Inanimate Life

INANIMATE LIFE

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INTRODUCTION

Why read this book?

Why study anything? Because the enterprise of mentally applying yourself to a particular topic is itself fulfilling. Like many journeys, study can be boring and tiresome and often you wonder if you are getting anywhere at all. But eventually you will reach a place where you not only can see how far you have gone, but a place where you can see things that you couldn't see before, or maybe you reach a place where things that you' ve seen before now look different and perhaps more understandable.

Knowing something about the organisms one sees while walking in the woods or any 'natural area' vastly enhances the enjoyment of the experience.

Fundamentally, this is a biology book. Why study biology? Living things are fascinating for a wealth of reasons—their diversity, their complexity combined with a fundamental simplicity, their functioning that begs for explanation, the multiple ways that living things exhibit organization, the multiple interrelationships between different living things. Also, there is clearly a fascination of biology that stems from the fact that people are indeed biological in nature.

Why study 'inanimate' (non-animal) life? This book studies a group of living things that are distinctive because they aren't human, or mammalian or even animal in nature (hence the title). In particular, why study plants, the primary subject of the book? There are at least three basic factors that make a study of plants particularly rewarding. First, plants are familiar organisms, things that are readily and commonly encountered, so much so that their fundamental biological nature is often ignored and they are simply considered inanimate components of the environment. Secondly, plants are extremely useful to human activities, not just as food but also by providing useful materials and chemicals. Because of this, the study of plants has a connection to a host of human endeavors. Thirdly, plants are the most conspicuous members of what is considered 'the natural world' or 'the outside'. Consequently, some understanding of plants can enhance the enjoyment of nature. An academic factor that makes plant study rewarding, and the reason for studying many inanimate (non-animal) organisms other than plants (e.g. fungi, bacteria), is that it enhances the understanding of other areas of biology by providing contrasting structures, development patterns, and physiologies when compared to familiar organisms.

There are many other reasons why the study of plants is rewarding, I'm confident that you will come up with additional reasons based on your own experience with the subject!

A brief history of the discipline of 'botany'.

This book is a 'botany book' and the book has been used in courses that are considered 'botany' courses. Most people associate 'botany' with plants, but this is a book studies a number of things that are not considered plants, why include them? The reason has to do with history and with classification.

Botany texts, like most of academia, have a great deal of inertia and, in terms of groups covered, this book perpetuates this. One hundred years ago, the field of biology was separated into botany and zoology, reflecting the binary taxonomy of the time that placed organisms into either the plant kingdom or the animal kingdom. Botanists studied organisms (plants, algae, some bacteria) that were green (contained chlorophyll) and also other forms of life (e.g. fungi) that weren't green but had some 'plant-like' features (cell wall, apparent lack of mobility, pattern of growth). As in any classification (more on this later!) there were organisms, most of whom were generally unicellular and small in size that had both 'animal-like' and 'plant-like' characteristics. These were often covered in both botany and zoology courses. Both textbooks and courses were 'survey' courses, going group by group through the members of the plant or animal kingdom.

As the 20th century progressed, more and more biological knowledge accumulated that revealed the commonality of all living things, topics like genetics, cell biology and biochemistry. Botany textbooks expanded adding elements common to all living things in addition surveying different groups. At the same time, botany and zoology departments merged into biology departments and introductory courses and textbooks reflected this merger.

Throughout the 20th century it became increasingly clear that the dichotomous classification (plants and animals) was undesirable for multiple reasons. In 1969, Robert Whittaker proposed a five-kingdom system, with three familiar groups ('Kingdoms' in a taxonomic sense)—plants, animals, and fungi, and two novel Kingdoms, protists and monerans. Monerans were prokayotes, primarily unicellular organisms with cells that lacked nuclei and other organelles. This was in contrast to the four other Kingdoms that had eukaryotic cells, ones that possessed a nucleus and membrane bound organelles. The novel Protist Kingdom contained photosynthetic groups (algae) and non-photosynthetic groups, including many 'problematic' groups that weren't obviously plants, animals or fungi. In spite of the taxonomic changes, most botany textbooks did not alter their coverage, only slightly changing how topics were organized. A few botany textbooks focused only on organisms considered to be in the plant kingdom, omitting photosynthetic protists (algae) and fungi.

With the start of the 21st century Whittaker's classification scheme fell out of favor, primarily because neither the protist group nor the monera group was a sound phylogenetic (evolutionarily-based, more details on this later) entity. 'Surveying' life in an accurate phylogenetic sense became more difficult, especially for the groups formerly considered protists, whose members do not group nicely. Where you used to have one group (protists) you might now have a dozen groups, all fairly obscure. And while five kingdoms could be managed, twenty kingdoms is more challenging. In spite of this, most botany textbooks in use today still approach to the subject as they have in the past: discuss the biology common to all organisms then survey the groups, with the precise groups surveyed varying between books.

As a consequence of the expansion of cell and molecular information, the amount of coverage of plants and of 'inanimate life' (everything other than animals) is drastically less than it was fifty years ago. The same can be said for other taxonomic groups: birds, fish, insects; but the problem is particularly significant for 'inanimate life' because it is fundamentally more obscure to most biology students and instructors. Additionally, the coverage given to what you might think of as organismal biology in general, what an organism is and how it functions, is very much reduced because the discussions of various groups are often dominated by taxonomic/phylogenetic/evolutionary aspects, with primary concern placed upon where a particular group might be put with respect to other groups.

This book is both traditional and non-traditional. Although the kinds of organisms this text studies is similar to most botany texts of the last hundred years, the approach to study is very different. This book is focused organismal biology, not phylogeny/taxonomy. It considers most of the groups that were covered in traditional botany texts, that is, 'EBA = everything but animals': plants, fungi, bacteria/archaebacteria, and most of the organisms that used to be placed in the protist category. But the approach to these groups is 'organismal' and comparative. It attempts to define the organism level of life (Chapter 1) and the classification of organisms (Chapter 2). The book then comparatively examines four features that define organisms: their structure (Chapters 3-10) their means of reproduction (Chapters 11-17), their acquisition of matter and energy (Chapters 18-25), and their interactions with conditions and with other organisms (Chapters 26-31). The approach is much more ecological (at the organism level) and much less phylogenetic/evolutionary than in botany texts or in introductory biology texts. A comparative approach, considering both the unifying features and the distinctive features of organisms, provides an enhanced perspective from which to consider the biology of plants.

This book is focused at the intersection of two biological phenomena: organisms and plants. In spite of this focus, it considers a wide area of biology — from cells to communities and from bacteria to fungi. It also considers a wide variety of organisms that are not now considered plants. Although this is intended as a botany textbook, it should be of interest to anyone interested in the scope of biology, even if they are not particularly interested in plants (something that it is hard for the author to imagine!!).

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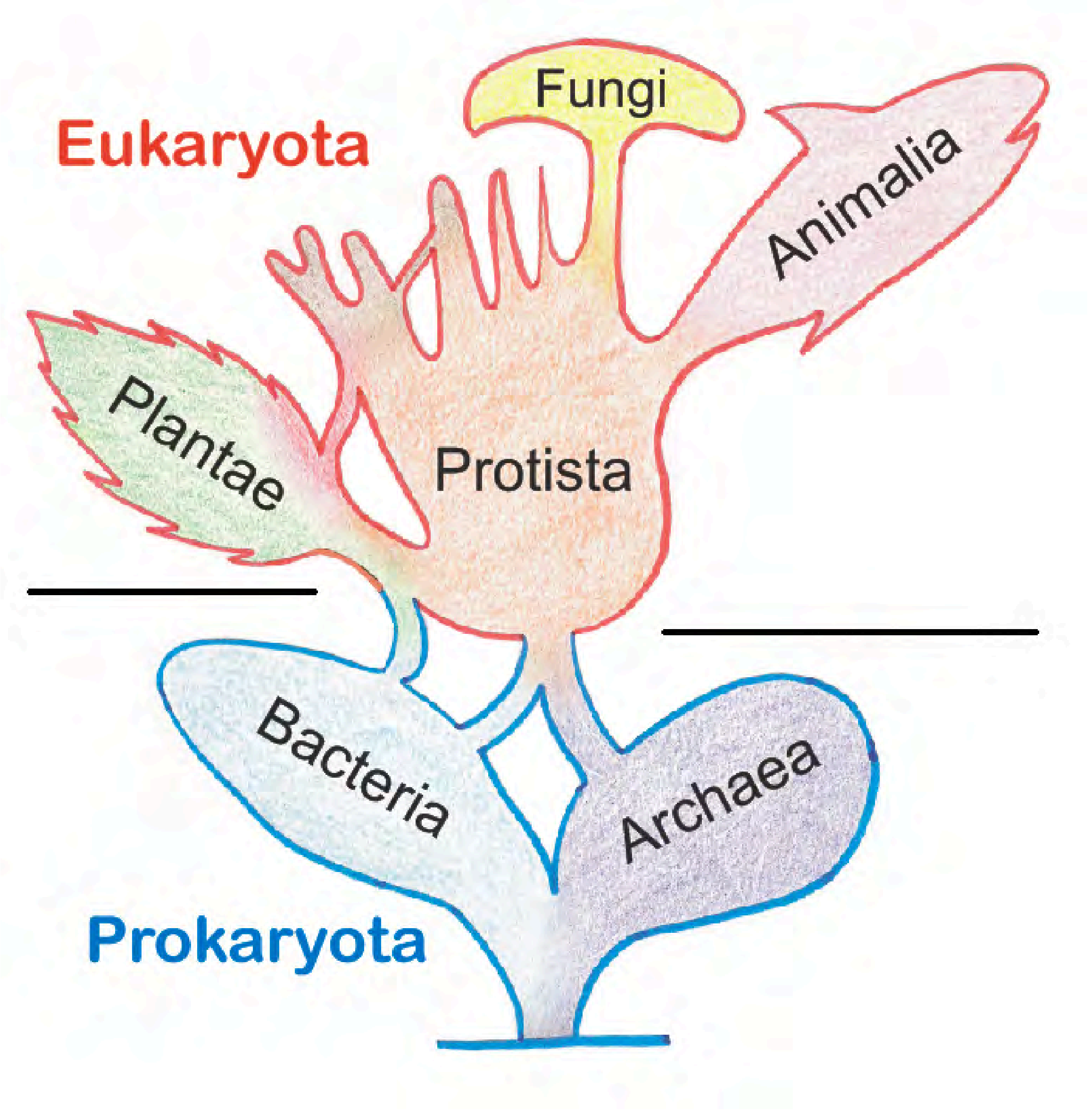

A ‘tree of life’ diagram depicting groups (basically the 5-kingdoms of Whittaker but with Monerans (aka prokaryotes) separated into Bacteria and Archaea) and evolutionary relationships. This text covers all but the animal branch.

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CHAPTER 1: ORGANISMS

This course is about organisms, biological things that most of us consider to be very familiar. The idea that life comes in packages called organisms is something that we all accept. And, for most students, the study of biology, at least initially, is focused on organisms, most often humans or things that are much like humans (mammals). Like a number of biological concepts, 'organism' is sometimes hard to pin down and there are certain situations where the concept of organism doesn't apply very well, especially for some of the forms of life covered in this course. An understanding of organisms is enhanced by viewing them comparatively and by viewing them from different perspectives. This course views organisms from four different perspectives, considering descriptions and comparisons of their (1) structure, (2) reproduction, (3) acquisition of matter and energy and (4) their interactions with each other and the conditions present in their environment.

Our first task is to try to define what an organism is. Let us start by looking at things that might be considered organisms:

Fig. 1 How many different organisms and kinds of organisms do you see?

The most obvious organisms are the moose. Their structure and development make their organismal nature easy to define. Other parcels of life, the grass, forbs, shrubs and trees may be more challenging to package as organisms. The next three figures present living things that perhaps are not as obviously organisms.

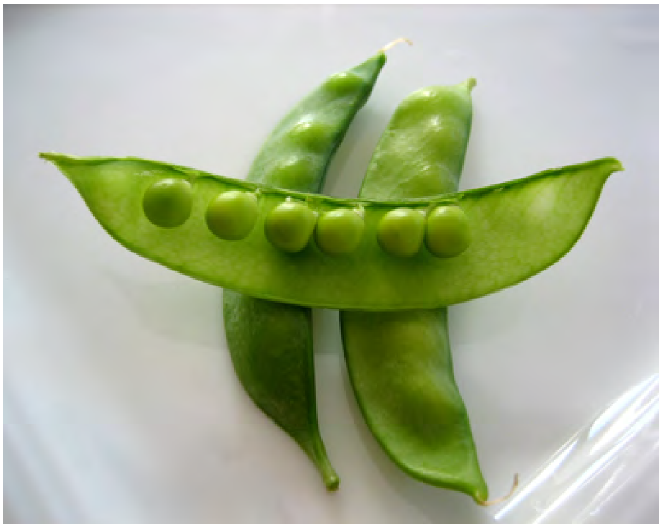

Fig. 2 Is a pea pod an organism? Are the seeds organisms? They certainly are 'living things', but what features might allow them or prevent them from being considered organisms?

Fig. 3 Cellular slime mold–a living thing with multiple lessons to teach about organisms.

Defining an organism

Fig. 4 The large 'leafy' structure attached to the tree trunk is a 'lungwort' lichen. Is a lichen an organism? They certainly are 'living things', but what features might allow them or prevent them from being considered organisms?

What are organisms? They are a manifestation of life, a 'living thing'. For most people organisms are the idea in their head when the term 'a living thing' is mentioned, but biologists appreciate that 'living things' don't have to be organisms, they could be parts of organisms (fingers, cells, membranes) or groups of organisms (populations, communities) and maybe even something that mixes life and non-life (e.g., cell walls, soils). Life itself is hard to define and it is manifested at many scales of time and space. It is important to appreciate that there are 'living things' that aren't organisms; organisms are just one manifestation of living things. But what is special about the organism that sets it apart from other levels of biological structure? Can we pin the word down?

"When I use a word," Humpty Dumpty said in rather a scornful tone, "it means just what I choose it to mean—neither more or less."

Words are essential to biology because they provide a means of communication and without some conformity on definitions communication can be difficult. At the same time, some words need to remain somewhat ambiguous because to pin them down too far renders them useless. Additionally, a word can shape thoughts and keep us from seeing phenomena. 'Organism' is perhaps such a word!! Here are some attempts to define an organism, each followed by some limitations of the definition:

- An organism is a fundamental unit of life: 'Fundamental' is a pretty vague term (which indeed might make this definition more useful!) but many would consider that a cell is the fundamental unit. It is important to realize that sometimes cells are organisms but sometimes they are just components of organisms. Most colleges teach a course on cell biology but (surprisingly!) courses on organisms are less common.

- An organism is a unit of life that can reproduce: One of the characteristics of organisms is that they can replicate themselves, but they are hardly unique biological entities in this respect—cells, DNA, organelles and sometimes even communities can replicate themselves. And one might be able (depending on definitions) to come up with organisms that lack this ability (see the discussion of caterpillars below).
- An organism is a cell or group of cells that is genetically distinct and genetically uniform. For familiar organisms (i.e., humans) this seems to work. Generally, a human organism is genetically distinct from its parents and from its offspring, and its cells are genetically uniform (except for sex cells). However, most unicellular organisms and many multicellular organisms produce 'clones' of themselves that are genetically identical but most would consider the offspring to be new organisms. Indeed, humans occasionally have identical twins, with two individuals that are identical genetically, and few (especially the twins!) would consider them one organism. Armadillos take this a step further and always give birth to genetically identical quadruplets.
- An organisms is a cell or group of cells that is spatially separated from other cells, a spatially discrete unit of life. Thus, individual cells are organisms (unicellular organisms) when they are **not** attached to other cells but if they are in a cluster (i.e., attached to each other) then the cluster is considered an organism. This works pretty well but there are problems:
    - Sometimes connections are hard to see and what we consider to be separate organisms (e.g., aspen trees) are actually connected below ground by their root systems. Is the tree an organism or the cluster of trees an organism?
    - Pieces of organisms break off and become spatially discrete (e.g., leaves fall off a tree)—are falling leaves organisms since they are now spatially discrete? What about egg and sperm, they are spatially discrete bits of life, should they be considered organisms?
    - It is common to have spatially discrete structures (e.g., lichens, corals, mycorrhizae) that are composed of cells that have very different genetic constitutions (lichens consist of a fungus and an alga, corals [often] consist of an animal and an alga; mycorrhizae contain a plant and a fungus). Generally, we consider associations of organisms to be a community, but maybe communities can be organisms?

  - What constitutes attachment? Mosses and lichens are attached to trees but most would not consider the combined entity to be an organism. Barnacles attach to whales but the combination is not considered a single organism.
- An organism is a unit of life that is 'self-sufficient', that can 'make it on its own': Mosses and lichens don't need the tree, they simply need to attach to whatever is available. In contrast, a liver needs the rest of your body in order to survive. Red blood cells circulat ing in blood are not considered organisms whereas *Paramecium* or an amoeba circulating in a pond would be because they can survive on their own. However, there really are very few organisms that are truly 'on their own' and self-reliant: cows need grass, cows need a particular group of organisms in their digestive system, pine trees need fungi associated with their roots, and, as we will study, **all** plants need bacteria and fungi. Almost all organisms depend on other organisms for their livelihood and it is very hard to use 'self-sufficiency' to define an organism.
- An organism is a unit of life that is distinct in time; it has a starting point and an ending point. For familiar (sexual, multicellular) organisms the start might be fertilization of an egg by a sperm and the end might be considered death. But organisms might start and end different ways. Consider a butterfly (the entity that can fly) : one might argue that it starts when it emerges from a chrysalis and ends with the death of the butterfly. Similarly, one could argue that a caterpillar is an organism that starts as a fertilized egg and ends as a chrysalis. This certainly isn't death but it is the end of the caterpillar. Thus, we might say that the thing we generally call a butterfly exists in two different forms, both of them organisms: a caterpillar and a butterfly. Or consider a particular interesting form of life called a cellular slime mold. It sometimes exists as amoeba-like single cells. The cells engulf other bits of material, both living and dead, grow and divide to form more amoeba-like cells. When conditions are right the cells aggregate, forming a multicellular slug a few millimeters long that moves briefly in a manner reminiscent of a slug and then stops moving and undergoes a transformation into a stationary entity with a base connected to a thin stalk standing up to 10 mm in height with a ball at the top of the stalk. In time, the ball breaks open, releasing single cells that are dispersed and can grow into more amoeba-like cells. Like butterflies (and, as we will see, like some plants), cellular slime molds have multiple forms, in this case three: one form that specializes in eating (the amoeboid cells), one specialized for moving (the slug) and another that specializes in reproduction (the fruiting body). Thus, some 'living things' exist multiple forms, and each of them might be considered 'an organism'. And each form has a starting point and an ending point but they may not be the

familiar ones of fertilization (union of an egg and sperm) and death.

- Organisms change through time, that is, they develop, changing in structure and in function. The simplest life-cycle pattern is a single cell that 'begins' when it is produced by the cell division of an existing cell and 'ends' when that cell divides to produce two daughter cells. Aside from growth, the basic structure (form) of the cell remains the same but internally (physiologically) there are a host of transformations (i.e., development) that allow for the acquisition of the materials necessary to form a new cell as well as changes that allow for division to take place. Multicellular organisms generally start with a single cell that proliferates to many cells, and the cells stay together after divid ing to produce a multicellular form that generally changes structure substantially, especially at the early stages of development. In many familiar organisms the cells that are 'passed on' (i.e., that can initiate the next generation) are of two types (e.g., egg and sperm) and they need to find each other and unite in order to form a cell that is capable of dividing to produce a new multicellular form. But this is often not the case, as we will see when we study reproduction, for many organisms a single cell released from a parent organism may undergo the developmental process that form a multicellular organism.
- The development of familiar (animal) organisms is usually quite regimented and results in a fairly consistent 'final' form. But we will see that the development of some 'inanimate' (i.e., non-animal) organisms is not as rigid and, in fact, many of the organisms that we will consider don't produce a 'final' form (an endpoint), they keep growing and growing. How do organisms end? The end of an organism doesn't have to be death by 'old age' ('wearing out') or by being ravaged by environmental conditions (e.g., cold weather) or biotic interactions (a disease or a predator). The end of some organisms is an aspect of development, e.g., the end of a caterpillar is the formation into a chrysalis, the end of the 'slug' stage of a cellular slime mold is its transformation into a stalked structure. This brings us back to the question of reproduction. As was mentioned above, one could argue that some organisms don't reproduce themselves: caterpillars don't make more caterpillars, they make butterflies; and butterflies don't make more butterflies, they make caterpillars. We will study a number of 'biological things' that exhibit life cycles that include multiple forms, each of which could be considered an organism and each of which 'passes on' (produces) a cell or a group of cells that develops to form the next stage (organism), eventually repeating the cycle. Thus organismal life is perpetuated through time but is manifested in different forms, each an organism. If we consider the individual stages to be organisms then what might we call the entity that includes all stages?

Usually it is also considered 'an organism' —monarch butterflies are both the caterpillar and the butterfly. This perhaps unfortunate because it obscures some interesting biology; and it certainly makes defining 'organism' more challenging. In an organismal sense monarch butterflies are clearly not the same as caterpillars, their structure and function are very different although they are connected to each other, not only through developmental patterns but also in a genetic, evolutionary and taxonomic sense.

- Organisms might be defined by their ability to grow. This requires the acquisition of material and the use of that material to make the organism bigger. Although generally this is the case, there certainly are some things that one might consider an organism that are not capable of growth: consider mayflies (the ones with wings, not the aquatic form). These organisms aren't capable of growing because they aren't capable of eating, their mouths are permanently closed! The same thing is true of the 'slug' form and the 'stalked' form of the cellular slime mold and, as we shall see, many plants transform from a form that is capable of growth to one that is not. Caterpillars grow but don't reproduce, butterflies don't grow but they do reproduce. The ability to grow is essential somewhere in the life cycle but does not have to be present in all organisms.
- One final aspect of organisms is that they are considered to be the unit of selection in Darwinian evolution, although occasionally arguments are made for selection at other levels of biological organization (genes, populations).

One of the purposes of this course is to give students a new perspective to understand life. Understandably, we all think that living things (i.e. organisms) are like humans. While all life is fundamentally the same in its chemical composition and in how it functions, there are substantial differences in the way they go about the business of living. We will examine a variety of organisms, some very familiar like pine trees and dandelions, some very unfamiliar like cellular slime molds, and our emphasis will be on comparing and contrasting a variety of features. This study should give students a new vantage point from which to study life's organization and behavior.

So, what are organisms? They are biological entities that can be defined in space (i.e. they have a boundary and a form–a **structure**) and can be defined in time (i.e. they have a beginning and an ending and a pattern of **development** between these times). They function in a way that ultimately results in their **reproduction**, i.e., making more of themselves. Reproduction necessarily requires the **acquisition of materials** so that **growth** can occur. Occasionally organisms have multiple forms and each of these forms can be considered an organism (e.g., caterpillar and butterfly; amoebae, slug and fruiting stages of a slime mold). In situations like these, an individual stage might not both grow and reproduce, but collectively, as result of the action of all the stages, both growth and reproduction are accomplished. As a result of their structure and their activities, organisms **interact** with their environment and with other organisms.

Fig. 5 The fruiting body of a stinkhorn fungus, a structure that facilitates reproduction. The fungus produces a very different structure to acquire materials and energy. One might consider it to be analogous to a flower, which is a structure that some plants produce that is associated with reproduction, while leaves and roots are structures associated with matter and energy acquisition.

This course will be studying a diverse group of organisms that at one point were considered plants, considering their structure and how it develops, their ability to reproduce, their acquisition of matter and energy, and their interactions with conditions and with other organisms.

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CHAPTER 2: TAXONOMY AND PHYLOGENY

Fig. 1 General Sherman, an organism with a name

While it is uncommon, people sometimes give names to individual plants. For example, in Sequoia National park stands 'General Sherman', considered to be the largest organism living on earth. Because organisms are discrete packages (i.e., with boundaries in space and time) it certainly possible to name them. But there are an awful lot of them and it is simply impractical to name them all. However, if one observes organisms, it is quickly apparent that they occur in groups, i.e. there are groups of them that look similar and thus the group can be considered an entity itself. Moreover, additional study will usually reveal that identified (i.e., defined) groups of organisms can often be: (1) subdivided into smaller groups and (2) lumped together into bigger groups; that is, that the diversity of organisms is organized into clusters of similarity and there are clusters of the clusters. These biological patterns seek an explanation: why do organisms come in groups and why are there groups of groups?

Even if organisms did not 'naturally' occur in groups it would be important for biologist to define groups; there is simply so much biological diversity that some sort of 'filing system' is required to organize it all. Thus, there are two aspects to organizing organisms into groups: (1) a practical aspect, producing a way to manage all the variety of organismal life, to arrange its vast diversity, (2) a mechanistic (process) aspect, producing a system that will allow biologists to understand mechanisms that result in the patterns of diversity, e.g., why there are groups. To a large extent these two aspects can be satisfied simultaneously, i.e., there are systems that categorize life easily and also allow users to study the processes (evolutionary mechanisms) that lead to the categories. However, the biological landscape is vast; clusters range from groups (species, or perhaps subspecies) that might have less than 1000 organisms that all 'look' very similar to groups (families, orders) that are comprised of millions of individuals, with members that do not 'look' very similar yet do possess some 'fundamental similarities.' With such a span in scale one should appreciate that there may be situations where a system that is useful to consider the evolutionary relationships (i.e., the **phylogeny**) between groups of organisms may not very handy as a filing system. Or, looking at it from a different perspective, classification schemes that easily organize life's diversity may not do so in a way that reflects the phylogeny of different groups. An example familiar to most biology students would be 'reptiles', a handy group in terms of classification (reptiles are vertebrates that aren't amphibians, birds or mammals), but a group that does **not** represent phylogeny. This book is primarily about organisms. And while in general it will use a phylogenetically based classification scheme, occasionally it will consider groups that are 'artificial' and do not reflect a phylogenetic entity, examples would be 'green algae' and 'gymnosperms'.

We will be dealing with scientific names, and the groups that they describe, throughout the book and it is important to appreciate the basis and the limitations of the naming. Shakespeare asks "what's in a name?" and answers with the implication that names are basically trivial. But names are profoundly significant in ways that often are not appreciated. Like water to a fish and air to humans, we are so immersed in names that we rarely stop to consider them. But names say much about humans, about how we think and what we think. Indeed, it is probably the case that names not only reflect how we think, they may actually **dictate** how we think. Names reflect the organization by which we view things and the way we process the information that we receive. While classification is useful whenever one is faced with a large number of variable entities, we need to consider to what extent our classification is a reflection of our thought (i.e., we are imposing order on something that isn't really ordered) , or a reflection of reality (i.e., there is an order that we are describing), or something in between. Stated another way, names reflect an organization and it is important to consider whether the organization is inherent to what is being named or inherent to our minds.

Keep in mind that naming is a grouping process, i.e., it is a mechanism to put 'things' (in our case biological things) together. Faced with diversity, humans lump things together into categories, putting similar things together into groups; this makes the diversity more manageable and this is what classification (naming) is all about. At the same time, one should appreciate that any classification, in fact, the very process of 'naming', results in a loss of information to the extent that any organism varies from the norm that characterizes the group. The name 'tree' sets up a classification of living things, one that is both useful and arbitrary; not all trees are the same and describing something as a tree strips an organism its individuality. The same could be said for the terms 'sequoia', '*Sequoiadendron*', and '*Sequoiadendron giganteum*'. For any named biological group, it is important to consider how 'real' the group is: do the entities naturally fall together or are we just putting them together as a means to simplify the system. If the groups are 'real' (valid) a biologist might consider what processes might relate to their validity; what process forms the group?

Thus the fundamental question to address when naming groups of things is what criteria will be used to group them. For instance, if you are classifying motor vehicles one might group them based on color, on manufacturer, or on type of vehicle. When considering organisms, deciding what criteria to group them on is a tough question: organisms are exceedingly diverse and they differ in myriad ways. Because living things have many, many characteristics, there are many different ways that they can be grouped. Moreover, until some goal has been attached to the classification, there is not 'right' way for it to be done; it is simply an arbitrary way to simplify a diverse system. Classifying cars based on color is certainly easy and, in some cases, might be useful, but it is not very useful if one's goal is to explain the overall patterns in car variation.

Two features make a classification easier to develop and make the entities thereby defined more 'real', i.e., an accurate representation of the reality. One feature relates to the pattern of variation. Consider a group of organisms that has only one characteristic, or perhaps only one characteristic that might distinguish one organism from another, for example, a group of organisms that are all the same except for length. Figure 2 (a) and (b) show two such groups of organisms, one where a classification (naming) is an accurate reflection of reality and one where it is not. Both plots are 'frequency histograms', showing the distribution of individuals of different sizes. The difference between the two is in the pattern of variation. The group of organisms in 2(a) is easy to classify into three groups because the there are 'gaps' in the distribution. A statistical way of describing what is shown in 2(a) is that one can define groups ('small', 'medium', 'large') so that the variation within a group is small compared to the variation between groups. The group of organisms in figure 2(b) is less easily classified because there are no gaps in the distribution of organisms of different sizes; there are no obvious groups, and whatever group you might define has as much variation within it as there is between that group and the remainder of organisms. Note that it certainly is possible to classify the organisms shown in 2(b); we could divide them into that are 'small' (less than 6 units in length), 'medium' (greater than 6 but less than 16 units in length) and 'large' (16 units or more in length). Although such a classification is arbitrary and not an accurate reflection of reality, this does not mean that it might not be useful.

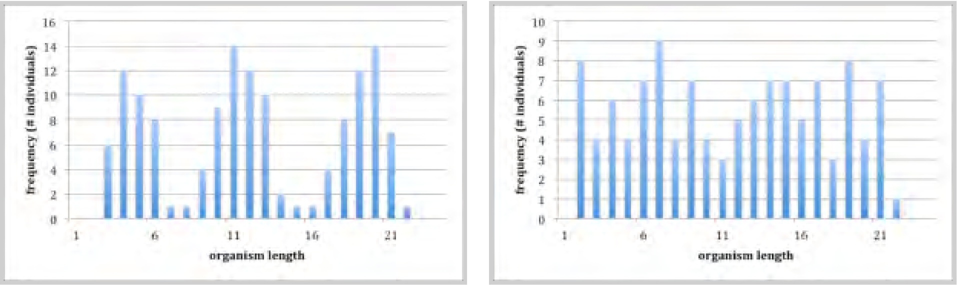

Fig. 2a (left) and 2b (right) Two examples of variation within a group of organisms. Both plots are frequency histograms, showing the number of individuals within a series of size classes.

A second factor that makes classification more 'real' is a correlation between different characteristics. If all the small organisms of figure 2(a) were round, the medium sized one's square, and the large ones cylindric, there would be a correlation between size and shape. This would make the categories (small, medium and large) more justifiable; it would make them more 'real'. Alternatively, if all the size groupings had all three shapes it would make the categories based on size (or based on shape) less real.

In general, organisms show variation that is discontinuous and they exhibit correlation in variation of different characters, and both these features make classification easier. These pattens of nature not only make classification of organisms simpler, by reducing the number of characters that one needs to consider, it also hints that there are better, or perhaps even a 'best', way to classify living things. This might be described as a 'natural' classification', one that is based on 'fundamental similarities'. This idea was apparent to early naturalists. Carl Linnaeus, who developed one of the first classification schemes, recognized that his technique of classification, although useful, was flawed because it was not 'natural', i.e., it put things together based on features that did not correspond to many other features. His categories were useful because they put organisms into bins and made their diversity much more manageable, but Linn ae us appreciated that there was an organization to the diversity of living things and that this organization was **not** always reflected in his categories.

If there was an organization to the diversity of living things, there should be a reason for this. Three hundred years after Linnaeus, Charles Darwin, who was an excellent student of classification (of organisms as varied as beetles, orchids and barnacles) , came up with an explanation for the correlated variation and for the observation that living things appeared to fall into 'natural' groupings: it was consequence of the process of evolution, the changes in the characteristics of groups of organisms through time. The fundamental similarity of groups of organisms was due to the fact that together they shared a common evolutionary ancestry. Indeed, Darwin's taxonomic acumen was highly significant to his elucidation of the process of evolution. He made two key observations that were connected to his understanding of taxonomy:

1. in widely separated parts of the world where conditions are similar, for example, deserts in South America and in Africa, organisms often look similar even though they are not 'fundamentally similar';
2. in one region of the world where conditions varied considerably within a relatively small geographic area, e.g., going from plains to mountains in southern South America, organisms that on first examination seem very different, upon closer study are 'fundamentally similar'.

The process of organic evolution explained both of these patterns; in the first instance, convergent evolution could cause organisms that are fundamentally different (i.e., not closely related) to look superficially similar; in the second case divergent evolution (adaptive radiation) could cause fundamentally similar (i.e., closely related) organisms to diversify and look different. It can be seen that although evolution explains different reasons why things might look alike, it does NOT, at least initially, explain how one might group things: should it be on the basis of 'basic, i.e. fundamental, similarity' and thus combine things that may not look that similar until ‘closely examined’ (see figure 3 which shows two different members of the cactus family, a leafy cactus and a more ‘normal’ looking cactus); or should things be grouped on the basis of ‘superficial similarity’, i.e. group things if, on the surface, they look similar (see figure 4 which shows two plants that look superficially similar yet are ‘fundamentally’ different).

The distinction may seem petty (i.e. what is the difference between superficial similarity and fundamental similarity), but it has real consequences because perceptions vary. For example, people commonly group flowers on the basis of flower color, which is one of the most easily perceived characteristics of plants, but it turns out to also be one of the most superficial.

Fig. 3 These two plants are closely related and both in the cactus family, yet they ‘look’ very different, with the *Pereksia* (on the left) having a more typical plant form with typical leaves and branches, while the saguaro cactus on the right has evolved a very different form with no obvious leaves, an unusual branching pattern and an abundance of spines.

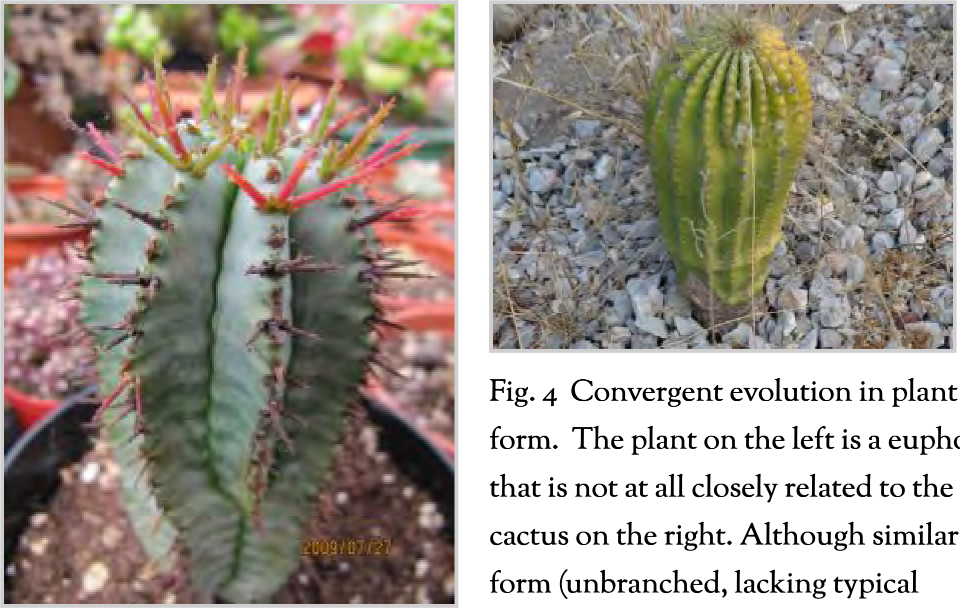

Fig. 4 Convergent evolution in plant form. The plant on the left is a euphorb that is not at all closely related to the cactus on the right. Although similar in form (unbranched, lacking typical leaves, having spines), this is not the result of a close evolutionary ancestry, but is the result of convergent evolution, two groups of plants 'converging' on a form that presumably is useful under arid conditions.

For one particular group of people, biologists, Darwin's theory of evolution did provide a rationale for grouping and naming living things, organisms should be classified based on their phylogeny, their evolutionary ancestry, i.e., their fundamental similarities. For those who are studying organic diversity it would desirable to group things based on 'fundamental similarities' (= evolutionary ancestry) because, among other things, it allows us to view the consequences of evolution. But we are still left with the question of how to recognize phylogenetic groups. From pre-Linnaean times through Darwin and up until the middle of the last century, sci entists searched for features that they thought reflected 'fundamental similarities'. After Darwin's ideas were accepted, scientists realized that what they were looking for were features that reflected the evolutionary past of organisms. But these characteristics are elusive entities and no one really knew if they had found one because most evolutionary history is impossible to trace—the fossil record is grossly inadequate except for large-scale overviews.

Over the last fifty years molecular biology brought new approaches to taxonomy. It allows organisms to be compared on the basis of similarities in the sequences of amino acids in proteins or sequences of nucleotide bases in nucleic acids (DNA, RNA). These are more than just new features to be compared; they are features that one can argue **do** reflect evolutionary lineage. Through time, changes accumulate so that the longer the time since two lines diverge the more differences that accumulate in the sequence of amino acids in proteins or nucleotide bases in nucleic acids. One might argue that this is how classification has always been done, that the assumption has always been that groups 'accumulate' more and more differences through evolutionary time, forming separate groups with divergent characteristics. Although this is true in a very general sense, classification has **always** involved 'character weighting', i.e., observers have always felt that some characteristics, ones that are less easily modified by natural selection should have more 'weight' in a classification than others, characteristics, e.g., flower color, that are readily shaped by evolution and thus might occur independently in two lines that are not phylogenetically related. The formation of groups is based not just on the accumulation of differences but rather the acquisition of key differences, the differences that reflect phylogeny. Molecular biology not only provides a tremendous increase in characteristics that can be compared. It additionally provides characteristics that are **unlikely** to be selected for by natural selection. This is significant because if two organisms share a feature this can be explained two ways: (1) it may reflect a common ancestry ('fundamental' similarity) , or (2) it may reflect a common selective force ('superficial' similarity). However, if two organisms share a feature that is unlikely to be selected for then the only explanation involves a common ancestry. Assuming that one wants a classification based on ancestry, then using molecular data provides multiple ways to trace ancestry.

One feature of biological classification from the time of Linnaeus to now, and a feature of most (but not all) classifications, is that they are hierarchical, with species grouped into genera, genera into families, families into orders, orders into classes, classes into phyla and phyla into kingdoms (and, some would add, kingdoms into domains). However, with the exception of species (whose definition we will consider later in the course), **none** of these levels is defined—a genus is a group of related species, but how closely related is never specified. Thus, although it is often the case that there is agreement that a group of living things represents a taxonomic entity, exactly what level that group should be placed at, and how this group relates to other groups, may be quite controversial. Moreover, the seemingly logical idea that groups should be organized on the basis of evolutionary ancestry doesn't mesh very well with a classification that has levels—evolution doesn't necessarily operate in a way to produce levels; and there is no reason to assume that the levels produced on one branch might coincide with levels on another branch. One can certainly devise classification schemes that more closely match the way that we believe evolution operates; but these schemes will not be as useful in pigeon-holing (categorizing) living things. As is the case with many concepts (and in fact with words themselves!) one must balance between utility and accuracy; useful concepts often distort reality but making them more real often renders them less useful.

Most biologists approach classification from a 'cladistic' viewpoint that is centered on the idea that evolution produces 'clades' (groups) as a result of the splitting of a previously existing clade. Seen through time one would see a branching diagram. In general, this probably reflects the pattern of evolution and the development of diversity. But we have good evidence that groups not only split but sometimes merge (e.g., the endosymbiont theory for the appearance of eukaryotes; secondary endosymbiosis and the origin of multiple algal groups) and neither cladistic approaches or a hierarchical system deals well with this possibility.

For most of this book we will speak of groups that are generally considered 'real', that is, a group of organisms that are set off, in terms of phylogeny and in terms of characteristics, from other living things. A non-phylogenetic classification of the groups covered in this book is here (Table 1). Because our focus is on organisms and their diversity, we will be less concerned with the exact placement of the group in a taxonomic scheme or the exact phylogenetic relationship between one group and others. Some of this information is covered in the phylogeny sections of the 'fact sheets' for specific groups found in the ***Organisms*** section of the book. But note that the text as a whole is NOT organized along phylogeny/taxonomy lines. In fact, I will refer to a number of 'artificial' (i.e., non-phylogenetic) groups. These are listed below and serve as examples of groupings that are known to be artificial yet are useful for reasons of history, ecology or convenience.

- 'inanimate life '— living things that are not animals (i.e., in the Animal Kingdom). Using a five-kingdom classification this would include Monera (i.e., prokaryotes), Fungi, Plants and Protists. A more ecological classification is shown here, along with a list that shows where the 'organism fact sheets fit in this classification.
- algae — aquatic photosynthetic organisms. This category spans most of the phylogenetic universe! Yet for ecological reasons, it is useful!
- macroalgae — multicellular or large colonial algae

- green algae — aquatic, photosynthetic organisms with multiple similarities to plants (pigments, cell wall chemistry, storage carbohydrates). This group is useful to know about, but for a host of reasons is difficult to define rigorously in a phylogenetic sense.
- gymnosperms — plants that have seeds but don't have flowers. This is an historical category that is still in common use and worthwhile to be aware of. It is an example of a grouping based on the lack of a particular characteristic, something that is not generally phylogenetically sound. Other examples of artificial groups based on what they lack are:
  - prokaryotes — cells without nuclei
  - protists — eukaryotic organisms that are not animals, fungi, plants or prokaryotes
  - bryophytes — plants (mosses, liverworts and hornworts) without vascular tissue
  - fern 'allies'— vascular plants without seeds

Further Reading and Viewing

- Go Botany Key by the Native Plant Trust. A "key" using characters to "identify" (i.e. give them a name) plants.
  - https://gobotany.nativeplanttrust.org/
- A Tree of Eukaryotes by PsiWavefunction. The modern way of classifying organisms, a phylogenetic "tree" flower.
  - A Tree of Eukaryotes link
- "Phylogenetic tree view" by The Botanist in the Kitchen. Some more phylogenetic trees.
  - https://botanistinthekitchen.blog/the-plant-food-tree-of-life/phylogenetic-tree-view/
- Plants by ScienceDirect. Some more plant classification.
  - https://www.sciencedirect.com/science/article/pii/S0960982211004374

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CHAPTER 3: BOUNDARIES

Significance of boundaries

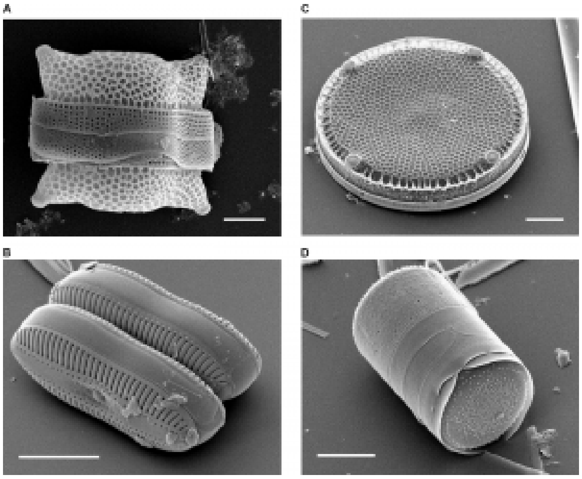

Fig. 1 These organisms are diatoms, sometimes described as organisms that live in glass houses because they are enclosed within an ornate structure made of the same material as glass, silica dioxide.

We have defined an organism as living material that is discrete (i.e., bounded) in space and time. Being distinct in space requires a boundary that separates the organism from the 'outside'. For single-celled organisms the boundary is the outermost component of that cell, and for most of the single celled organisms studied in this course that outermost component is a cell wall, but the chemical and physical nature of the wall varies considerably. For some unicellular organisms there is no cell wall and the outermost layer is a structure called a cell membrane. For multicellular organisms, the boundary is the collective of all the (generally specialized) cells on the organism's perimeter, its dermal tissues. For most of the organisms studied here the dermal cells have a cell wall and also a specialized coating on the outside. This chapter examines the physical and chemical nature of organism boundaries and also considers the significant functions of the boundary, starting with its influence on something called flux, the movement of materials in and out of the organism.

TOPICS

- Boundaries and flux
- Structural, chemical and physical nature of boundaries
    - Membrane

Fig. 2 A coccolithophore, whose external boundary consists of multiple plates of calcium carbonate.

    - Walls
        - Polysaccharide cell walls
            - plants, fungi, bacteria, archaebacteria
        - Inorganic cell walls
        - Internal cell walls
    - Dermal tissue
    - Coatings
- Boundaries and structure
- Boundaries and movement
- Boundaries and communication

Boundaries and flux

One reason the boundary is significant because it represents a barrier to movement into and out of the organism. This movement can be described as a 'flux' and flux can be modeled as being a function of three parameters present in the following formula (which is actually a model of what causes materials to move):

Flux = (driving force * surface area) / resistance

While in many ways this equation is a simplification, it does point out the three fundamental properties that determine the flow of materials into and out of the cell:

- Driving force—this is generally approximated by the difference in the concentration of something on the inside vs. the outside, but in the case of heat flow the driving force is the difference in temperature; considering the movement of fluids (e.g., air, water) the driving force can be pressure differences. In all these situations, the bigger the driving force, the more flux there is.
- Resistance—the resistance can be described as the difficulty with which materials can move from the outside to the inside, or vice versa. Some materials readily allow the movement of molecules (or heat) through them, i.e., they have a low resistance. Other materials only reluctantly allow materials (or heat) to move through them, i.e., they have a high resistance. It is important to appreciate that resistance depends on the substance/ molecule one is keeping track off; a boundary may have a very high resistance to some molecules and a very low resistance to others. (related terms are conductance and permeability, which, for our purposes, are the reciprocal of resistance)
- Surface area — the more surface area through which materials can flow, the more flux.

As will be discussed in the next chapter, the surface area is determined by the shape and size of the organism. The driving force is determined by where the organism is and what is going on inside and outside of the organism. Organisms can manipulate fluxes by manipulating the driving force. Most of the discussion of these mechanisms is beyond the scope of this book but we will mention some in Chapter 22. In the case of the flow of materials or heat into and out of cells, the resistance to flux is determined by the chemical and physical characteristics of the boundary between the organism and its environment.

Besides being important in influencing the flux of materials into and out of organisms, boundaries serve other important functions that will be discussed after describing different types of boundaries.

Structural, chemical and physical nature of boundaries

Cell membrane

The chemical nature of the cell membrane should be familiar to biology students: a phospholipid bilayer with proteins imbedded in and through it. The two sides of this membrane are ‘w et’ (i.e., hydrophilic) due to the attraction of polar water molecules to the charged phosphate groups of the membrane. The interior of the membrane is dry (i.e., hydrophobic) because lipid molecules carry no charges and have no regions that are even partially charged and to which a polar (= partially charged) water molecule might be attracted. However, there are tubular proteins passing through cell membranes. These tubular proteins may have a ‘wet’ in interior, providing for water filled channels running from the outside to the inside. Some of these channels allow selective passage of ions and many of these can be manipulated (opened or closed). Although the chemical nature of the hydrophobic layer is different in the Archaea, the basic structure of membranes is fundamentally the same for all organisms. Significant to organism function is that the membrane is quite permeable (low resistance) to small, uncharged molecules (significantly O_2, CO_2 and H_2 O) but not very permeable (high resistance) to charged molecules (ions) and to larger molecules, especially if they are not soluble in lipids. The cell membrane generally has little strength and readily yields to internal and external forces, that can cause the cell to change shape. Organisms lacking a cell wall in terrestrial environments cannot be very tall because the force of gravity flattens them. This can be overcome with an internal skeleton (vertebrates) or an external one (exoskeleton), which is a rigid boundary.

Cell walls

In contrast to the consistent presence and composition of the cell membrane in the cells of organisms, cell walls show much greater variability. Many organisms (e.g., almost all animals) have no cell wall. For the organisms that possess walls, its composition is quite variable (Table 1), although some of its structural features are more consistent.

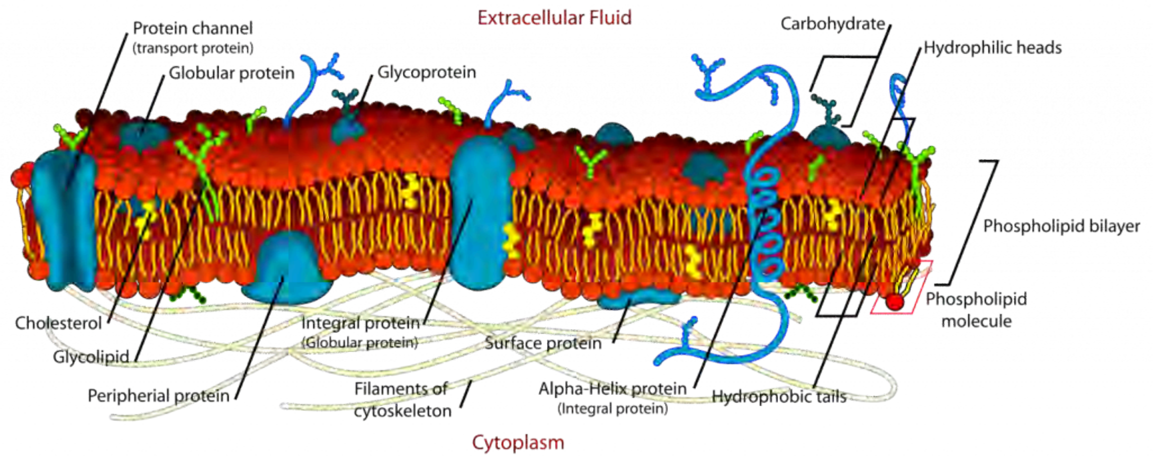

Fig. 3 A representation of a membrane serving as a boundary to cells and organelles.

Polysaccharide cell walls

The cell walls of **plants, fungi, water molds, brown algae, red algae** and (most) **green algae** have a similar structure and chemistry. These cell walls are composite structures, and can be considered to be gels. They consist of fibers made of elongate carbohydrate polymers that resist being stretched. These are imbedded in a matrix of different carbohydrate polymers that are highly hygroscopic (water absorbing) (Fig. 4).

Two common fiber materials are cellulose (found in plants, water molds and green algae) and chitin (found in fungi). Cellulose is a polymer made up of glucose monomers, as is the more familiar polysaccharide, starch, but the two have very different roles, one structural and one energy storage. Chitin is also a polysaccharide polymer but the subunits (N-acetylglucosamine) are hexoses with a nitrogen attached (Fig. 5).

The fibers of cellulose and chitin are consist of multiple (20-100) individual polymer molecules that interact with neighboring molecules to form a crystalline structure of the fiber. These fibers are significant in multiple ways: (1) because there are multiple molecules and they are bound to each other, the fibers, and the wall they are present in, are considerably 'stronger' (see below) than would be the case if the individual molecules did not interact to form fibers; (2) the fiber is difficult to digest because the component polymer molecules are not very accessible to enzymes and the fiber itself is not soluble in water, in spite of the fact that the monomers units, e.g. glucose, are very soluble in water.

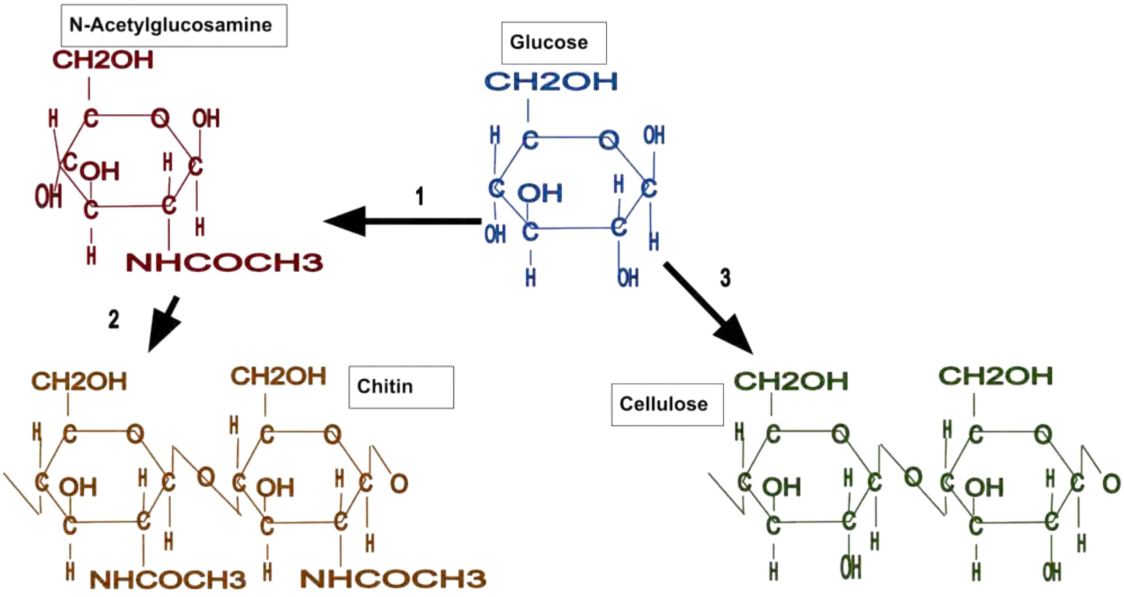

Fig. 4 Chitin and cellulose. Both generally occur as chains with hundreds or thousands of monomers connected together, always with the same linkage between individual monomers. Not shown is starch, which, like cellulose, is a polymer made up of glucose units but the linkage between individual glucose molecules is different.

The fibers of chitin and cellulose are deposited in a matrix of other polysaccharide polymers whose composition is much more variable. This is because the polymer 'chain' consists of several subunits, not just one, and also because the linkages between subunits are more variable, not always the same one, and not always 'end to end' but with branching (one subunit connected to three other subunits, not just to the ones 'in front and behind' it). While these polymers are given names (hemicellulose, pectin, agaropectin), the names refer to groups of chemicals and not to a specific chemical structure and composition. Some of these chemicals bind to cellulose or chitin fibers, connecting them to each other and providing more structure to the cell wall and also allowing the cell walls of adjacent cells to be bound to each other.

Although they are made primarily of polysaccharides, these cell walls contain some protein molecules. The function(s) of the proteins are not known with certainty. They are probably not particularly significant structurally in the way that the chitin and cellulose are and the way that the intracellular proteins tubulin and actin are. The protein component of the cell wall is probably significant in being able to change, through enzymatic action, the structure of the rest of the wall, e.g., during cellular growth when the wall

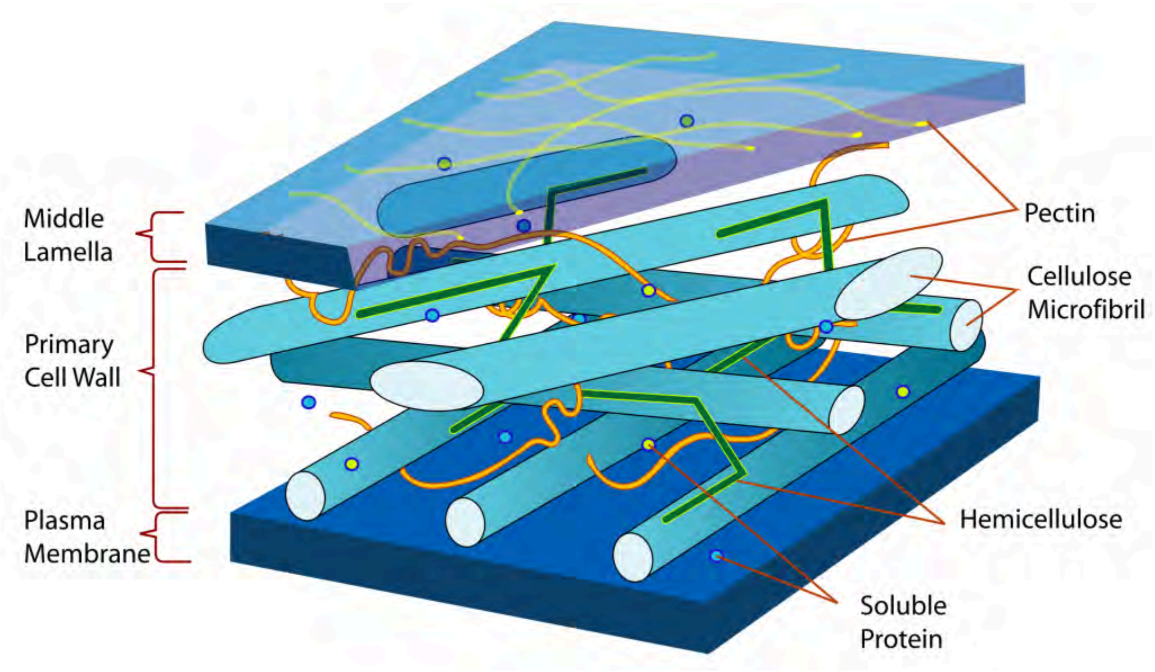

Fig. 5 A representation of the primary cell wall of plants, consisting of fibers of cellulose imbedded in a matrix of water absorbing pectins and hemicellulose. The middle lamella is the area between two adjacent cell walls.

'relaxes' and allows the internal pressure of the cell to bring about growth (Chapter 25). Wall proteins are probably also significant in allowing material to get through the cell wall (both inward or outward).

Generally, carbohydrate cell walls readily absorb water and can be considered to be a hydro gel. The absorption of water comes from the adhesion of water molecules to the carbohydrate components of the cell wall, in particular the 'matrix' polymers (e.g., pectins, hemicellulose) plus the cohesion of water to itself. The hydrophilic nature of the cell wall makes it highly permeable (low resistance) to the movement of water (as a result of either diffusion or as a result of pressure differences, i.e., mass flow (m ore discussion on this when discussing material movement, Chapter 24). Small water-soluble molecules also move readily through the wall both as a result of their individual diffusion and as a result of being dissolved in water that may be moving via mass flow. However, dissolved ions may be slowed by becoming bound to charged components of the polysaccharides.

Under some circumstances, the cell wall of plants can shift from being hydrophilic to being hydrophobic as the result of the deposition in the cell wall of 'water-proofing' materials called cutin and suberin. These materials are found in cell walls of certain plant tissues and their ability to retard the movement of water is significant. Both suberin and cutin are mixtures of multiple compounds including polymers with hydrophobic subunits and wax molecules. Like the lipid portion the cell membrane, these chemicals are 'dry' (hydrophobic) and water movement through walls with these materials is much retarded. While there are some chemical differences between the two, the primary distinction between cutin and suberin is location. Cutin is deposited in a coating called cuticle, present on the external walls of cells located on the outside of the aerial portions of plants. Suberin is deposited in the walls of certain cells as they are produced. Suberin is found in the above-ground portion of the plant in places where growth or mechanical damage has eliminated the cuticle. Suberin is also found in the below-ground portion of most vascular plants in a cylindrical tissue called the endodermis, whose significance will be discussed later.

A final component found in some polysaccharide cell walls is lignin, a material absent in non-vascular plants (e.g., mosses) but found in the cell walls of most vascular plants, and a material that is highly significant to their evolutionary success, i.e., their prevalence in today's flora. Structurally, lignin is similar to pectins and hemicellulose, i.e., a matrix that surrounds cellulose fibrils. Lignin is produced in what is described as the secondary cell wall, a component of the cell wall present only in certain cells. The secondary cell wall is laid down after cells have stopped growing, necessarily so because lignin is a rigid material that will not yield readily, therefore preventing the cellular expansion needed for growth. Lignin is the material that makes wood tissues woody. It is stiff and rigid and allows plants to be tall by resisting the compressive force of gravity. Like hemicellulose and pectin, lignin is a complex polymer with subunits that are not all the same and are not always connected the same way. Moreover, the subunits of lignin are not sugars, they are phenolic molecules chemically quite different from sugars. Lignin polymers extend in three dimensions, forming a solid material. Lignin is hard to digest and its breakdown products are phenols, chemicals that are poisonous to many organisms. Hence, lignin is resistant to degradation. The secondary cell wall is deposited inside of the primary cell wall and it necessarily shrinks the space available to the membrane bounded cytosol, sometimes eliminating it almost completely. Most cells with secondary cell walls are short-lived and are structural, providing function to the plant when they are dead.

Bacterial cell walls

Not all bacteria possess cell walls but the ones that do possess a wall material unique to bacteria called peptidoglycan. As the name implies, peptidoglycan has components that are peptides (sequences of amino acids) and components that are sugars (carbohydrates). Unlike the polysaccharide wall materials described above that are chains of monomers, peptidoglycan polymers form a mesh, a three-dimensional molecule (like lignin) with units linked not just end-to-end but also above-and-below and side-to-side. Also significant is the fact that many bacteria, including 'gram-negative' bacteria and cyanobacteria, have an 'outer membrane', a second phospholipid membrane that occurs outside of a thin peptidoglycan cell wall. Some bacteria possess one additional layer, an 'S-layer', a protein layer on the very outside of the cell, outside the outer membrane of gram-negative bacteria and the peptidoglycan cell wall layer of gram-positive bacteria.

Archaea cell walls

Recall that Archaea and Bacteria are prokaryotes and used to be considered a single group. One of the several features that distinguish Archaea is a distinct cell wall structure one that lacks peptidoglycan. The chemical composition of Archaeal cell walls is diverse and some have a cell wall composed of a carbohydrate/peptide material similar to peptidoglycan. Like some Bacteria, most Archaea are bounded on the outside by an S-layer, a self-assembling structure composed of globular proteins or glycoproteins.

'Inorganic' cell walls'

All of the cell wall materials discussed so far would be considered 'organic', a flexible term whose exact meaning wanders considerably. In this context it refers to 'biological materials', molecules found in living things, as opposed to inorganic molecules, those generally found in non-living things, e.g. rocks/minerals. Two important cell wall materials, calcium carbonate and silica dioxide, are most commonly found as minerals in rocks. However, these minerals are in some sense 'organic' because they can be produced by biological processes, cells produce conditions whereby calcium carbonate or silicon dioxide is precipitated out of solutions. In fact, their presence in some rocks is completely due to their manufacture by marine organisms whose remains became deposits at the bottoms of oceans and eventually in rocks. The 'White Cliffs of Dover' (Fig. 6) are formed from a massive deposit of coccolithophores, a type of marine algae that produces distinctive looking calcium carbonate plates as its outside boundary (Fig. 2). Although not as common or extensive as calcium carbonate cliffs, there are similar deposits of 'diatomite', a sedimentary rock formed from deposits of diatoms, another unicellular photosynthetic organism that produces an external skeleton, i.e., a cell wall, made of silica dioxide (Fig. 1). Exactly how the material is precipitated in such a precise, and often ornate, manner is not known with certainty.

Fig. 6 The white cliffs of Dover are a calcium carbonate (chalk) deposit formed by billions of individual coccolithophore 'skeletons' from organisms that lived in a Cretaceous sea. Similar deposits are found in Nebraska and Kansas.

'Internal' cell walls

A few organisms have an unusual structure where wall-like materials (i.e., structural components) occur just inside the membrane. One example is gram negative bacteria where there is a wall inside a membrane, but these bacteria also have a second membrane in its normal location, inside the cell wall. In contrast, dinoflagellates have plates of cellulose enclosed in membranes that occur inside of the plasma membrane. Cryptomonads have wall-like glycoprotein plates both inside and outside of the plasma membrane, forming a structure called the periplast that is unique to this group of organisms.

Dermal tissues of multicellular organisms

Most multicellular organisms have groups of cells, called dermal tissues, that form a 'skin' to an organism. These cells / tissues will be considered anatomically in a later chapter but they generally are cells tightly bound to each other (no spaces between them) so that they collectively form a boundary to the organism. Often these cells have different components in their cell wall (e.g., cutin, suberin, lignin) and/or produce a secretion on the outside (cuticle, see below) that is important to their functioning. Additionally, many multicellular organisms produce structures, organs, that have specialized boundaries that are significant to their role. In inanimate life the most common of these are organs associated with reproduction, e.g., spore cases (sporangia), fruits and seeds. The 'skin' of these structures may be important in protecting the structures inside, e.g., the sporangium of mosses, the outside of an acorn (a fruit wall), the seed coat of apple seeds (in the latter two cases it is lignin depositions in the cell walls of dermal cells that are particularly important). The 'skin' of reproductive structures must eventually open up and allow the dispersal/release of its contents and sometimes features of the 'skin' actively participate in dispersing its contents (see discussion below on 'explosive' movements). In other situations, the permeability of the coating, in particular how much water/oxygen enters, can significantly influence the behavior of the enclosed structures.

Specialized coatings

Some organisms /colonies of organisms cover themselves or part of themselves with some sort of coating. A number of algae and bacteria coat themselves in a polysaccharide gel outside of the cell wall. A striking example of this is with some species of *Nostoc*, a colonial, filamentous cyanobacterium that sometimes forms gelatinous sheets or spheres that may be several centimeters across (Fig. 7). The bulk of the sphere is a polysaccharide secretion deposited outside the cell walls of individual cells. Coatings may be significant to the organism for a variety of reasons including: retention of water, protection, adhesion to substrates, keeping a colony of cells together, buoyancy. Similar coatings are sometimes important in producing biofilms, communities of one to several organisms including bacteria, archaea, fungi and others, that coat surfaces (e.g., dental plaque) and are sometimes important ecologically and to human disease).

Fig. 7 *Nostoc*, a cyanobacterium, can form spherical structures up to several centimeters in extent (left photo), the result of polysaccharide secretions. The photo on the right shows the filaments of the algae, the spaces in between the filaments are filled with polysaccharide hydrogel secretions.

Cuticle

Most plants, who are terrestrial organisms exposed to a drying atmosphere, have a coating on the outside called a cuticle (Figure 8) that lessens water loss. The cuticle is a complex mix of chemicals including cutin (mentioned above as a component of some cell walls) and other similar (hydrophobic) constituents. The cuticle is much more impermeable to water (it has a high resistance to water movement) than the membrane because it is substantially thicker and also because proteins do not span across it. The cuticle's high resistance to water movement is significant because it lessens water loss from plants to the atmosphere. However, the cuticle is also impermeable to gases, in particular carbon dioxide, and this feature has important consequences for photosynthesizing plants. The cuticle is produced by the cells on the outside of the plant, and the outer part of the cell walls of these cells have extensive deposits of cutin. In addition, hydrophobic materials are deposited completely outside of the cell wall (outside the area where cellulose microfibrils are present). The mechanism whereby materials can be deposited outside of the cell walls is not completely understood.

In addition to reducing water loss, the cuticle is a physical barrier to the entrance of organisms into plants, and it also serves to absorb and reflect UV radiation, thereby pro-

Fig. 8 Hosta leaves showing the hydrophobic nature of the cuticle which causes water to mound up into spheres.

tecting tissues within. Also, the dryness of the cuticle, along with other specific chemical features, makes it a very inhospitable place for the growth of other organisms, adding to its protective function. The cuticle of many plants may be ruptured by growth from within (discussed later). In these cases, the protection of the cuticle is replaced by a new layer or layers of cells that are produced with suberin in their cell walls, forming the outside portion of what we know as bark.

Spropollenin

Pollen grains (of seed plants) and the spores of a variety of organisms are coated with sporopollenin, a chemical that is particularly resistant to degradation and is thought to be significant in protecting against desiccation, oxidation and enzymatic degradation. It is the resistance of sporopollenin to breakdown that allows pollen buried several hundred million years ago in sediments to be preserved and recognized. Its exact chemical nature has not been determined (partly because it is so hard to breakdown!) but it has some similarities to cutin in having hydrocarbon components as well as phenolic components.

Boundary diversity

The following table summarizes boundary materials for organisms that we cover (plus a few others) grouped grouped by whether they are unicellular or multicellular and whether or not they possess a cell wall.

Cell walls, cell membranes and structural integrity

One reason that an organism's boundary is significant is because the boundary resists physical forces that are acting on the organism. These forces can come from the outside (e.g., wind, gravity) or from the inside (internal pressure). For unicellular organisms it is the strength of the boundary that prevents (or allows) deformation that would come about as a result of these forces. For multicellular organisms it is the boundaries of individual cells and also their linkages to each other that determine how the organism will respond to external forces.

Osmotic forces

A common factor that might cause a cell to change shape is 'osmotic disruption', brought about by osmosis, the diffusion of water. All other things being equal (more in Chapter 22) water moves by diffusion from areas where it is purer (i.e. has less solutes) to areas where it is less pure (has more solutes). Since living things acquire and manufacture solutes and the impermeability of the cell membrane allows these solutes to be concentrated inside cells, cells are often are in situations where water is going to spontaneously move into them. The cell membrane offers little resistance to expansion and is not able to be stretched. Consequently cells/organisms with only a membrane will burst if exposed to pure water, or any water that is purer than that inside the organism, unless they have mechanisms to eliminate the water. The presence of a cell wall outside the membrane solves this problem because it resists expansion. This allows the cell to pressurize, and this pressure prevents the entry of more water (note that diffusion is NOT just dependent upon differences in purity, as it is often described. It is also dependent upon pressure, more in Chapter 24).

Table 1

Boundary and organism type	Organisms	Features
Unicellular organisms with no walls	Some bacterial groups	Mostly parasites
	Cellular slime molds	For parts of their life cycle they do have walls
	Plasmodial slime molds	Like a giant amoeba
	Euglenoids	No wall, but the membrane is reinforced with protein filaments forming a structure called a pellicle, often exhibiting parallel striations on the outside
	Cryptomonads	Wall-like materials (glycoproteins) both inside and outside of the plasma membrane, forming a structure called a periplast.
	Dinoflagellates	Often possess multiple 'plates' of cellulose that lie interior to the cell membrane
Multicellular organisms with cells with no walls	Animals	Many do have coatings ('skin') that are groups of cells
Unicellular organisms with cell walls of some sort	Bacteria (most), including all Cyanobacteria	Wall contains a peptidoglycan polymer with polysaccharide and amino acid components. Some bacteria have a second, 'outer membrane' outside the peptidoglycan layer
	Archaea	Wall contains a polymer similar to peptidoglycan with polysaccharide and amino acid components
	Diatoms	Wall is made of silica (SiO_2) — Silicon (Si) is an element that most organisms do not accumulate. The wall is also distinctive because it is not organic (i.e. carbon based), does not absorb water and is very rigid

Boundary and organism type	**Organisms**	**Features**
	(some) Green algae (Chlorophyta)	A variety of wall materials (and sometimes none at all) many green algae have walls containing cellulose, a polymer of glucose
	Haptophytes (Coccolithophores)	Wall consists of round plates of calcium carbonate outside the cell membrane
	Bread molds (Zygomycota)	Cell walls are composed of chitin, a polymer of acetyl glucosamine units (essentially sugar units with a nitrogen attached). The same material is found in the exoskeleton of insects and mollusks.
	Water molds (Oomycota)	Cell walls are contains cellulose, a polymer of glucose units.
Multicellular organisms with cell walls	Club fungi (Basidiomycota)	As is the case in all fungi and in the bread molds, the cell wall is composed of chitin, a polymer of acetyl glucosamine units (essentially sugar units with a nitrogen attached).
	Sac fungi (Ascomycota)	Same as Club fungi
	Red algae (Rhodophyta)	Wall contains cellulose and sulfated polysaccharides.
	Brown algae (Phaeophyta)	Wall has small amounts of cellulose with large amounts of alginate, a polysaccharide polymer composed of uronic (sugar-acid) units
	Green algae (Chlorophyta)	Wall varies but some with cellulose as the main constituent; other green algae have mannans (polymers of mannose), xylans (polymers of xylose), glycoprotein polymers and some have no wall at all
	Plants (mosses, conifers, flowering plants)	Cell wall contains filaments of crystalline cellulose connected by hemicellulose polymers and imbedded in pectin polymers. Many plant cells develop an inner secondary cell wall containing cellulose and lignin, a complex, phenolic polymer.

It is important to note that the strength required to resist expansion is 'tensile' strength. The cell 'resists' water absorption because components of the wall (e.g., cellulose or chitin microfibrils) are resistant to being stretched.

If the cell with a cell wall were in an environment causing it to lose water, e.g., an aquatic habitat high in solutes or in a terrestrial habitat where organisms are losing water to a drying atmosphere, water would diffuse outward and the presence of a wall would not prevent the cytosol from collapsing unless the membrane were somehow glued to the cell wall to prevent it. This is not thought to be the case. Moreover, for plant cells with only primary cell walls (no lignin reinforcement) or fungal cells, the wall is not strongly resistant to compression and if water leaves the cell the cell will shrink in size (collapse). Note that although cellulose fibers have a high tensile strength, they are not very resistant to compression, i.e., have little compressive strength. Consider a string (which often times is actually a collection of cellulose microfibrils): you can pull on the string and it resists stretching but it is very easy to collapse the string, it has very little compressive strength.

Walls and 'structural integrity'

Cells and organisms do need compressive strength to: (1) provide protection from certain predators who would like to crack them open to get to the goodies inside, and (2) allow the organism/cell to resist various forces in the environment, e.g., gravity. Resisting forces becomes more significant if organisms are bigger, especially for organisms in terrestrial environments where the surrounding medium (air) provides little support. In terrestrial environments, organisms will be collapsed by gravity if they are more than a few centimeters in height unless they have structural strength to resist it. Three-dimensional wall materials (e.g., peptidoglycan, calcium carbonate, silica dioxide), can resist compression but these wall materials are only present in very small organisms. Plants are 'big' and terrestrial, how do they resist gravity? Walls with lignin, another 3-dimensional material, will resist compression, but not all plant cells have lignin. Plant cells lacking lignin have structural integrity against gravity because of the combination of water, a membrane that 'holds' solutes but allows water movement, and a cell wall that has tensile strength. Water is very difficult to compress as long as it is contained in something that doesn't allow water to escape. It might seem that water should be able to be 'squeezed out' of cells by the force of gravity but this doesn't happen because water movement out, as a cell is squeezed and pressurized by gravity, is balanced by water movement in due to purity (the low water purity inside is because of solutes, Chapter 24). To summarize: plant cells without lignin resist the force of gravity because is incompressible (high compressive strength) and is located within a selectively permeable membrane surrounded by a cell wall with tensile strength.

This structural feature is demonstrated in wilting plants. Deprived of a supply of water, many plants are unable to resist the force of gravity and to maintain their structure. The cells, mostly with only primary cell walls (no lignin) in and of themselves cannot resist compression, they need water, and if re-watered a wilted plant will once again stand up against gravity Fig. 9). Woody plants, at least the woody parts of woody plants as well as some herbaceous plants do not wilt because they have cells with secondary walls containing lignin that provides the compressive strength to resist the forces of gravity.

Fig. 9 Wilted plants. The plant on the right has been deprived of water and has lost the ability to resist the force of gravity, causing the leaves to droop. When re-watered the plant is able to re-pressurize its cells and to once again regain its normal form. The ability to resist gravity is a result of the combination of a cell membrane, a cell wall, with the diffusion of water creating pressurized cells.

Although most cell walls resist expansion, the resistance is not absolute and cells can yield (i.e., expand) to some extent when pressures increase inside them. The yielding of cell wall is both elastic (the wall yields, but returns to its original form when the force, internal pressure, is eliminated) and also plastic (the wall yields but does not return to its original shape if the internal pressure is reduced). Because cell walls are present even in newly created cells, plastic deformation is essential for cellular growth.

Considering a tree trunk being pushed by the wind, the windward side needs tensile strength, the lee side needs compressive strength. Woody stems are almost entirely composed of lignified cells that have both tensile strength from the cellulose and compressive strength from the lignin. Such a composite material is comparable to 'reinforced' concrete (concrete poured around wire/steel rods) or fiberglass (resin poured around glass fibers), where the matrix of concrete/resin provides compressive strength and the fibers of wire/glass provides the tensile strength. Moreover, the lignin in plant cells was deposited while the cellulose was under tension, because the cell was pressurized when the lignin was deposited in the secondary cell wall. This produces a composite material like pre-stressed concrete, a concrete made by pouring concrete around steel cables that are under tension. Pre-stressed concrete has superior strength when compared to regular reinforced concrete. Finally, a tree trunk blown by the wind not only has to have structurally strong cells, the cells need also to stick to each other because separations between cells will cause structural failure, and indeed when stems break or lumber fails it is both because of separations between individual cells and also failures within individual cells.

Boundaries and organism movement

Organisms move by manipulating their boundaries relative to the environment. For familiar organisms (lions and tigers and bears) this is done with appendages (legs, fins, tentacles) whose positions are manipulated internally. This is comparable to the movement brought about by flagellae and cilia, which are extensions of the boundary of cells that often provide motility to unicellular organisms, including most of the groups covered here: most archaea (e.g. *Halobacterium*), most bacteria (e.g. *Agrobacterium*, *Rhizobium*), euglenoids (e.g. *Euglena)*, dinoflagellates (e.g. *Gonyaulax*), cryptomonads, some of the green algae (e.g. *Chlamydomonas*). Flagellae and flagellar motility is commonly found in the reproductive cells (e.g. sperm, zoospores) of most multicellular organisms, and, as considered in Chapter 2, these cells might be considered organisms. Thus flagellated mobility is near ubiquitous, lacking only in a few groups, all of them 'inanimate', being absent in all red algae, all flowering plants (and almost all seed plants), almost all fungi (except in some Chytrids), and almost all diatoms.

But there are other means of movement and the diversity of organisms that we cover illustrate a diversity of movement mechanisms, all of which, like flagellar movement, are related to manipulation of boundaries. Some examples are given below:

Flagellar motility

Cytoplasmic streaming

Like amoebae, the amoeboid cells of **cellular slime molds** move by pushing and pulling on their boundary by means of microtubules, keeping the volume of the beast constant while changing its form. This allows them to move through their environment or to flow around a particular food item. **Plasmodial slime molds**, though much bigger and multi nucleate, are able to move in a similar manner. Their cytosol is seen to stream back and forth but more so in one direction, propelling the organism in the direction of greater flow.

Euglena motion

Organisms in the Euglena group can move by both flagellar movement and by a movement that involves reshaping their form, comparable to an amoeba or slime mold.

Growth

Fungi and plants move by growing, which requires the extension of boundaries into new territory. This process will be covered later but it requires the extension of individual cells, accomplished by the pressure inside these cells exceeding the tensile strength of the cell wall and also exceeding the resistance to movement provided by the medium that they are moving through (e.g., soil).

Stomatal movement

Vascular plants and a few non-vascular plants have the ability to change the shape of pairs of cells (guard cells) in the skin tissue of (generally) leaves, thereby opening pores (stomata) in the leaf surface. This is accomplished by means of changing hydration levels of cells, thereby changing their pressure and shape and in turn opening a hole in between them. Stomatal movement ties into two topics of this chapter: (1) the change in shape in guard cells is a consequence of asymmetric deposition cellulose microfibrils in the cell walls, (2) the opening of stomates dramatically changes the dermal permeability to carbon dioxide and water, allowing water to escape the leaf and carbon dioxide to enter.

Leaflet/organ movement

In addition to moving by growing, a number of plants are able to move appendages, usually leaves. This is accomplished in a manner similar to the operation of stomates: by changing hydration levels of specific cells and groups of cells, thereby changing their pressure and volume and in turn changing their shape. In flowering plants, the changes in cellular shape happen in special cells at pivot points that allow leaves to move. In mosses, changes in cellular shape happen in all the cells of the 'leaves' (microphylls) , sometimes causing them to twist and curl up next to the main axis of the moss. Most mosses also possess appendages called peristome teeth at the end of the spore-producing capsule. Changes in the hydration of the cells in these teeth change their shape, which allows the capsule to close in times of high humidity, when spores are less likely to be dispersed, and open in times of low humidity, when spores are more likely to be dispersed. Although not a boundary movement, a similar mechanism and motion happens with groups of cells called elaters that are present in the sporangia (containers where spores are produced) of horsetails and liverworts and whose movement aids in the dispersal of spores.

'Explosive' movements

Mentioned earlier was the fact that as cells absorb water and expand, the change in size may be elastic, in which case energy is being stored in the wall; this energy can be utilized to cause movement. Such an energy storage and a resultant movement is significant in spore and seed dispersal. A container, which may be a cell (e.g. the basidium of club fungi (Basidiomycota) or may be a container with a wall of dermal cells (the fruit of dwarf mistletoe or squirting cucumber, both flowering plants) becomes pressurized and stores energy in the wall(s). Then a part of the wall(s) breaks open and the pressure is rapidly released, expelling the contents (spores or seeds). A similar phenomenon occurs in ***Pilobolus***, a **bread mold (Zygomycota)** except that what is expelled is the whole spore container (sporangium), occasionally with other organisms hitching a ride. Dehydration can also result in movement. Cells in the fruit wall of some fruits (e.g., witch-hazel) and also in the spore containers (sporangia) of many ferns dehydrate as the fruits/sporangia mature. Dehydration results in shrinkage that is resisted by the cohesive strength of water bound to cell wall materials. More and more force builds up as more and more water is lost. Eventually the force exceeds the cohesive strength of the water in the walls of the cells, again causing the structure to rupture. This is often accompanied with an extremely rapid change in the form of the fruit/ spore capsule that can result in the forceful release of seeds/ spores, like a catapult.

Boundaries and communication/sensation

A final point about boundaries is that they play a role in the sensation of the environment and communication between organisms. Organisms need to sense their environment, which means that either signals need to get through the boundary or alternatively that there exists a sensor molecule that extends through the boundary and allows a molecular interaction outside to cause a response inside. Both of these things happen. It is also the case that important signals are actively transported out of organisms and that some signals are components of the boundaries (e.g. cell wall compounds, or derivatives of enzymatic action on cell wall compounds). A great example of this is the communication between Rhizobium, a nitrogen fixing bacteria and the plants they associate with.

Further Reading and Viewing

- “Squirting Cucumber: The Plant That Explodes” by Animalogic. Exploding fruits.
    - https://www.youtube.com/watch?v=LLBgoIn8Dtw
- “Exploding Cucumbers! | Slo Mo #36 | Earth Unplugged” by BBC Earth Unplugged
    - https://www.youtube.com/watch?v=wOIHzl2h9a8
- “Exploding myths about seed dispersal” by Stuart Gillespie
    - https://www.ox.ac.uk/news/science-blog/exploding-myths-about-seed-dispersal

- “See the Plant Kingdom’s Hidden Microscopic Wonders” by Michael Greshko. Nice images of plants, see in particular the first image showing the cuticle coating on part of a moss and images 3 and 11 that show the interlocking nature of a plant epidermis (“skin”) cells as well as the stomates. And images 17 and 18 show the “glass houses” of diatoms.
    - https://www.nationalgeographic.com/science/article/photography-plants-cells-diatoms-xylem-phloem-microscope
- “The Formation and Function of Plant Cuticles” by Trevor H. Yeats, Jocelyn K.C. Rose. Good technical discussion of the plant cuticle.
    - https://academic.oup.com/plphys/article/163/1/5/6110956
- *General Microbiology* by Linda Bruslind. Good discussion on the membranes of archaea.
    - https://open.oregonstate.education/generalmicrobiology/chapter/archaea/

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- Chitin, glucose, and cellulose © Arion422 is licensed under a CC BY-SA (Attribution ShareAlike) license
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CHAPTER 4: ORGANISM FORM: COMPOSITION, SIZE, AND SHAPE

In the famous Star Wars bar scene, an attempt was made to illustrate diverse organisms. It was a remarkably unimaginative effort: all of the life-forms illustrated had a striking resemblance to humans, all about the same size and with the same basic components (e.g., head, legs, arms). Without going outside this planet one can come up with a much more diverse set of organisms, as I hope this chapter demonstrates. Organisms vary from each other in multiple ways but in this chapter, I will focus on three aspects, two of which, size and form, are very straightforward, but the third aspect, composition, is less familiar. These characteristics have been shaped by evolution, and evidence of convergence (unrelated groups converging on a common form) and divergence (related groups showing a variety of forms) abound. Consequently, although form, size and composition are extremely important to an organism's biology, they are remarkably poor indicators of phylogeny. This makes attempting to characterize the form of larger taxonomic entities (class, order, phylum) challenging, if not impossible. Composition, size, and shape are interrelated and significant to other aspects of an organism's biology. Moreover, they are also often dynamic, changing during the existence of an organism.

TOPICS

- Composition
  - Unicellular
  - Multicellular
  - Colonial
  - Coenocytic
- Size
- Size and shape considerations
- Organism shape: spheres, flatten ed, cylinders

Fig. 1 Add to the Star Wars bar scene??? This organism changes composition, form and size throughout its life with the most noticeable form being a cylinder about 10 cm in height topped with a sphere.

Composition

What are organisms composed of, i.e., what are they constructed of? A later chapter will consider composition in chemical and molecular terms. In this chapter 'composition' refers to an organism's cellular nature. Most would agree that all organisms are made of cells, but is it one cell or many? And are the cells all the same or do they differ? And are the cells 'typical' in their organization? Here are four composition types, two of which are very familiar, and two of which are less so:

- **unicellular organisms** — the organism is a single uninucleate cell
- **multicellular organisms ('complex multicellularity')** — the organism is made of multiple (usually many) cells but the cells are different shapes and have a specific organized arrangement that involves tissues and organs
- **colonial composition ('simple multicellularity')**— the organism is made of multiple cells but the cells are generally similar in size and shape with no obvious tissues and organs
- **coenocytic composition** — the organism is made of 'atypical' cells, atypical in that

they have multiple nuclei, sometimes thousands of them. The entire organism is sometimes just a single cell that has many nuclei, or it may be composed of multiple units, that might be called cells, except that they are generally larger than normal and have multiple nuclei.

Unicellular Organisms

In spite of the fact that plants and animals, the two groups of organisms that most people are familiar with, are multicellular, unicellular composition is by far the most common type of organism. Clearly it is a successful way for an organism to be constructed and most of the 'living' that happens on earth is a consequence of unicellular life. As will be demonstrated by the examples of unicells that are covered here, there is a tremendous diversity in unicellular organisms.

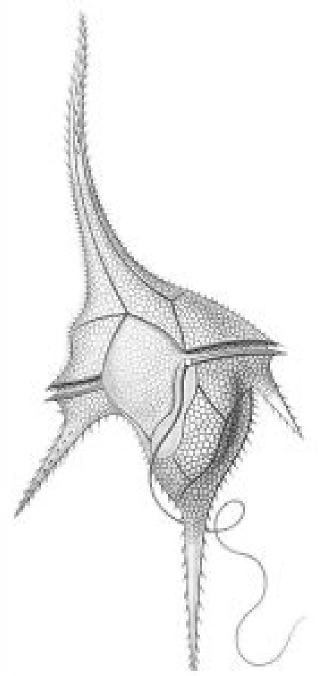

Fig. 2 Dinoflagellate

Unicellular organisms are NOT always simple in form and function. They may be very elaborate in form e.g., diatoms and dinoflagellates (Fig. 2). While any cell is a complex entity, there are many unicellular organisms with components functionally analogous to the (multicellular) organs of more familiar organisms. For instance, *Euglena* cells possess a remarkable amount of internal organization, including organelles (eye spot, contractile vacuole) that perform functions covered by whole organs (eye, kidney) in multicellular organisms. Also, *Euglena* (Fig. 3) (along with many bacteria and unicellular algae) can move as a result of coordinated re-positioning of extensions that are not multicellular legs, wings or fins but rather an extension of the cell, called a flagellum; additionally, *Euglena* and other unicellular organisms can also move by altering the form of the cellular body, comparable to what earthworms do, but, unlike earthworms, it happens without the aid of muscles and other tissues.

Most organisms go through a stage or stages that is/are unicellular (e.g., spore, gamete, zygote) and these unicells, many of which can be considered organisms because they are often distinct spatially and temporally, are often very elaborate in structure and func-

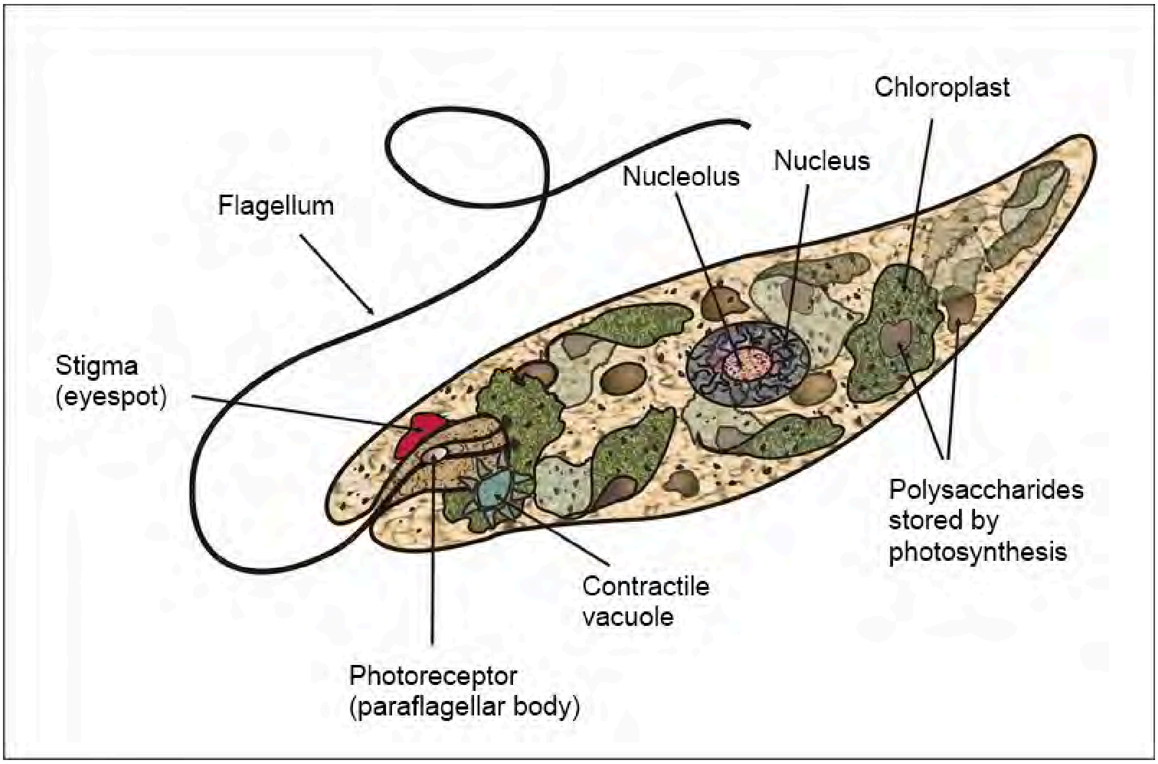

Fig. 3 Euglena

tion. Examples that will be discussed later are the sperm of multiple groups of plants (e.g., ferns, mosses), often referred to as a spermatozoids (Fig. 4).

Although being unicellular is rightfully considered a primitive condition, yeasts are unicellular fungi and demonstrate that the unicellular condition can sometimes 'reappear' in a lineage that previously had some other type of composition, i.e., that unicellularity is sometimes a 'derived' condition. The vast majority of fungi are colonial/multicellular but yeasts have appeared independently multiple times in several different fungal groups and they do NOT represent the primitive condition. In many yeasts the unicellular growth habit is tied to environmental conditions and the organism can be induced to grow in a colonial matter by adjusting conditions.

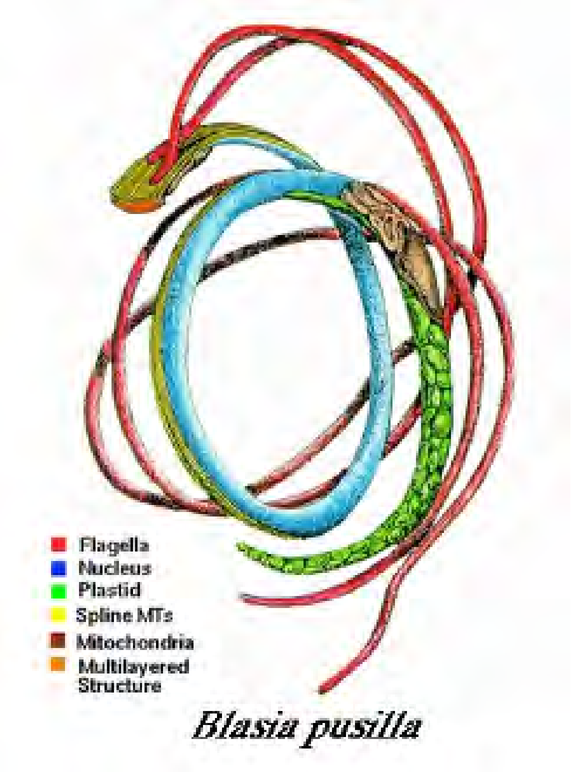

Fig. 4 The spermatozoid of a liverwort.

Colonial Organisms

Fig. 5 Slug and sporocarp forms of the cellular slime mold Dictyostelium.

Colonies of cells (colonial organisms) can form two ways. The less common way is for individual cells to come together to form a colony. This behavior has evolved multiple times, several times in the bacteria (in groups described as 'social bacteria') and also in the cellular slime molds like Dictyostelium. (Fig. 5) Colonies produced this way will contain cells that are not necessarily all the same genetically. The second and far more common way to form a colony is a result of repeated cell divisions where the daughter cells adhere to their parent. For a cell with a cell wall, the adhesion between daughter cells is accomplished with an adhesive layer deposited between the new cell walls that are produced during cell division (cytokinesis).

In colonial organisms, repeated cell divisions produce an organism with many cells attached to each other but the cells are all (or almost all) identical. This type of composition is sometimes described as ‘simple multicellularity’ or ‘plurocellularity’ that is distinguished from ‘true multicellularity’ or ‘complex multicellurity’, or sometimes just ‘multicellularity’ by a variable set of criteria that usually include cellular differentiation and the production of tissues (more on this in the next chapter). A wide variety of colonial forms are possible and result from the patterns in the planes of cell division. For example filaments (Fig. 6) are formed if the plane of cell division is always the same, producing a chain of cells connected top to bottom.

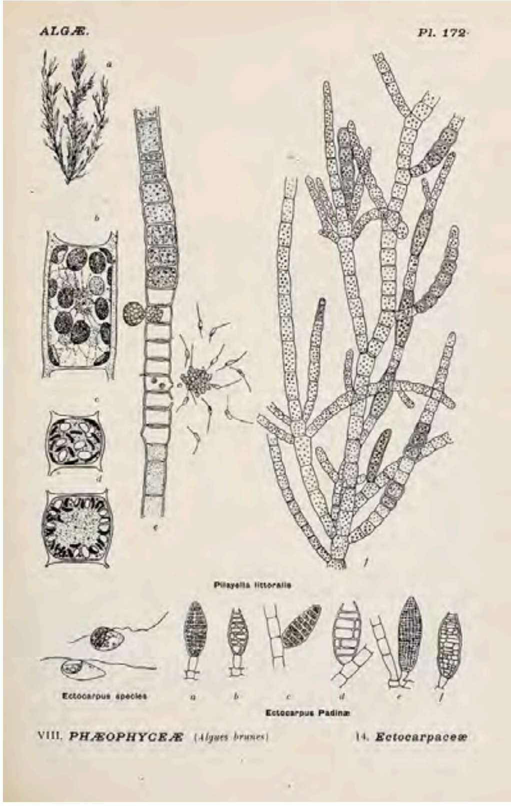

Fig. 6 Branched, filamentous growth in the brown algae *Ectocarpus*

Fig. 7 Two dimensional sheets are produced by the colonial growth in Ulva, a green algae.

Filaments can grow from the basal end (if the original cell continues to divide but the daughter cells do NOT divide) or it can grow from the tip (if the original cell does NOT divide and the daughter cells repeatedly do divide) or it can grow throughout the filament. Filaments may branch if some cells in a filament divide in a direction roughly parallel to the direction of the filament; flattened **sheets** (Fig. 7) are produced if cells repeatedly divide in two perpendicular planes; globular clusters of cells are produced if the original cell and its derivatives divide repeatedly in multiple planes.

Filamentous growth is found in archaea, bacteria, (Fig. 8) and fungi and many of the groups that used to be put in the Protist Kingdom, in particular the green, red and brown algal groups and some diatoms. It is also found as a brief stage in most mosses and ferns (Fig 10).

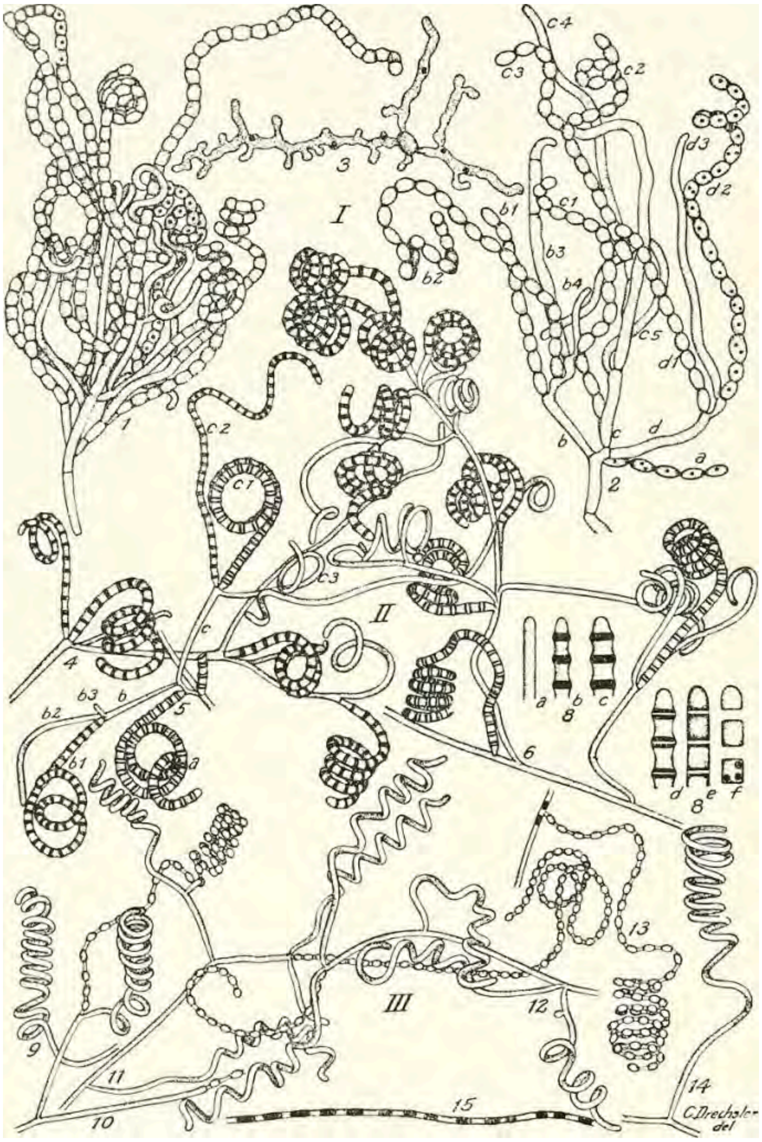

Fig. 8 Actinomycete bacteria generally have a filamentous form.

Most fungi exhibit a distinct type of filamentous growth where the filaments, called hyphae, grow from the tip but commonly branch, both at the tip and below it, and with

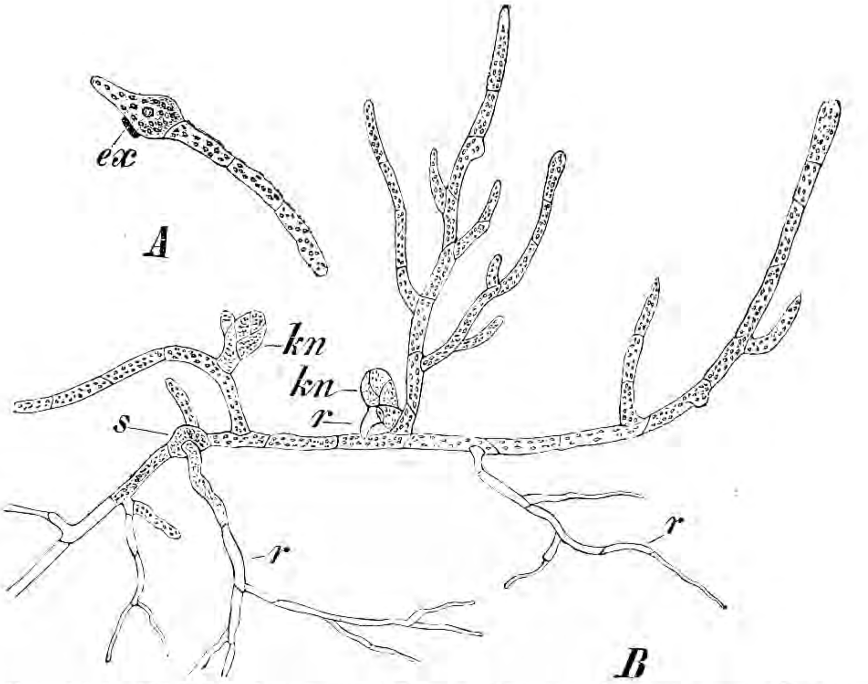

Fig. 313. Funaria hygrometrica. *A* keimende Spore, *ex* Exine. *B* Protonema mit Knospen *kn* und Rhizoiden *r*, *s* Spore. Vergrössert. (Nach Müller-Thurgau.)

Fig. 9 A protonema, the filamentous growth (from a spore) of the haploid stage of a moss. Less commonly a two dimensional sheet is produced.

the branches capable of fusing with other hyphae to form what is called a mycelium, an interconnected, anastomosing mass of hyphal filaments (Fig. 10).

Two dimensional colonial growth, forming sheets one-to several cells in thickness, is most commonly found in photosynthetic forms, primarily in the algal groups. It also is present in some of the non-vascular plants: all of the hornworts and some of the liverworts (Fig. 11) , where it is present in the haploid (gamete-forming) form but not the diploid, (spore producing) form (see Chapter 13). Spherical colonies are occasionally found, particularly in the green algae.

The advantages of colonial growth, i.e., of having cells aggregate or having daughter cells remain attached to parental cells, may be different in different situations. One advantage is size; it allows for much larger organisms than a single cell, and larger size is sometimes, but not always, advantageous. As discussed below, size affects interactions between

Fig. 10 The filamentous growth of fungi consists of unicellular filaments (hyphae).

organisms and their environment. Colonial growth may be successful because it allows for exploration of the habitat: an organism in a marginal habitat may be sustained as it explores for greener pastures. The larger size of colonies makes possible the exploitation of different habitats/regions. For example, algae are able to exploit both a substrate (for attachment) and the water column (for light and nutrients). Most workers feel that colonial growth (simple multicellularity) is a step on the way to complex multicellularity, but the abundance of highly successful (i.e., diverse and plentiful) colonial forms indicate that colonial growth is itself an advantageous composition type.

Coenocytic Organisms

Probably the least familiar composition type is coenocytic, where the organism's cells, or sometimes its single cell, is multinucleate. This results from repeated nuclear cell divisions that are unaccompanied by splitting of the cytoplasm (cytokinesis). Part of the significance of the coenocytic condition has to do with size. Cell size may be limited because

Fig. 11 Marchantia, a 'thalloid' liverwort whose structure consists of flattened sheets of cells. This the haploid form of the plant. The rounded structures that are visible are associated with reproduction (Chapter 13)

a single nucleus can only control a limited volume of cytosol and for the cell to get bigger there needs to be additional nuclei. Coenocytic cells are usually large and sometimes extraordinarily so. An extreme case is found in the plasmodial slime molds (e.g., *Physarum*), an amoeba-like organism that consists of a single wall-less cell that may be as much as a meter in length with hundreds of thousands of nuclei (Fig. 12). The form of slime molds is dynamic, owing to the ability of the cytoplasm to flow in channels inside the single cell, thereby allowing the organism to explore its environment, engulf food, and even climb up over obstacles. Unlike wall-less plasmodial slime molds, coenocytic organisms with walls can produce specific, permanent forms, but not the way that form is typically created in multicellular organisms (adding cells to create a form), but instead as a result of the creation of shape in individual large cell(s). The bread molds (Rhizopus). produce rhizoids, stolons and stalked reproductive structures, all formed out of a single cell with multiple nuclei (Fig. 13).

Similarly, the notorious invasive green algae *Caulerpa*, can appear very plant-like, i.e., with 'stem and leaves ', but it's remarkable size and complexity occurs without recourse to cells and tissues.

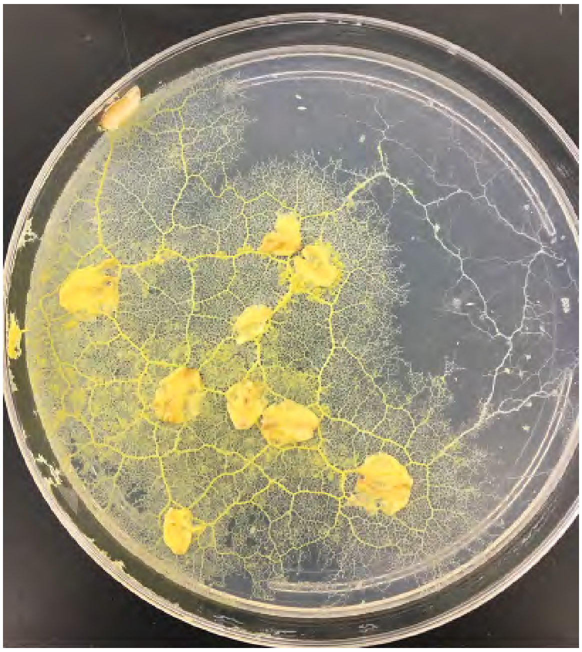

Fig. 12 The plasmodial slime mold, Physarum, consists of a single large cell

Many coenocytic organisms are very similar in form to colonial organisms, most commonly filaments but also sheets and spheres. The 'fungal' structure of hyphae and mycelium that is cellular (i.e., colonial) in the sac fungi (Ascomycota) and club fungi (Basidiomycota) is coenocytic in the bread molds (Zygomycota) and the mycorrhizal forming Glomeromycota. And this same fungal-like coenocytic form is found in a non-fungus group, the water molds, e.g., the plant pathogen *Phytophthora*. The structure of water molds explains why the group used to be placed in fungal phylum and also why grouping things by 'looks', i.e., form, is dangerous! Water molds are now placed in a group that includes brown algae and coccolithophores, two groups that are not at all fungal like nor coenocytic.

Many would not consider these coenocytic organisms to be unicellular, even though technically many are. They are closer to a colonial organism. If one defines organ as a component of an organism that provides a particular function (e.g., anchorage, elevation) then it is apparent that organs can be formed in both colonial and coenocytic organisms (Fig. 14), in both cases without the presence of specialized cells and tissues.

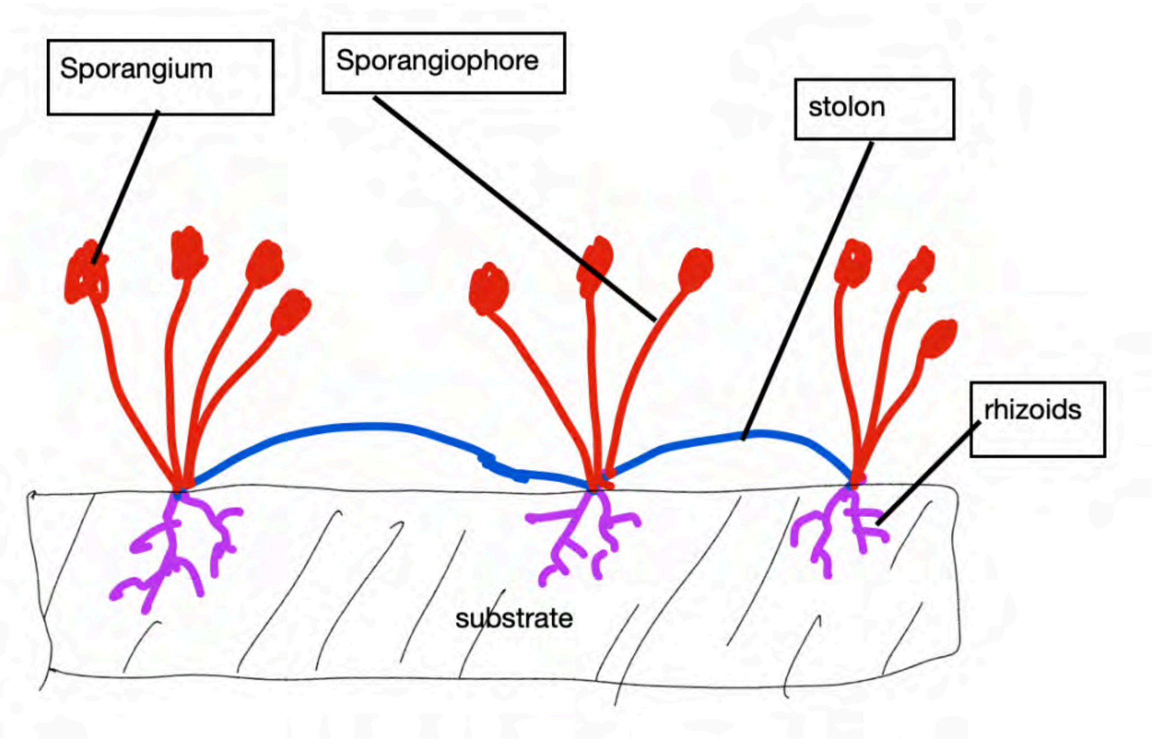

Fig. 13 Representation of the structure of the bread mold *Rhizopus*, showing rhizoids, stolons and sporangiophores. Before forming these structures the fungus exists as a mycelium.

Multicellular Organisms

Most workers would not unify all organisms composed of two or more cells as 'multicellular' but developing criteria for useful definitions (e.g., 'simple vs. complex' multicellularity) is challenging and there is no universal agreement as to where to draw lines. For most researchers 'true' multicellularity involves specialization of cell types, a topic that will considered in the next chapter. The introduction to the 'Organisms' section of the book lists inanimate life based on mode of nutrition and cellular nature, with links to specific groups of organisms.

Fig. 14 Caulerpa, a coenocytic green algae that forms stems, blades and holdfasts (the extent of the vertical structures is 10-30 cm)

Organism Size

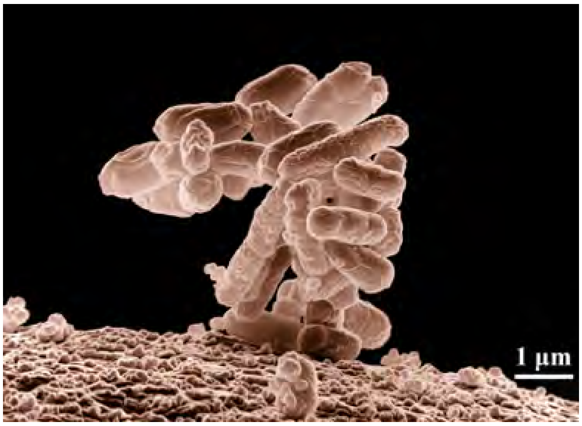

Fig. 15 Escherichia coli bacterial cells

Organisms vary tremendously both in volume and their extent in three dimensions. The smallest organisms (Table 1) are prokaryotes (bacteria and archaea) , unicellular organisms that lack nuclei or other cellular organelles, with longest dimensions typically of a few um (= 10^{-6} mm) and volumes of less than 1 um^3 (= 1 femolitre, where a billion (10^9) femolitres equals 1 ul; a quadrillion (10^{15}) femolitres equals 1 litre). These tiny organisms are usually shaped as spheres, rods or spirals. Although most prokaryotic cells range from 0.5 to 10 um, there are a few giant prokaryotes whose cells might be up to 500 um in length, meaning that they can be seen with the naked eye, albeit as a speck.

Unicellular eukaryotes possess cells with nuclei and other cellular organelles. They are generally bigger (10-100 um) than prokaryotes although there are a number of unicellular eukaryotes with small cells, in particular the yeasts (unicellular fungi, generally with cells less than 10 um). The fact that unicellular organisms are *almost* always small in size is generally thought to be a consequence of the need for nuclear control of cellular activity: larger size is difficult because in large cells messages (mRNA, proteins) moving by diffusion take too long to get from the 'control center' (the nucleus, the ribosome) to all parts of the cell. This idea is supported by the following observations:

- coenocytic cells, which have multiple nuclei, are often much larger than cells with a single nucleus
- larger unicells often exhibit cytoplasmic streaming which provides for more rapid movement of signals throughout the cell
- larger unicells (found in plants, fungi and algae) possess a large central vacuole that takes up much of the cell's volume and that is in some ways a metabolic 'dead space' that is relatively inactive (or at least not as dynamic as the cytosol); consequently, the amount of cytosol that the nucleus must 'control' is actually much smaller than appears based on cell size

There are a few extremely large unicellular organisms, *Acetabularia*, (Fig. 16) standing up to 5 cm tall, being one of them. *Acetabularia* is unique not just for its size but also because it demonstrates that 'organs' ('rhizoids', 'stems', 'leaves') are possible even in organisms that are unicellular. *Acetabularia* cells are over 1000 times larger than typical eukaryotic cells, with maximum dimensions of over 50,000 um (= 50 mm = 5 cm).

[Other large unicells e.g., bread mold (*Rhizopus)*, *Physarum* (plasmodial slime mold) are coenocytic and the case could be made that they really should not be considered unicellular.]

Most organisms over 100 um in size are colonial, coenocytic or multicellular. While the cells of coenocytic organism vary greatly in size, the cells of colonial and multicellular organisms are commonly 10 – 100 um in their maximum dimension and the organism's overall size is determined by how many cells are produced/accumulate. Some of the particularly large organisms that we will consider are: redwoods, up to 85 m in height and weighing an estimated 2100 metric tons (= 2100 * 10^3 kg = 4620 * 10^3 pounds = 2310 tons); giant kelp (brown algae) up to 50 m in length; 'Pando', a clone of trembling aspen that

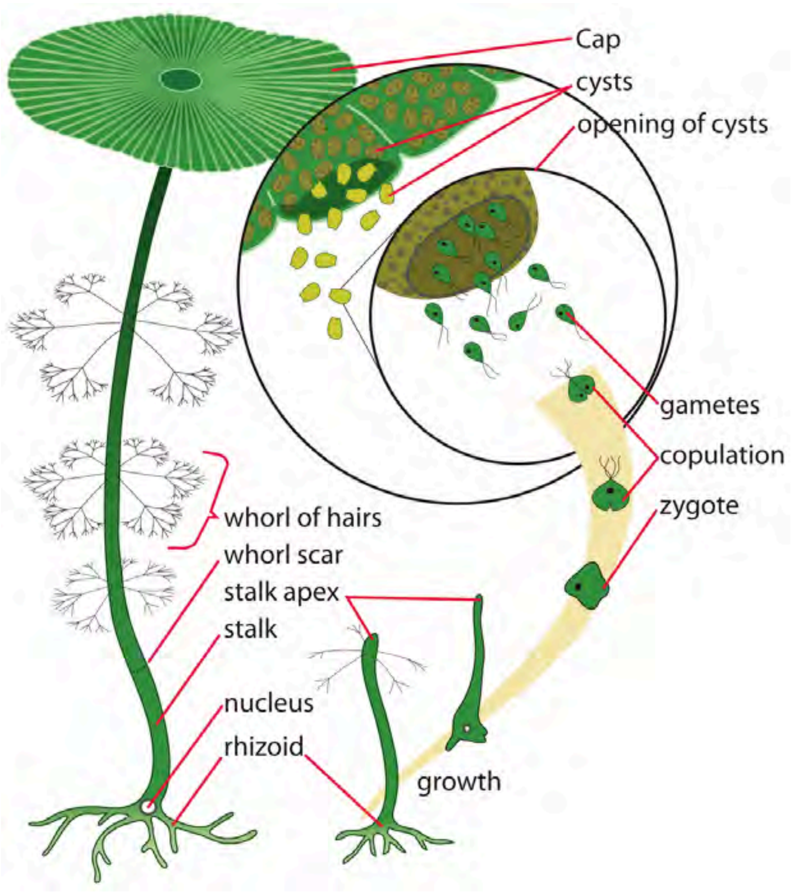

Fig. 16 Acetabularia are among the largest unicellular/ uninucleate organisms, standing up to 5 cm tall and with a well-defined structure

weighs over 6 million kg, extends over 43 hectares and may have an age of 80,000 years (more in the discussion of *Populus*); and a honey mushroom (*Armillaria*) that extends over 4 square miles (1000 hectares), weighs an estimated 55,000 kg and is considered to be 2400 years old.

Size and shape—influence on surface area & interactions with the environment

Size and shape are particularly significant because they dictate the degree of interaction between the organism and the outside environment. Appreciate that the conditions inside organisms are different from those on the outside; this is part of what defines life. The

Fig. 17 A clone of aspen, all connected below ground, extending several hectares.

second law of thermodynamics (which we will consider in Chapter 24) dictates that differences between the inside and the outside diminish with time: if some chemical is concentrated inside an organism it will tend to leak out; if something is excluded from an organism it will tend to leak in; if an organism is warmer than its environment it will cool; if an organism is cooler than its environment it will warm. Whatever conditions an organism develops to promote its life functions will tend to disappear because the second law dictates that systems change to develop uniformity, i.e., there is a tendency for the inside to become more like the outside. Given this, one might think that having little interaction with the external environment is 'best'. However, interaction with the environment is essential: (1) to obtain materials — food, oxygen, minerals—that are needed to maintain life, and (2) to rid the organism of 'materials' that it produces, e.g. heat and carbon dioxide, that will bring it harm if allowed to accumulate. The size and form of an organism control how it interacts with the environment that it is in. Significantly, size and form affect two important parameters that are related but not exactly the same thing, **the surface area of contact** with the environment and **the volume of the environment in**

proximity with the organism. Both of these parameters are important in controlling the interaction between the organism and its environment.

The significance of surface area is familiar idea. More surface area allows for more interaction with the environment, which may or may not be beneficial. For any shape, smaller objects always have a greater surface area per unit volume than large objects (Table 1).

Table 1. Influence of size on surface area: volume ratios for spheres, cubes and cylinders with heights ten times longer than the radius.

shape	**dimension (in arbitrary units) r = radius,s = side**	**volume (units^3)**	**surface area (units^2)**	**surface area: volume (units^{-1})**
sphere	r = 0.1 units	0.004	0.126	31.5
sphere	r = 1.0 units	4.19	12.6	3.01
sphere	r = 10 units	4190	1257	0.3
cube	s = 0.1 units	0.001	0.06	60
cube	s =1.0 units	1	6	6
cube	s = 10 units	1000	600	0.6
cylinder	r = 0.1, height = 10 x r	0.314	0.691	22
cylinder	r= 1.0, height = 10 x r	3.14	69.1	2.20
cylinder	r= 10, height = 10 x r	31.4	6911	0.22
formulae	sphere: volume = 4/3 (pi) $(r)^3$; surface area = 4 (pi) $(r)^2$			
	cube: volume = $(s)^3$; surface area = 6 $(s)^2$			

	cylinder: volume = height (pi) (r)^2; surface area = 2 (pi) (r) (height) + 2 (pi) (r)^2

Keeping volume constant, a sphere has the minimum surface area of any shape, and departures from an isodiametric shape increases the surface area and thus the surface area: volume ratio (Table 2). If one compares the surface area of two common shapes, 'filaments' (elongated in one dimension) and 'sheets' (elongated in two dimensions) **while keeping the volume constant**, the degree of elongation increases the surface area, and elongation in two dimensions has a greater effect than elongation in one dimension (Table 3).

Table 2. Surface areas of different symmetric shapes (sphere, cube, cylinder with diameter = height), all with the same volume, arbitrarily set at 1 unit cubed.

shape	dimensions	surface area = surface area / volume
sphere	radius = 0.62	4.83
cube	side = 1	6.0
cylinder	diameter = length = 1.08	5.49

Consequences of form and size

To see how surface area and form are significant we will use the example of the flow of heat from a warmer environment to a cooler cell, but the same principle would apply to the heat flow from the cell to the environment or the movement of materials, e.g., nutrients in to the cell or waste products out of the cell. Because smaller objects have relatively more surface area than larger ones, smaller organisms heat up more quickly than larger ones. In fact, because of effective heat exchange between them and their environment, small organisms are always very close to the same temperature as their environment. Only large organisms, with a small surface area to volume ratio, can develop temperatures substantially different from their environment. Considering shape, spherical bodies, with the least surface area per unit volume, heat more slowly than any other shape when put in an environment that is hotter than it; the more deviation from a spherical shape the faster it will gain heat. If you had three pieces of ice, one spherical, one filamentous and

Table 3. Surface areas different shapes when volume is kept constant but the length or width is extended. Data for cylinders and cubes shapes elongated in length 10-fold and 100-fold (to form elongate cylinders and cuboidal threads), or elongated 10-fold and 100 fold laterally to form disks with increasing radius or cuboidal sheets (i.e. a sheet made of cubes). All shapes have the same volume, arbitrarily set at 1 unit cubed.

shape	dimensions	surface area = surface area / volume
thread	length = 10 x diameter	8.34
thread	length = 100 x diameter	17.28
disk	diameter = 10 x length	10.32
disk	diameter = 100 x length	40.69
rectangular sheet height 10 x length and width	0.464 x 0.464 x 4.64	9.04
rectangular sheet height 100 x length and width	0.215 x 0.251 x 21.54	21.73
rectangular sheet height 1/ 10 length and width	0.215 x 2.15 x 2.15	11.09
rectangular sheet height 1/100 length and width	0.0464 x 4.64 x 4.64	43.92

one disc-shaped, all of the same volume, the disk would melt first, then the filament and last the sphere. Assuming equal volumes for ice cubes, the best ice cubes, if you want them to last (not melt), are spherical ones, the best ice cubes if you want them to cool the drink that they are in, are shapes that deviate the most from spheres

A second influence of form: the extent of environment that is explored

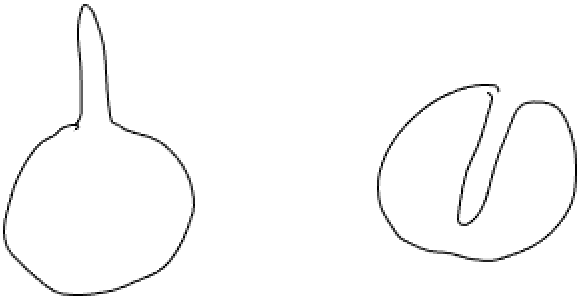

Fig. 18 Two spherical organisms with the same volume and surface areas but the different form causes their interactions with the environment to differ.

An often-overlooked fact is that organisms change their environment around them. In the example just given, the transfer of heat to the cell results in a cooling of the environment adjacent to cell. The cooling of the environment next to the cell will reduce the gain of heat by the organism and diminish the significance of surface area to heat transfer. Because of this, a second characteristic related to form becomes important: the volume of the environment that is within some distance (the distance depends characteristics of transfer) of the organism. To see why, consider two spherical organisms with a cylindrical 'distortions' of their otherwise spherical boundary: one has an 'outie' (a projection that extends outward), the other has an 'innie' (an invagination that penetrates into the organism) (Fig. 18).

As long as the dimensions of the projection / invagination are the same, both the cells will have the same surface area, yet the heat exchange between the 'outie' cell will be faster than that from an 'innie'cell. This is because the conditions of the environment inside the 'innie' projection will become more similar to those of the organism than to the conditions of the bulk environment outside of the cell. The volume of 'the environment' that is in the 'innie' is small and the surface area between the innie and the cell is relatively large, consequently as the 'innie' part of the environment loses its heat to the cell it would become less and less significant a source of heat. Thus, the additional surface area resulting from the 'innie' would become of little consequence in terms of interacting with the environment. In contrast, the additional surface area of the 'outie' can remain more effective in facilitating heat transfer because this area is surrounded by the environment, not the cell. Hence surface area by itself is not always the best measure of how much interaction an organism (or object) might have with its environment.

A consequence of this is that form is important in influenc ing the transfer of materials between the organism and the environment in two ways: (1) by determining surface area of a given volume of organism, and (2) by influencing the volume of the environment that is in close contact with the cell. Although an ‘innie’ does increase surface area, this does little to influence the volume of environment close to a cell; an ‘outie’ does much more. The significance of how much of an environmental volume is explored depends on several factors including the rate at which heat or material is conducted through the environment and the rate at which heat or material can be transferred from the environment to the organism. If the environment transfers heat or material readily, or if the rate of transfer into the cell is slow, the importance of how much environment is explored is of less importance.

Consider another example of two cells with the same number of multiple outies, extensions outward, and the same surface areas. One has the outies close together, the other has them spaced out (Fig. 19). The cell with spaced out extensions explores more of the environment than the other and will be able to acquire more heat or material from its environment (or lose more heat or material to its environment), especially if the rate at which heat or materials move through the environment is relatively slow, or the rate at which they are absorbed/lost is relatively fast. A parameter can be calculated that is the volume of environment within some distance of the cell surface; outies that are close to each other are less effective in increasing the amount of environment being ‘accessible’ than are more separated outies.

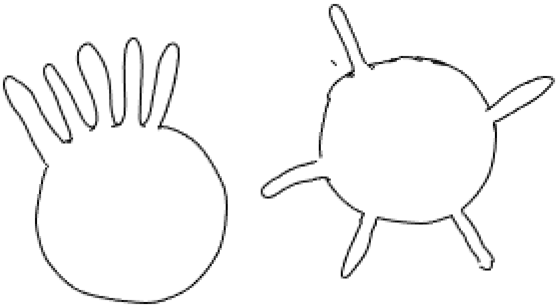

Fig. 19 Two organisms with the same volume and surface area but which differ in their interactions with their environment.

Some (perhaps) familiar situations demonstrate the importance of form and some of the complications related to it. The microvillae, small projections of small intestine that extend out into the gut track, are often cited as being important in the absorption of materials from the gut because they provide increased surface area. This is certainly the case but it should also be pointed out that the movement of material through the gut track, a result of peristalsis, is what allows the additional surface area to be significant.

Without peristalsis continually bringing 'fresh' material to the dense stand of microvillae, the increased surface area would be of little utility. Peristalsis changes the environment next to the microvillae. Root hairs, cylindrical extensions from the cells on the outside of roots, are another situation where increased surface area is cited as being significant to the water absorption function of roots. This may not always be the case, especially when the root hairs are extremely dense and if water is abundant, which allows it to move more readily through the soil. However, roots and root hairs don't just absorb water, they also acquire nutrients and the impact of root hairs may be different for different nutrients compared to the impact for water. Moreover, the conductivity of the soil to water and minerals is very strongly affected by how much water is present, a very dynamic property for most soils. Root hairs probably do multiple things that are significant for absorption of water and minerals: (1) increase surface area, (2) increase the volume of soil in close proximity to the root, (3) improve contact between the root and the soil by preventing gaps (air spaces) which would drastically reduce absorption of water and nutrients, (4) perform metabolic functions that facilitate nutrient absorption, e.g., active transport.

Shapes of Organisms

While there are a wide variety of shapes of organisms, three common forms are cylinders, sheets and spheres. Many organisms are composites of different shapes, i.e., they have some pieces that are one shape and other pieces that are another shape, e.g., many animals have cylindrical appendages attached to a spherical core. Most above-ground plants are composed of flattened sheets (leaves) attached to cylindrical stems. Both the above-ground and below-ground form of plants typically are filaments that branch repeatedly, a form that is also found in fungi. Common forms for the organisms covered in this text are outlined in the Table 4.

Spheres

As mentioned above, spheres have a minimum surface area per unit volume. Assuming that there is a specialized boundary on the outside of the object, be it unicellular or multicellular, a sphere would require the minimum amount of boundary, which often is composed of relatively expensive materials. Spherical shapes are also more mobile in many situations owing to their reduced drag, which in general increases with surface area. While there are a number of roughly spherical animals, spherical **multicellular** organisms from

Table 4.

shape	examples	notes
spheres	many unicellular organisms, some colonial and multicellular ones	low surface area to volume ratio and small amount of environmental volume explored per unit of organism
flattened	many colonial and multicellular algae including sea lettuce (*Ulva*) and kelp (*Laminaria*) ; the haploid form of all hornworts and many liverworts	high surface area to volume ratio, often significant for photosynthetic organisms to absorb more light
cylinders (branched or unbranched)	most fungi, many green and red algae, some bacteria, the roots of vascular plants	both a high surface area to volume ratio and potentially a large amount of environmental volume explored per unit of organism
cylinder with (non-cylindric) appendages	some macroalgae (red, brown and green); most plants–including most mosses, many liverworts and almost all vascular plants	the appendages typically are flattened and photosynthetic and their shape increases the amount of surface area exposed to light

other groups, in particular the groups we are covering, are uncommon. However, the form is commonly found organisms that are unicellular: many bacteria, many unicellular green algae, dinoflagellates, cryptophytes and coccolithophores are roughly spherical in shape and the shape occasionally occurs in colonial organisms (some green algae). Spheres are also common in dispersal units: pollen, seeds, spores, all of which are entities that might be considered organisms. And spherical shapes are also a common shape for the structures (organs) that contain elements to be dispersed: sporangia (spore containers), fruits (seed containers), anthers (pollen containers). The advantage(s) of spherical shapes no doubt varies on circumstances and may also reflect other constraints on development. In rare occasions, round shaped seeds, fruits and even whole plants may aid in the dispersal of propagules by wind and gravity. A whole-plant example of the this is the tumbleweed, whose spherical shape promotes the dispersal by the wind of the seeds which are released from the rolling plant. Spherical forms are typical of the (usually underground) storage organs of flowering plants: corms, bulbs and tubers and this is probably a consequence of surface area to volume considerations.

Flattened structures

Flattened structures are especially common in photosynthetic organisms, undoubtably because of the importance of intercepting light. While it is often stated that flattened shapes 'intercept more sunlight' than other shapes (e.g., maple leaves vs. pine needles), this is misleading; similar amounts of light can be acquired given any particular shape. What is significant is how much volume is required to produce a given area of light absorbing surface, and also how much total surface area is required. Table 5 compares morphological characteristics for three different leaf shapes: cubes, sheets and filaments. In each situation the assumption is made that one 'face' of the shape is facing the light source and that light absorption only occurs on this surface. As can be seen the same amount of light could be intercepted by ten cuboidal leaves, each 10 x 10 x 10 cm in size, or ten filamentous leaves, each 100 x 1 x 1 cm or by ten planar leaves 10 x 10 x 1 cm. While both filaments and planar leaves can produce the same amount of absorbing surface per unit volume of leaf, cuboidal leaves 'cost' much more (illuminated area: total volume) (Table 5). The difference between filamentous leaves and planar leaves is that planar leaves reduce the total surface area required to produce a given amount of absorptive surface. It is probably these two factors that are significant in ensuring that light absorbing surfaces are generally planar: thick leaves require volume that cannot be used effectively for photosynthesis; filamentous leaves produce excess total surface area which may be costly in terms of other factors, e.g., water loss for terrestrial organisms.

The flattened structure may be the entire organism (some green, red and brown algae, some liverworts (including *Marchantia*, hornworts) or, most commonly, the flattened structures occur as leaves / leaf-like structures off of a cylindrical stem.

Table 5.

shape	number of leaves	dimensions	total volume	total surface area	illuminated area / total area	illuminated area / volume
cuboidal	10	10 x 10 x 10	10000	6000	1 / 6	1: 100
filamentous	10	100 x 1 x 1	1000	4020	1 / 4.02	1: 1
planar	10	10 x 10 x 1	1000	2400	1: 2.4	1: 1

The above treatment is superficial and some complicating factors should be noted: light is usually not only absorbed by one surface of any structure as the sun's position changes during the day and season; light penetrates through a surface to layers below; although most leaves move only minor amounts during the day or season, some leaves change position to 'track' the sun; and some leaves change position to reduce solar exposure. And, in spite of the trend of generally planar light absorbing surfaces, there are multiple examples of filamentous 'leaves'(e.g. conifer needles, asparagus branches) and also examples of spherical 'leaves.'

A planar shape is also sometimes found in propagules, the dispersal stages of organisms, where the flattened 'wing' aids in dispersal in the air. Interestingly, wings are primarily found in relatively large propagules, the seeds and fruits of seed plants, with dimensions greater than a few millimeters. 'Wings' are uncommon in aquatic organisms and in small propagules: e.g., spores and pollen. Although most conifer pollen has two 'wings', they are not particularly flattened and, in spite of the fact that conifers are wind pollinated, the role of the wings may not be to aid in dispersal but rather to orient the pollen grain after it has been dispersed.

Cylindrical structures

Cylindrical structures are extremely common, both as parts of organism and as the whole organism. Cylindrical unicellular organisms are found in rod-shaped bacteria and archaea; filamentous colonial forms are represented by some bacteria, many cyanobacteria, colonial diatoms, many green algae and some red and brown algae. For most of these colonial organisms, the filaments are all one cell thick, but, especially in the red and brown algae, the filaments may be thicker, often several cells thick. There are many coenocytic green algae that are filamentous.

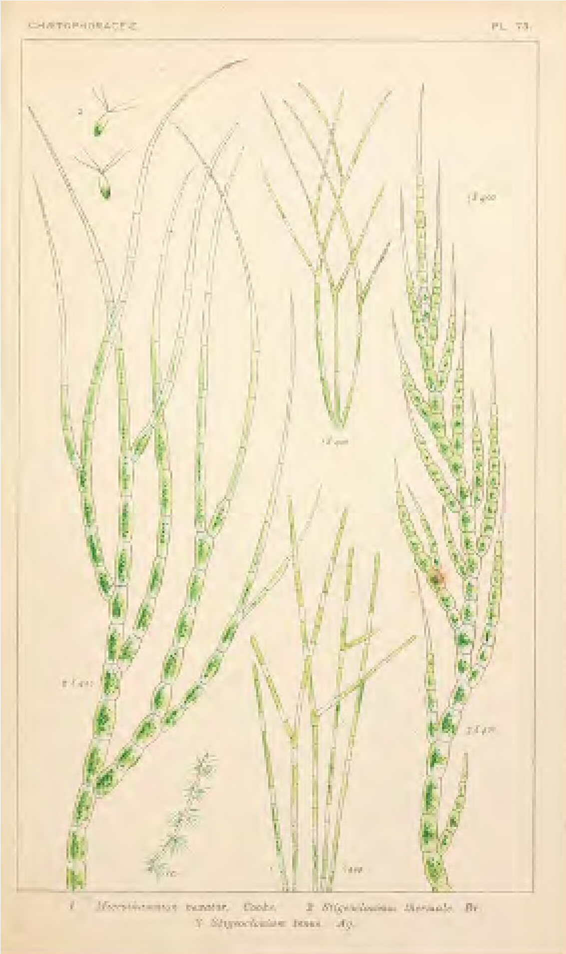

Fig. 20 Cylindrical form in filamentous green algae.

Fig. 21 Laminaria consist of a base of branching cylinders, a cylindrical stalk and a flattened sheet forming the blade.

A branched filamentous structure is particularly effective as a 'feeding' (for fungi) or 'mining' structure (for plant roots) that explores an environment for resources. Such a form is also effective in providing anchorage because it allows for extensive interaction between the organism and its substrate. In contrast to roots, which have dual functions of absorption and anchorage, the holdfasts of algae and rhizoids of mosses, liverworts and hornworts perform little absorption but primarily serve an anchorage role. Across the diversity of organisms, what it is that forms the branched structure and the size of the branched structure vary tremendously. Unicellular chytrids (fungi) form 'rhizoids' for absorption and anchorage that are extensions of a single cell. The 'arbuscules' (literally meaning 'little tree') of Glomeromycota fungi are also extensions of parts of the fungal cell that enters into plant root cells. Root hairs are also extensions of individual cells. The rhizoids of mosses, liverworts and hornworts are usually a filament made up of a string of individual cells. Holdfasts of macroalgae are made up of thousands of cells and the roots of vascular plants are multicellular and made up of multiple tissues with multiple cell types.

Cylinders with non-cylindrical appendages

Cylinders also function to position organs in favorable locations, e.g., the stem of plants or the stipe of the larger algae, distributing flattened leaves/leaf-like structures in order to obtain more light. The vast majority of plants, ranging from mosses, most liverworts and all vascular plants , have an above-ground structure that can be described as a 'stem with leaves'. Typically, the cylindrical stem branches and is erect but sometimes it is unbranched and sometimes it is prostrate, running along the ground surface.

Phytopthora, a water mold, is a parasite that grows inside plant leaves and produces branched structures that emerge from the leaf through stomates, regulated pores in the leaf surface, and form cylindric, branched structures that produce and release reproductive structures.

Cylinders (stalks) also repeatedly serve to elevate structures that are producing propagules (mobile reproductive structures) and thereby facilitate dispersal of propagules. The ubiquity of the structure reflects the structure's significance in multiple situations over quite a range of size s: from stalks as short as 1 micron in myxobacteria, to 1 millimeter in slime molds, to 1 centimeter in mosses, to meters in height in vascular plants. The cylindrical stalks can be parts of a cell (bread molds, some slime molds), made of a single filament of cells (fungi), a collection of intertwining filaments (fungi) or truly multicellular (some fungi, mosses, vascular plants). Generally, such structures are found in terrestrial organisms with stalks that carry propagule-producing-structures upward into the air. Even a very short upward extension can enhance dispersal by allowing the propagules to be released above the most sedentary part of the boundary layer, the layer of still air that blankets all objects, and in particular the ground. Apparently, such structures are not as advantageous in aquatic situations because they are much less common. In some situations, a stalk is significant not by moving the propagule-producing-structure up (relative to gravity) but because it moves the structure outside of the organism's own body or outside the body that it is growing inside of (e.g., fungi, some parasites).

As the last example demonstrates, cylinders are significant to a number of organisms as a means of mobility, to arrive at new places. Although most of the organisms that we study are considered immobile, they are capable of movement that is due to growth, and a cylinder is an effective structure to cover territory. Examples include: horizontally running above ground stems (stolons) and below ground stems (rhizomes) of plants, the 'stolons' of bread molds, rhizomorphs of fungi, horizontal 'runners' in *Caulerpa*, a green alga.

Further Reading and Viewing

The first six deal with the question of multicellularity; the last with fungal structure.

- "Fungi took a unique evolutionary route to multicellularity: Seven key challenges for fungal multicellular life" by László G. Nagy et al. Fungi took a

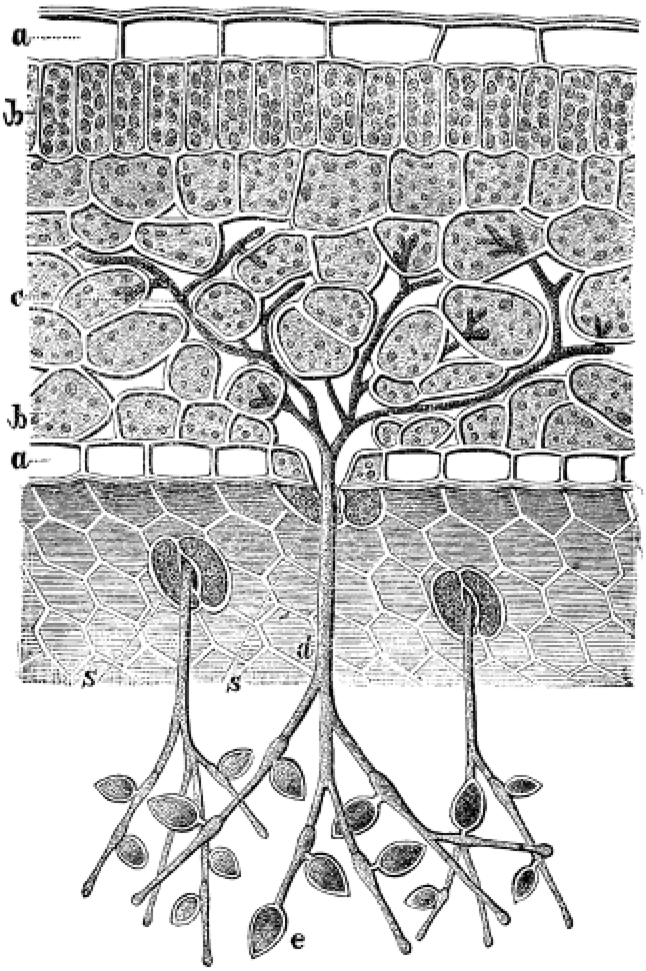

Fig. 22 Phytopthora, a water mold, is a parasite that grows inside plant leaves and produces branched structures that emerge from the leaf through stomates, regulated pores in the leaf surface, and form cylindric, branched structures that produce propagules that are released for dispersal.

unique evolutionary route.

  - https://www.sciencedirect.com/science/article/pii/S1749461320300269

- "Role and Evolution of the Extracellular Matrix in the Acquisition of Com-

plex Multicellularity in Eukaryotes: A Macroalgal Perspective" by Bernard Kloareg et al. Complex multicellularity.
  - https://doi.org/10.3390/genes12071059
- "Independent Emergence of Complex Multicellularity in the Brown and Red Algae" by J. Mark Cock, Jonas Collén. Multicellularity.
  - https://link.springer.com/chapter/10.1007/978-94-017-9642-2_16
- "The momentous transition to multicellular life may not have been so hard after all" by Elizabeth Pennisi. Multicellularity.
  - https://www.science.org/content/article/momentous-transition-multicellular-life-may-not-have-been-so-hard-after-all
- "Volvox, Chlamydomonas, and the Evolution of Multicellularity" by Stephen M. Miller et al. Volvox, chlamydomonas, evolution of multicellularity.
  - https://www.nature.com/scitable/topicpage/volvox-chlamydomonas-and-the-evolution-of-multicellularity-14433403/
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  - https://bsapubs.onlinelibrary.wiley.com/doi/10.3732/ajb.1300314\
- "How Fungi Work" by David Malloch.
  - http://website.nbm-mnb.ca/mycologywebpages/NaturalHistoryOfFungi/Physiology.html

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CHAPTER 5: CELLULAR STRUCTURE IN INANIMATE LIFE

The discovery of the first cell is often attributed to Robert Hooke in the middle of the 17th century. But people had observed cells before (fish eggs, frogs' eggs, birds' eggs). What was significant about Hooke's observation was that he noted that organisms, at least some of them, were composed of smaller entities that he called cells. He was able to see them in part because he was using the recently developed microscope. But what also made the cells visible were that they were plant cells, cells that not only are larger than most animals cells but also have cell walls that outline each cell, are rigid and do not collapse when the material is cut into thin sections. The material he was looking at was cork, the outer bark of a tree, and what he was observing was the remnants of cells that were no longer alive; their existence was preserved because of their thick and persistent cell walls (Fig. 1).

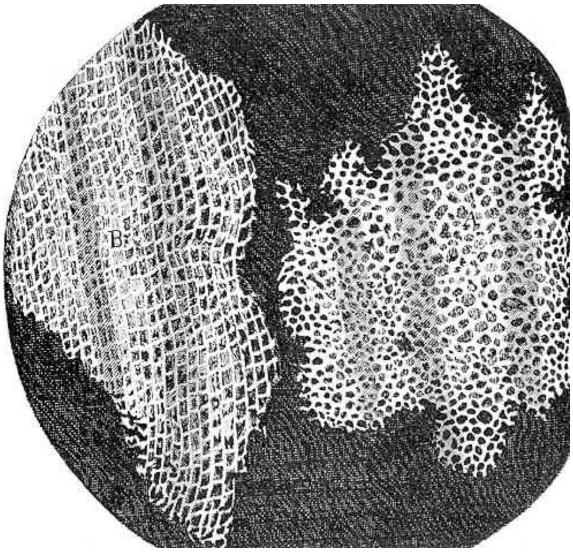

Fig. 1 Robert Hooke's drawing of the cells of cork published in the book Micrographia, published in 1665.

While Hooke's observations illustrated that at least some parts of some organisms were composed of smaller units, the generalization that all organisms were composed of one to many 'fundamental units', cells, was not to be fully realized for another 200 years when 'cell theory' was proposed and championed. Although people were very aware of fish eggs and frog eggs, they had not appreciated that when the eggs turned into tadpoles the material was first divided up into many, many small units, each with the same basic construction. With time, these units diversified from each other and transformed into groups to serve specific roles. These are arranged in a particular way to produce a complex whole, a frog embryo. Think of making castles out of legos. A similar transformation occurs as the fertilized egg of plants transforms into a plant embryo, although the egg cell of plants (about 20 um) is 100 times smaller than those of frogs and about five times smaller than those of humans.

One of the great themes of biology is the unity and diversity of life: how organisms can simultaneously be so similar and so different. The same concept also applies to cells and is fundamental to 'cell theory': living things are made up of cells, whose basic organization, chemical composition and organization is similar; but these cells are also diverse in terms of shape and function and the diversity is seen both between different organisms (plant cells are different from animal cells) but also within (multicellular) organisms.

Diversity of cells within an organism is one, and for some people the only, criterion for a multicellular organism, not simply that they are made of multiple cells but that at least some of the cells differ from one another. Before describing the diversity of cell types found in some of the organisms that we cover, we will consider additional criteria that might be used to define multicellularity.

TOPICS

- Multicellularity
- Cell Structure of Fungi
    - Chytrids
    - Coenocytic, filamentous fungi — bread molds and Glomeromycota
    - Septate fungi — Club and sac fungi
- Cell Structure in water molds
- Cell structure in algae
    - Brown algae
    - Red Algae
    - Green algae

Multicellularity

Can a unicellular organism be multicellular? One might think that this is absurd, yet it can be true, depending on definitions. An illustrative case is the Apicomplexa, a group that includes is the causal organism for malaria, *Plasmodium.* Members of this group are always unicellular but have multiple cell types (Fig. 2), cells that look different, behave differently and live in different places. Most biologists would not consider the Apicomplexa to be multicellular and would rather consider it as a biological entity with multiple forms, but in a developmental sense it raises the same question that multicellularity poses: if one cell is identical genetically to another cell, how can they end up looking and behaving differently?

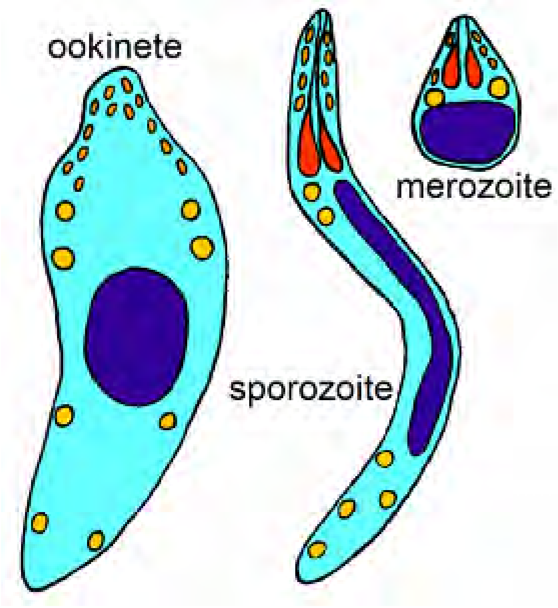

Fig. 2 Different cell types form by Plasmodium.

If you study the life cycle of *Plasmodium* carefully you will note that some of the cellular diversity is associated with reproduction and the sexual process, a topic that will be dealt with in more detail later but for now simply note that **most** organisms produce different cells that are associated with reproduction and/or sex. *Chlamydomonas*, a unicellular green algae (Fig. 3) , produces bi-flagellate cells that all look and behave alike except for: (1) some cells look different because they lose their flagellae and divide twice to produce four cells while still within the parental cell. Eventually the parental cell wall is digested and the four typical-looking cells are released, (2) some cells look normal but are 'special', functionally different, because they are able to fuse with other 'special cells'. Cells become 'special' because of changing conditions, e.g., nutrients become less available. (3) the cell formed by the fusion of two special cells develops into a very different looking cell, one with no flagellae and a thick cell wall. It also functions differently, because it is metabolically inactive. Eventually it becomes active and divides to produce four typical looking (bi-flagellate) daughter cells that are released after the cell wall is digested and weakened. These three atypical cell types are associated with sex and the process of meiosis (Fig 3, right-hand side of the diagram) will discussed in more detail later, along with a consideration of reproduction (left-hand side of Fig 3).

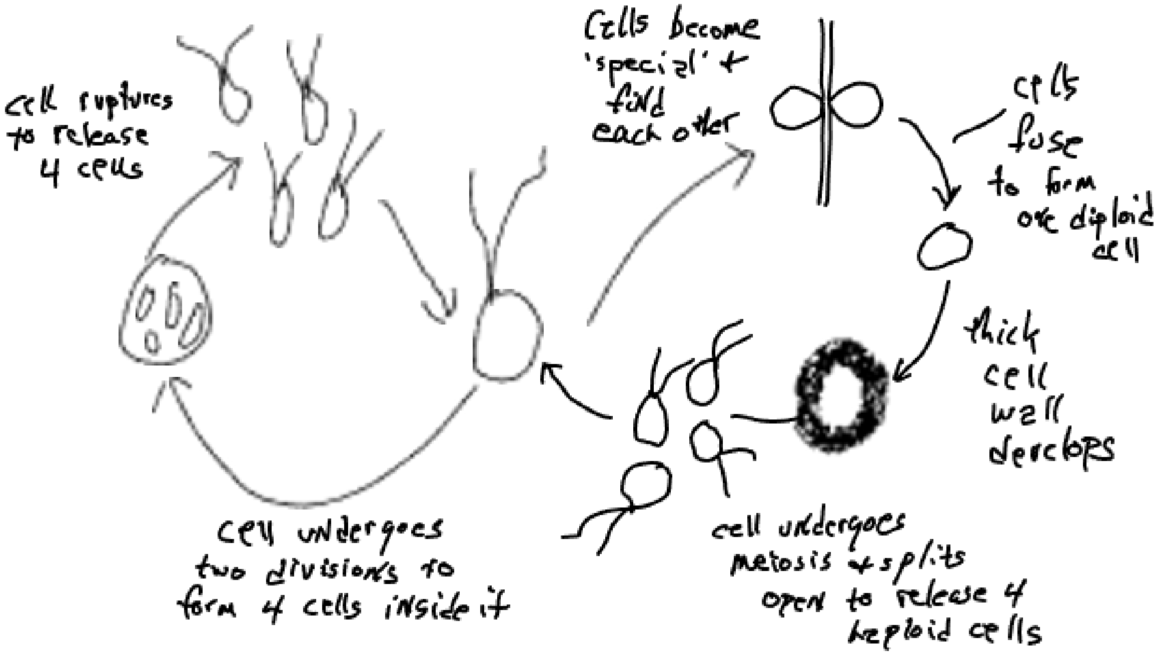

Fig. 3 Sexual (on the right) and asexual (on the left) reproduction in the unicellular green algae Chlamydomonas.

Obviously very few would consider unicellular organisms like *Plasmodium* or *Chlamydomonas* to be multicellular in spite of the fact that they may exhibit multiple cell types. The point is that the possession of different-looking or different-behaving cells (e.g., egg, sperm, zygote, spore) that are associated with the reproductive or sexual process are not sufficient to label an organism as multicellular. This is trivially true for unicellular organisms but is also true for colonial organisms that are made up of multiple cells that are almost all the same and is the reason for the distinction between 'simple multicellularity' and 'complex multicellularity'.

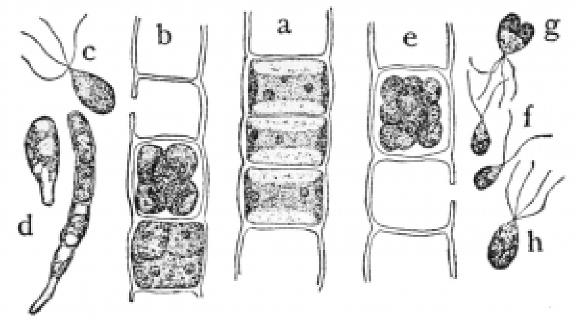

Fig. 4 Cell types in Ulothrix, a filamentous green algae.

Consider the filamentous green algae *Ulothrix*, (Fig. 4) which exists as strings of cells, most of which all look alike (see the center part of the drawing labelled 'a'), but sometimes some of the cells transform (i.e., develop) to produce mobile cells that have four flagellae ('c' in the diagram) and are released from the filament. These cells can establish new filaments by attaching to a substrate and dividing to produce new filament ('d'). Other cells transform and produce and later release cells with only two flagella ('f'). These cells must find another bi-flagellated cell, fuse with it ('g'), then undergo meiosis to form four quadriflagellate cells ('h') that can attach to a substrate and form new filaments.

Another example of simple multicellularity with diverse cell types associated with reproduction and sex is found in *Oedogonium*, (Fig. 5) another filamentous green alga. Most cells are cylindric with lengths about five times longer than their width. But there are also egg cells that are shorter and bulge in the middle, and there are much shorter sperm producing cells, with lengths the same or shorter than their width. Both these cell types develop holes in their walls that allows the short cells to release mobile sperm and allows the sperm to enter into the egg cells, resulting in the production of cell with genetic information from two parents. This develops into a dormant spore (zygospore) that is eventually released from the filament. An additional cell type can develop from the normal cells as they develop flagellae and eventually are released from the filament as cells capable of forming new individuals.

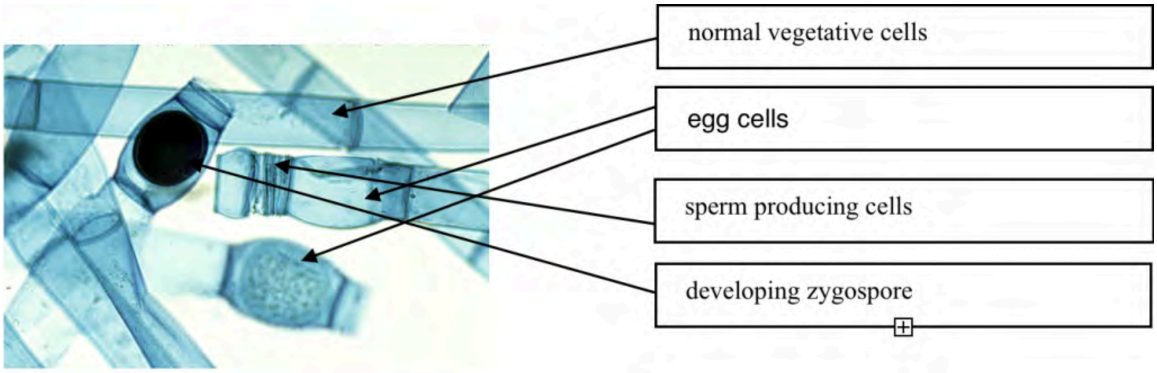

Fig. 5 Cell types in Oedogonium.

These examples demonstrate common cell types associated sex and reproduction and found in organisms with colonial growth (showing 'simple multicellularity'): (1) cells that are capable of fusing with each other, called gametes that are sometimes differentiated into egg and sperm, (2) zygote, a cell formed by the fusion of gametes, (3) zoospores, flagellated cells specialized for mobility (dispersal in space) (e.g. the cell labelled 'c' in the *Ulothrix* diagram), (4) inactive, dormant cells that allow for dispersal in time. In general, these are called spores (but note that zoospores are NOT inactive). These inactive cells are called endospores in bacteria and akinetes in cyanobacteria. In a number of organisms (e.g., *Chlamydomonas*, *Oedogonium*, bread mold*)* spores develop from zygotes and are called zygospores. We will see a number of different types of spores in the fungi.

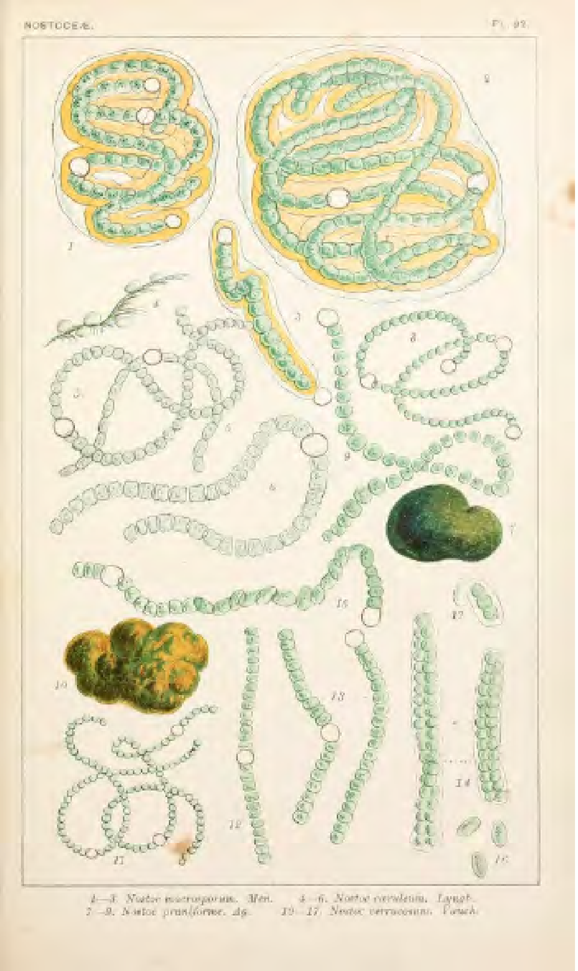

Fig. 6 Anabena, (a cyanobacterium) filaments, the clear cells are heterocysts that 'fix' nitrogen and make it available to other cells

To repeat, none of the examples considered so far would be considered multicellular even though they produce multiple cells, some of which are very different structurally and functionally from others. What additional features contribute to the case for 'true multicellularity'? One feature is mutual dependency. Most of the cells of *Anabena*, a cyanobacteria, have chlorophyll and photosynthesize to feed themselves. *Anabena* also produces cells called heterocysts that lack chlorophyll and are unable to photosynthesize. They are 'fed' by adjacent, 'regular' cells. Heterocysts are significant because they can take dinitrogen gas, a form of nitrogen that 'regular' cells cannot utilize, and convert it into a form that the regular cells can utilize (more details in Chapter 22). Hence, the heterocysts and the regular cells depend on each other. At least some workers would consider the dependency of one cell type on another to be a criterion that makes *Anabena* multicellular. Another feature that *Anabena* demonstrates and that is significant to the concept of multicellularity is material movement (food, nitrogen compounds) between the cells of the organism. This really is a form of intercellular communication, and many workers consider intercellular communication to be a key requirement defining multicellularity. Features that enhance communication include trans-cellular connections, plasmodesmata in the case of plants.

Another criterion that has been applied to define 'true multicellularity' is a three-dimensional cellular organization, i.e., not just cells added continuously (without and endpoint, i.e. indeterminate development) in one dimension (a filament) or added in two dimensions (a sheet), or added in three dimensions. True multicellularity to some workers requires a developmental program that produces a distinct three-dimensional form that requires that the size, shape and activities of cells be influenced by a combination of location (where they are in the organism) and where they came from (cellular heritage). Such a structure requires extensive communication and coordination between cells. Note, however, it does not necessarily require tissues made up of different cell types.

Workers who study the evolution of life believe that simple multicellularity (colonies) has appeared at least twenty-five times. Complex multicellularity (or what some would call 'true' multicellularity), but defined without the requirement of multiple cell types and tissues, has evolved at least ten times: once in the group that led to animals, once in the green algal group that led to plants, once in another green algal group that did not lead to plants, twice in the red algae, twice in the brown algae, three times in the fungi, and several times in the prokaryotes. If the definition of multicellularity requires tissues with multiple cell types (not associated with sex and reproduction) then the number of multicellular groups is much reduced: just animals, plants and a very few fungi.

The cellular structure of select groups of inanimate organisms, organisms that might be considered multicellular, is described below. Excluded are the vascular plants; these are considered in the next chapter.

Cellular Structure in Fungi

While many biologists characterize the fungal group as being 'multicellular', many clearly are not. Three fungal groups are coenocytic and none of these are easily characterized as being multicellular. And unicellular fungi, which exist in several fungal groups, would certainly not be considered multicellular. The fungi that might be considered as possessing complex multicellularity do so for only a small portion of their existence and only in a small portion of their structure. Almost all fungi produce a filamentous structure, a hypha (plural hyphae), that is not multicellular and most fungi are better described as being colonial, a filamentous organism with no specialization of cells whatsoever. In three of the fungal groups the hyphae lack cross walls and are coenocytic but the two largest groups of fungi do produce cross-walls (Fig 7) and exhibit simple multicellularity. Hyphae grow from the tip and can bifurcate to branch in two. Branching can also occasionally occur away from the tip. Hyphae may also fuse with one another, thereby producing an anastomosing structure. The network of hyphae thus formed is termed a mycelium. The typical mycelium is a feeding structure with a dynamic (growing and dying simultaneously), diffuse, form that is well suited to obtain nutrients: it possesses both a great deal of surface area for absorption and it also penetrates a large environmental volume, allowing it to 'mine' a substrate for nutrients. The feeding mycelium is the digestive system of fungi and simultaneously serves as: (1) a structure to digest food, (2) a 'small intestine' to absorb nutrients (3) a circulatory system to move nutrients to other parts of the fungus and ultimately to reproductive structures. Note that none of these functions are associated with specific cell types, tissues or organs.

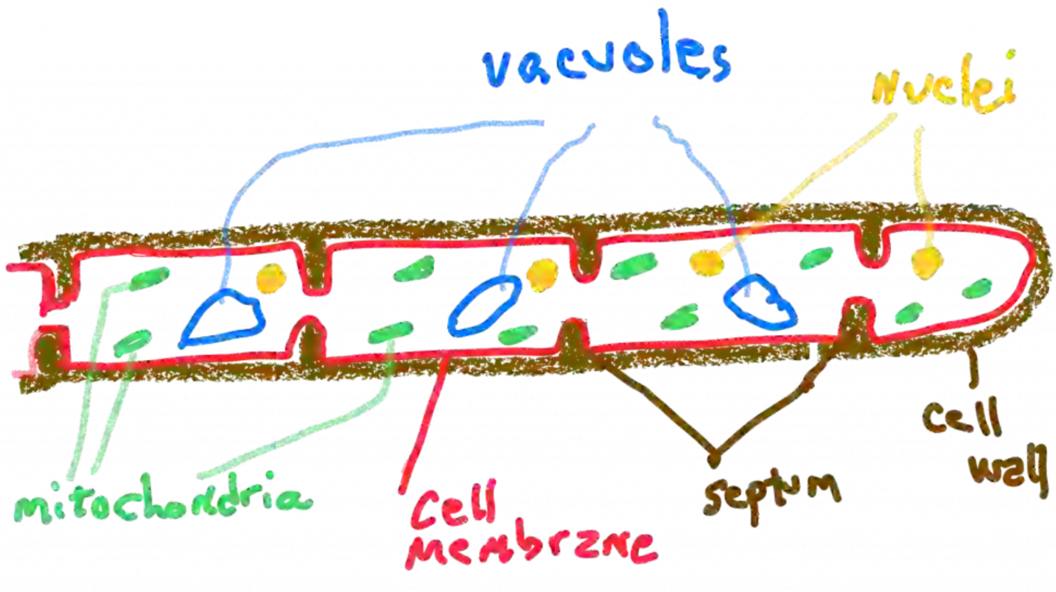

Fig. 7 Illustration of septate fungal hyphae. Note that the cross walls (septa) delineating individual cells do not span the entire cell, leaving a pore that allows materials to move between cells.

Two fungal groups are considered cellular because they do have cross-walls of sorts. These are called septa (singular septum) and they only partially seal off cells because they are perforated by pores that are large enough to allow many materials (ribosomes, mitochondria and sometimes nuclei) to move from one cell to another. Thus, the composition of these fungi is in between coenocytic and cellular. The cellular structure of specific groups of fungi are described below.

Chytrids

The fungal group considered most primitive (probably better described as the group that diverged at the earliest time from the rest of fungi) are the Chytridiomycota (chytrids). Chytrids are small aquatic organisms, both marine and freshwater, with some existing in the film of water surrounding soil particles. Most are microscopic, usually the size of a typical unicellular organism (less than 100 um). They may be truly unicellular (one nucleus) or coenocytic (multiple nuclei). Many produce forms that are roughly spherical. Several chytrids form what are called rhizoids, root-like extensions off of the main body that attach them to a source of nutrition, often pollen, the spores of other organisms, or a single cell of a living or dead multicellular organism. Besides attachment, the rhizoids also serve to increase surface area and allow for more effective digestion and absorption. A few chytrids form filaments (hyphae) that occasionally branch to form a very small mycelium. The group is distinguished from all other fungi by having flagellated, mobile, spores.

Coenocytic, filamentous fungi

Two additional fungal groups, the bread molds (Zygomycota) and the Glomeromycota, are substantially bigger than chytrids and produce a coenocytic hyphae and form mycelia. While both these groups lack specific cell types, some do form specific structures which one might term organs, except that they are parts of cells, not composed of cells. For many bread molds these structures, stolons, rhizoids and sporangiophores, are relatively large and can be seen with the naked eye. In the Glomeromycota the ‘organs’ are much smaller structures, but again are parts of cells, not cells. The Glomeromycota are the fungi that, together with plants, form endomycorrhizae, associations between plant roots and fungi. In endomycorrhizae, the fungus penetrates individual root cells (‘endo’ means inside) and inside these cells the fungus form two structures, tree-like arbuscules and spherical vesicles (endomycorrhizal fungi are sometimes called vesicular-arbuscular mycorrhizae or simply VA mycorrhizae). These structures are extensions off of the coenocytic hyphae. Arbuscules are structures with some similarities to the the rhizoids of chytrids. They serve no anchorage role but are significant in increasing the area of contact between the fungus and the plant, thereby allowing for greater material movement between them. Vesicles are spherical bodies that are thought to store materials for the fungus and which may develop into spores.

Septate fungi—Club and Sac Fungi

The two largest groups of fungi, club fungi (Basidiomycota) and sac fungi (Ascomycota) are not coenocytic. They produce hyphae that are septate, with cross walls to delineate individual cells. As the growing tip of a hypha extends, nuclear divisions (mitosis) are coordinated with the cellular divisions (cytokinesis) that produce new cross walls with a substantial pore. These cross walls are oriented perpendicular to the long axis of the hypha. As a result, new cells, each with a nucleus, are sequentially produced at the tip as it grows. The tip cell is also capable of occasionally dividing in a manner to cause the tip to bifurcate, to split in two, forming a branch. Branching sometimes also occurs away from the tip, the result of an outgrowth from a previously formed cell.

Under certain conditions the hyphae of Ascomycota and Basidiomycota may also form much more compact mycelia, usually associated with reproduction, and some of which approach in form structures that are more typical of multicellular organisms. These structures may range in organization from an amorphous mass of compact hyphae (aka a dense mycelium), termed a stroma, in which 'fruiting bodies' (spore producing structures) are formed (see tar-spot disease), to much more defined and determinate structure such as a typical mushroom with a stalk and cap. The stalk generally serves to enhance the dispersal of spores that are produced in the cap. Most of the organisms that produce mushrooms are club fungi (Basidiomycota) but a few are cup fungi (Ascomycota), and both groups produce fruiting structures that are not at all mushroom-like (e.g. bracket fungi). Both groups produce a wide variety of fruiting body forms, all developing as a result of pattern of growth of multiple hyphae. Although these structures are clearly organized and produce a consistent (determinate) three-dimensional final form, they generally show little evidence of tissues or specialized cell types, except those directly associated to sexual reproduction.

Another dense, compact hyphal structure produced by septate fungi is called a fungal cord or a rhizomorph. It consists of a multiple hyphae running parallel and glued to each other, forming a thread that may be several millimeters in diameter (cf. to a fungal hypha which typically is ten-times smaller in diameter than a human hair). Rhizomorphs are the result of repeated hyphal branching at very low angles to the orientation of the parent hyphae, consequently allowing the branch to stay closely associated and fused with the hypha that produced it. The result is a structure with little capacity to feed (or lose water) when compared to a diffuse mycelium, because of its reduced surface area and reduced penetration of its environment. But the rhizomorph is specialized for mobility and allows the fungus to traverse low-nutrient space or environmentally hostile (e.g., dry) space and potentially arrive in a more favorable location. When and if the rhizomorph arrives in a nutrient rich zone the growth form reverts to a diffuse mycelium suited for nutrient absorption. The extension of rhizomorphs requires transport of nutrients in order to feed the tips of hyphae (where growth is occurring) using nutrients that are being acquired at some distance from the tip. This transport function is served by specialized, large diameter hyphae, analogous to tubes found in brown algae and vascular plants. Another specialized cell type found in rhizomorphs, and located toward the outside of them, are thick walled 'sheathing hyphae' that have a structure again similar to some cells (fibers) found in vascular plants. These give the rhizomorph structural integrity and make it is less likely to be severed, something that is of much more consequence to a rhizomorph than to an individual hypha.

A few fungi produce structures called sclerotia, again a dense mass of hyphae, but sclerotia often develop into distinct forms and sometimes show specialization between a hard outer 'rind' and inner cells. The cells on the interior often have substantial food reserves and sclerotia are typically overwintering structures, structures that can become dormant. The stored food allows the sclerotium, which is sometimes dispersed, to survive the winter and resume growth when favorable conditions return.

Cellular Structure of Water Molds

The water molds, or Oomycota are similar in form to the bread molds (Zygomycota) with both groups being composed of coenocytic filaments, hyphae, that collectively form a mycelium but show no cellular specialization other than cells associated with reproduction. The group includes some important plant pathogens, including late blight of potato, sudden oak death syndrome and 'damping off' diseases. In spite of the name, they aren't molds (fungi) and many are terrestrial not aquatic (although the representative of the group that is most commonly seen, at least if you have an aquarium, is a white fuzz occurring on dead fish). Water molds were once grouped with the fungi because of morphology but they are now considered to be in the heterokont grouping that also includes brown algae and diatoms.

Cellular Structure of Cellular Slime Molds

During the unicellular part of cellular slime mold's existence there obviously is no cellular differentiation, but when aggregation occurs the cells acquire different fates and one might consider this to be reflective of complex multicellularity. In particular, and of evolutionary significance, only some cells of the aggregate ultimately end up producing reproductive cells. Other cells, e.g., the cells in the stalk of the spore producing structure, contribute to reproductive success by elevating the spore producing structure but gain no evolutionary advantage for 'doing a good job' since they are not necessarily represented in the next generation. This is in contrast to the more normal situation in multicellularity where all the cells of a multicellular organism are derivatives (and hence share a genetic composition) with the original 'starter cell', typically a zygote or a spore. Because of their unusual path to multicellularity, the determinators of cell fate in cellular slime molds is an area of active study. There are no obvious visual/structural differences between the cells of the slug or the fruiting structure but their positions are different, some are on the outside, some inside; some are near the front, some are behind. And position appears to be important in determining cell fate, including the position at the time of aggregation. Moreover, there is strong evidence that cell fate and 'knowledge' of position is a result of communication via chemical signals, one of the criteria that workers consider to be a defining aspect of complex multicellularity.

Cellular Structure of Algae

Algae are an artificial grouping of aquatic photosynthetic eukaryotic organisms whose classification remains in some flux. Many algae are unicellular or are colonial ('simple multicellularity') and do not show any cellular specialization except for cells associated with sex and reproduction. Most of these organisms are small: microscopic, or barely visible to the naked eye. But there are three groups of algae, colorfully named the red algae, brown algae and green algae, that include forms that are described as 'macroalgae'. They are large (i.e., not microscopic, generally at least 0.1 m in extent) and with an organized structure, often consisting of organs: cylindric stems and branches, flattened blades, air sacs, root-like holdfasts and other features. Almost all of the brown algae and most of the red algae could be described this way. This 'macro' form is proportionately less common in the green algae where many members are smaller and where a considerable number of forms are unicellular or colonial (filaments). Using the more lenient definitions of multicellularity, most macroalgae would be considered multicellular. Using more restrictive definitions, in particular requiring intercellular connections and communication that allows for cooperation between cells, substantially reduces the number of macroalgae that are considered 'truly multicellular'. Nonetheless, it appears that rigidly defined complex multicellularity has evolved independently at least two times in each of the three macroalgae groups (along with three times in the fungi, one time in animals and twice in bacteria).

Brown algae

This group used to be considered a phylum but now is considered as an entity further down the taxonomic scale (a class, or a family, or a level in between). While almost all brown algae are macroalgae, many lack cellular differentiation and an obvious tissue organization. The structure is basically filamentous, with the filaments branching and interacting with each other to form a distinct structure, similar to the way that certain fungi produce mushrooms out of hyphae. It appears that 'true' multicellularity, with the presence of cellular differentiation and tissues, has evolved twice in this group, once in a line that includes rockweed (*Fucus)* and once in a line that includes giant kelp (*Laminaria*). In both these groups there are distinct organs (holdfast, stipe, blade, air bladders) along with some cellular and tissue differentiation; in particular, there are cells specialized to allow for the long-distance movement of carbohydrates throughout the organism. These cells are analogous (not homologous!) with transport cells of vascular plants and have similar features: they are elongate cells with large diameters and with multiple trans-cellular cytoplasmic connections between adjacent cells. Another distinct cell type, also analogous with what is found in vascular plants, are cells with thickened cell walls that provide for structural integrity, allowing a large organism to hold together in spite of being pushed and pulled by ocean currents and/or waves.

Red Algae

The red algae group has roughly four times the number of species as the brown algae and is more diverse in terms of morphology. A substantial number are macroalgae with a definite organized structure. As was the case in fungi and some brown algae, their three-dimensional complexity is a consequence of the growth and interactions of multiple filaments. Tissues can be described in some forms, with the cylindrical portions ('stems') having distinct outer and inner layers and possessing cells distinguished by their size and pigmentation. Some red algae are crust forming ('crustose') and exist as a coating on the surface of various substrates. In many crustose forms there is a layered organization, with the filaments next to the substrate having different cells from those above. Some of the crustose red algae develop a layer of dividing cells near the top surface whose action allows the crust to thicken and also allows for the development of reproductive structures.

Green Algae

Of the three algal groups that include macroalgae, the green algae group is by far the largest (15,000 species), with many unicellular, simple filamentous and other colonial forms. Consequently, the macroalgae are a much smaller portion of the total species. Some of the macroalgae are siphonaceous, often composed of multinucleate filaments that interact to form a three-dimensional form. Most modern (cladistic) phylogenies divide the green algae into two groups, one of which, in addition to including (some) green algae, contains all of the organisms considered plants. Both groups exhibit a variety of forms, including some macroalgae with 'complex' multicellularity, showing three-dimensional growth, cellular connections and distinct cell types. Some of the green macroalgae (e.g. Caulerpa) are siphonaceous, producing a large complex form out of many large, multinucleate cells.

Further Reading and Viewing

- "Are mushrooms the new plastic?" by Eden Bayer. Interesting application of fungal structure to make organic "styrofoam" evocative design:
    - TED talk
    - Company site

- “Amazing Science: Ten Craziest Things Cells Do” by Wallace Marshall. A video on remarkable cells.
    - https://www.ibiology.org/cell-biology/amazing-science-ten-craziest-things-cells/

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- Anabena filaments © Cooke, M. C. (Mordecai Cubitt), b. 1825 is licensed under a Public Domain license

CHAPTER 6: ORGAN, TISSUE, AND CELLULAR STRUCTURE OF PLANTS

Fig. 1 A hornwort, a plant whose simple structure is described as a thallus and shows very little organized structure.

Most workers consider plants to be a monophyletic group derived from green algae. All plants are considered 'truly multicellular' although there are some members with very little cellular specialization and only very rudimentary tissue and organ structure (Fig. 1). The majority of plants, and the ones that most people observe, are 'vascular plants', a monophyletic group whose name refers to particular cell types and tissues that they possess. The remaining plants, non-vascular plants (mosses, liverworts and hornworts), are often put together in a group. However, grouping organisms on the basis of what they lack is generally not useful in a phylogenetic sense and it certainly is not in this case: non-vascular plants do not form a 'natural grouping'. Moreover, none of the three groups appears to be more closely affiliated with vascular plants than the others. Thus, the plant group is best separated into four units (generally put at the phylum level): mosses, liverworts, hornworts and vascular plants. Mosses, liverworts and hornworts are all small, often less than a centimeter in height, but they can extend over a considerable area. They do vary in form and exhibit three basic body plans that do not follow the phylogenetic groupings. These are delineated below.

Non-vascular plants, and all plants, alternate between two stages: a haploid, gamete producing form (gametophyte) and a diploid, spore producing form (sporophyte) (Chapter 11). In all of the non-vascular plants the gametophytes are much more likely to be encountered because of their greater size and longevity. When present, sporophytes often appear to be an appendage of the gametophyte which, in a structural sense, they are. For vascular plants it is the sporophyte plant that is dominant (much larger on longer lived) and the gametophyte stage will only be considered briefly here but will be described more fully when considering sex and reproduction (Chapters 13 and 14).

TOPICS

- Non-vascular plant gametophyte structure
    - Simple thalloid forms
    - Complex thalloid forms
    - ‘ Stem and leaf’ forms
- Non-vascular plant sporophytes
- Vascular plant sporophyte structure
    - Organs, tissues and cell types
    - specialized organs
    - special cell types

Gametophytes of non-vascular plants

Simple thalloid forms

A thallus refers to a body form that lacks organs and tissues and is relatively amorphous, often occurring as a flattened sheet. In all of the hornworts (Fig. 1) and some of the liverworts the form of the gametophyte is a simple sheet of cells, a few cells thick, often thin enough so that the thallus is translucent. There is no cellular specialization within the thallus, although the lower surface produces unicellular rhizoids that attach the thallus to the substrate. These cells lack chlorophyll and therefore must acquire nutrition from the photosynthetic cells above.

Complex thalloid forms

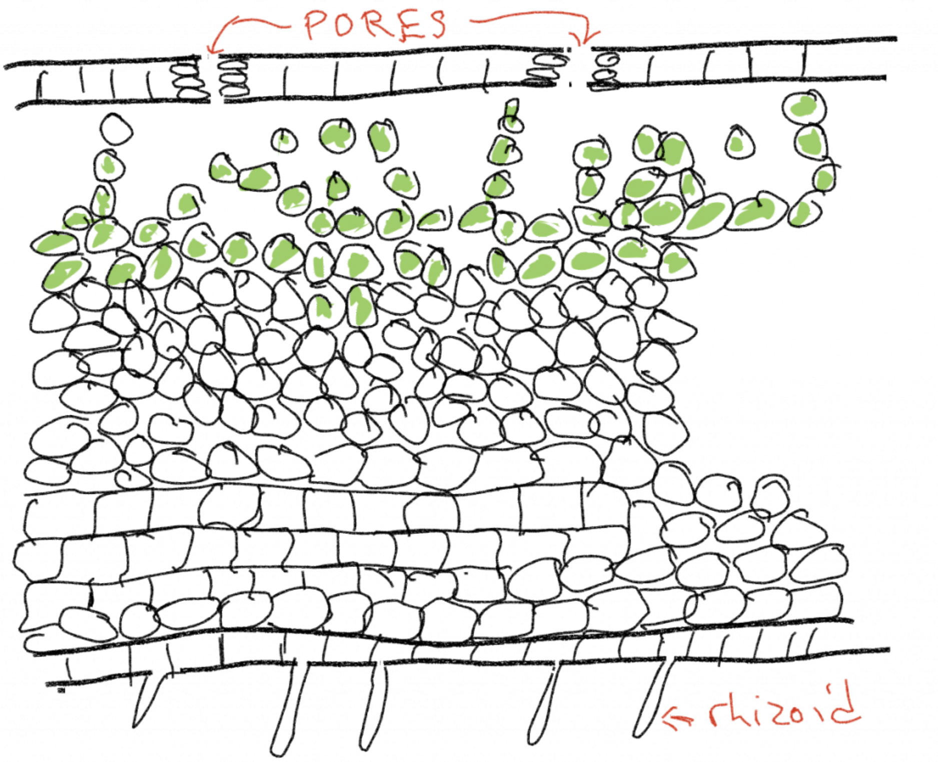


Fig. 2 Cross section through a complex thalloid liverwort

This form is present solely in the liverwort group. Like the previous form there are no obvious organs except those associated with sexual or asexual reproduction (see *Marchantia*. The thallus consists of flattened sheets that spread over the substrate (soil, rocks or tree trunks and branches, leaves) and commonly bifurcates, splitting in two. The thallus is often over 20 cells thick and has discernible layers. There is an upper 'skin' (epidermis) that is coated with a cuticle and often is regularly perforated by pores. The pores are formed by barrel shaped clusters of cells that span the epidermis and, at least in some forms, are capable of closing the pore under dry conditions. Below the epidermis is a porous layer of cells, i.e., cells are not tightly packed and have air spaces in between them. Cells of this layer have abundant chloroplasts. Generally, the largest air spaces are below the por es. The porous nature of the upper thallus is a feature that is also be present in most vascular plant leaves and is significant in allowing carbon dioxide to diffuse to photosynthesizing cells. Lower layers of the thallus are less porous and have cells that lack chlorophyll. The lower epidermis often produces rhizoids, i.e., some of the cells have thread-like extensions that anchor the organism to the substrate. Structures associated with asexual reproduction (gemmae cups), and structures associated with sexual reproduction (antheridiophores and archegoniophores) are sometimes observed extending from the upper surface (see Marchantia), their structure and function will be discussed later in the chapter.

Stem and leaf form

This is the form found in most mosses and many liverworts. The organism has a cylindrical 'stem' to which are attached small planar appendages, 'leaves', that are typically two mm or less in length and increase the light absorbing area.

Fig. 3 The 'stem and leaf' form of nearly all mosses and many liverworts consists of a stem upon which are born multiple small 'leaves'.

The 'leaves' generally do not have a cuticle and are only one-cell thick, although moss leaves commonly are thickened with more cells along their center-line, forming a nerve (costa). The stem is often less than 2 mm in diameter and generally shows little cellular specialization. Rarely, in a few moss species there are cells (hydroids) that are specialized for water transport by being elongate and hollow (i.e., the cell has died and the cytosol is absent), with openings in their slanted end-walls that allow water movement between cells. Similarly, a few mosses possess cells (leptoids) that have features that facilitate carbohydrate transport. Although hydroids and leptoids function in ways similar to cell types in vascular plants, they lack lignin and are not considered vascular tissue. They represent convergent evolution, not a close relationship between vascular plants and the few mosses that possess them.

Similar to vascular plants (see Chapter 10), the orientation of the stems greatly influences the 'look' of the plant. Most 'stem and leaf' liverworts and many mosses are prostrate, running basically parallel with the substrate that they are growing on. But many mosses have vertically oriented stems that give them a very different appearance. Also analogous to the form of vascular plants, mosses and liverworts vary in branching frequency, with some species showing little or no branching (occurring as single erect stems) and others showing extensive branching.

Fig. 4 A moss with a prostrate growth habit, with stems running horizontally and infrequent branching.

Fig. 5 Another moss lacking vertical stems and showing extensive and regular branching of creating a fern-like form.

Fig. 6 'Leaf and stem' form of two mosses: The bright green moss is erect, unbranched and standing 3-4 cm in heigh with leaves almost 1 cm long. The yellow green moss also has a 'leaf and stem' structure but the plant is prostrate and the leaves much smaller, similar to the liverwort shown below.

Fig. 7 ‘Leaf and stem’ form of a ‘leafy’ liverwort. The ‘leaves’ are ~2 mm in size and attached to a cylindrical 1 mm stem. This is just one of the three growth forms found within the liverwort group, the others being simple and complex thalloid forms. Most leafy liverworts show prostrate growth.

Sporophytes of non-vascular plants

Fig. 8 Sporophytes of *Polytrichium* moss. These grow out of the tops of the 'leafy,' green, gametophytes. In the foreground are light brown new sporophytes (tan) just emerging from the tops of gametophytes.

The diploid, spore producing form (sporophyte) of all the non-vascular plants emerges out of the gamete producing form (gametophyte) and is generally short-lived and is sometimes completely embedded in gametophyte tissue. Although they are sometimes green and photosynthetic, they have no flattened parts to increase photosynthetic light absorption and must depend on the gametophyte for carbohydrates during some or all of their existence. In hornworts, the sporophyte is a thin cylinder that splits open longitudinally, from the tip, to release spores. In liverworts and mosses, the most common sporophyte form is a 'ball on a stick', with a roughly spherical spore producing structure (sporangium) at the end of a stalk that in most cases serves to elevate the sporangium to a higher position, presumably to aid in spore dispersal. However, in some liverworts (e.g., Marchantia) and mosses (e.g., Sphagnum) it is a structure on the gametophyte that actually provides the elevation. The sporangium opens to release spores by splitting apart (liverworts) or through an opening (mosses) whose size is regulated by teeth that move in response to humidity, closing the opening under humid conditions. In some liverworts the sporophyte is extremely small and although it is not elevated, its stalk is produced in an umbrella shaped organ (the archegoniophore) that is elevated.

Organs, tissues and cells of vascular plants

Although non-vascular plants are clearly successful, existing and thriving in most terrestrial habitats, their size and activity is impacted by their limited ability to grow upwards. This inability was overcome with the appearance in vascular plants with the appearance lignified cell walls that can resist the force of gravity and the appearance of vascular tissues possessing cell types that make possible long-distance transport of water and carbohydrates. Vascular tissue allowed terrestrial autotrophs to exist as two connected entities, both essential to the other: a water and nutrient absorbing structure and a photosynthetic structure. The three organs of vascular plants, roots, stems and leaves, reflect the basic biology of terrestrial autotrophs: leaves acquire sunlight and carry out photosynthesis to 'feed' the organism, roots explore the soil and acquire the water and nutrients that is required for photosynthesis and growth, and stems connect the photosynthetic part with the water-and-nutrient acquiring part and also serve to distribute leaves effectively in their aerial enviro nment. Each of these three organs possess three fundamental tissues: a 'skin' (dermal tissue), transport tissue (vascular tissue), and ground tissue (everything else, the tissue that fills the spaces between dermal tissue and vascular tissue).

Cells of vascular plants show substantially more specialization than is found in non-vascular plants and multiple cell types have been defined, primarily on the basis of the following features, summarized in Table 1.

1. **Whether the cell is alive or dead at maturity**. A number of plant cell types are significant to organism function only after they have died. In particular, cells important for water transport, for structural integrity (keeping the plant from falling over when the wind blows), and for mechanical protection are often dead when they are performing these function s. Obviously, the cell is functioning before it dies, but its most significant contributions to the organism as a whole are when it is dead. These cells 'die young' as a result of a programmed cell death, i.e., a genetic program is triggered in these cells that causes it to die 'on its own'. Although the cells are only alive for a short period of time relative to the life of the organism,

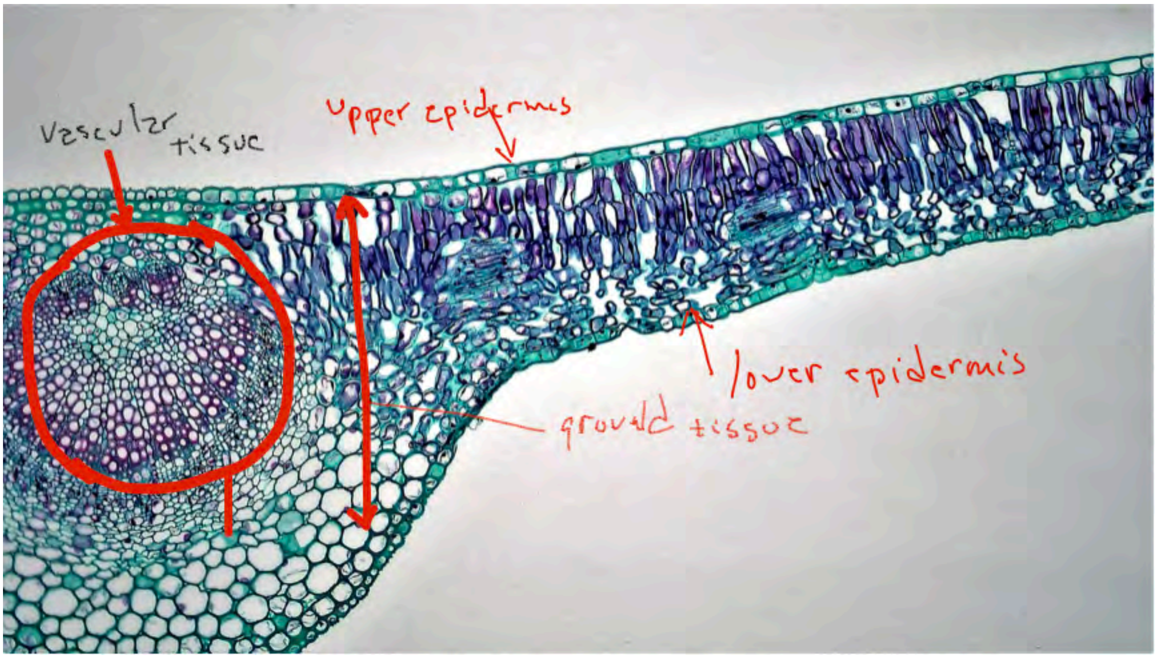


Fig. 9 Cross section of a leaf showing three fundamental tissues (dermal, vascular and ground tissues) and several different cell types

they contribute to the longevity of the plant for a prolonged period after their death and by so doing contribute to its evolutionary success.

2. **Cell wall characteristics.** All plant cells have what is called a primary cell wall described in Chapter 3. It is composed of cellulose microfibrils imbedded in a matrix of hemicellulose and pectins, molecules that bind cellulose microfibrils to each other and also absorb water, forming a gel. The primary cell wall is present as the cell is growing and when the cell expands the wall is yield ing to the pressures that are present inside the cell. The cell stops growing when the cell wall stiffens and no longer yields to the pressures generated inside it. At this point some cells deposit a distinct type of cell wall material, called a secondary cell wall, inside the primary cell wall. Since the cell is not growing, the more secondary cell wall that is deposited, the smaller the space inside the cell wall becomes. When the cell dies, this space, where the cytosol (usually with a large vacuole) used to be, is termed the lumen. Like the primary cell wall, the secondary cell wall contains cellulose microfibrils, but they are imbedded in a matrix of lignin, not hemicellulose and pectin. Lignin is a complex polymer composed of phenolic subunits. Unlike the primary cell wall, the secondary cell wall has substantial compressive strength and does not need a cell membrane and the pressurization of water inside the cell in

order for the cell to resist compression (details on this process are discussed in Chapter 22). Killing plant cells with only primary cell walls drastically affects their structural integrity (cooking spinach dramatically demonstrates the effects of killing plant cells on plant form). A cell with a secondary cell wall is rigid even after the cell has died and the membrane is gone. Corn stems stand erect even after the plant is dead because of cells with secondary cell walls. Lignin is the material that makes some plants woody, tough and rigid, but non-woody plants (e.g., corn) may possess lignified cells that are important structurally. Plants or plant parts (e.g., spinach and many other leaves) with cells possessing only a primary cell wall are called herbaceous and are much less resistant to forces produced by gravity or the wind. Such plants/plant parts lose all structural integrity if the cell membrane is destroyed or if lost water is not replaced (see Fig 9 in Chapter 3).

3. **Cell shape**. Plant cells come in a variety of shapes. Many cells are round or nearly so, or rectangular with their long dimension being two to ten times that of the short dimensions. Other cells are very elongate with their long dimension being up to 1000 times that of their diameter. Generally, the long axis of cells runs the same direction as the long axis of the plant, i.e., up and down the stem /root.

These features are summarized below. Specific cell types will be considered in more detail when considering the functioning of these tissues.

Specialized organs of vascular plants

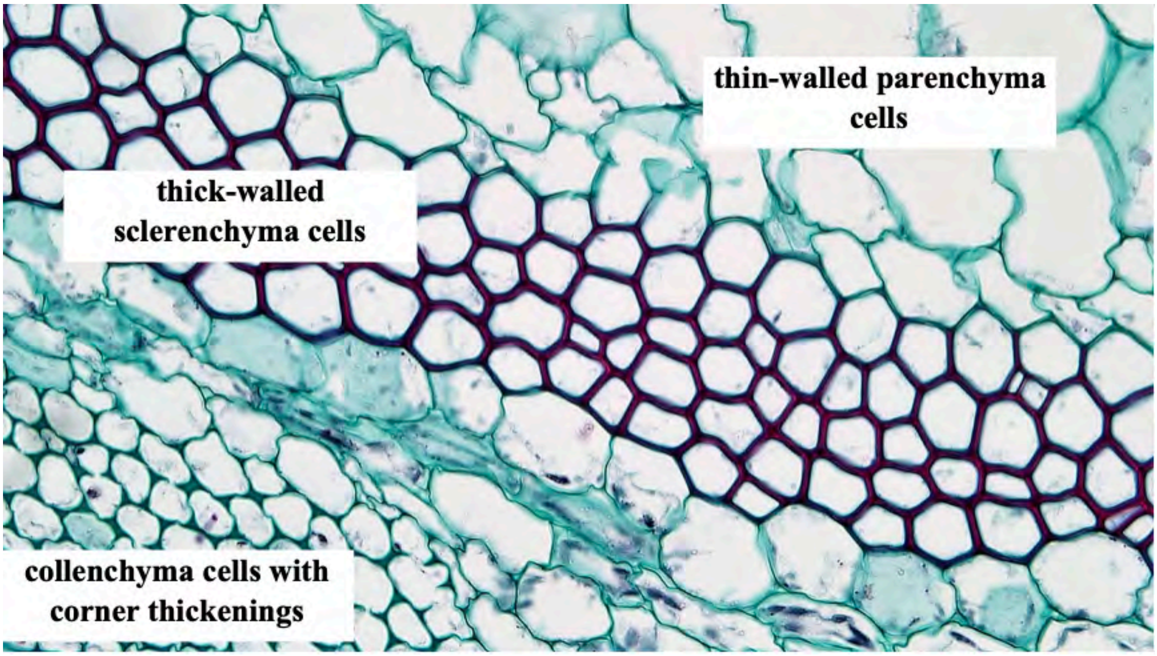
The three basic organs of vascular plants are roots, stems and leaves but commonly these organs have become specialized for specific functions and do not look 'typical'. The most readily observed of these are stems devoted to reproductive structures: the flowers of angiosperms and the cones of conifers, clubhouses. Generally these specialized stems have specialized leaves that may or may not be recognized as such. These structures are considered in more detail in chapter 14 and 15 dealing with reproduction. Stems and also roots are often modified to store carbohydrates, with the modification usually involving a simple enlargement of the structure, e.g. the root of a carrot, the stem of kohlrabi, the leaves that form onion bulbs. Often the specialized structure is produced in a specialized way, e.g. potatoes are modified stems but they are produced below ground, onions and cabbage are both round structures formed by densely produced leaves either above ground

Table 1. Vascular plant cell types. Note that some workers would classify fibers, tracheids, and vessel tube elements as types of sclerenchyma cells. Similarly, some workers consider sieve cells and sieve tube elements as types of parenchyma cells.

Cell type	Cell wall	Shape	Live at maturity?
Parenchyma	Generally, only primary, but occasionally with secondary walls	Round, rectangular, generally not elongate	Yes
Collenchyma	Primary only but it is usually substantially thickened, often in the corners of the cell	Elongate	Yes
Sclerenchyma	Thick secondary wall, leaving a very small lumen	Variable	No
Fibers (sometimes considered a type of sclerenchyma)	Thick secondary wall, leaving a very small lumen	Elongate	No
Tracheids	Secondary wall deposited in a variety of patterns or sometimes uniformly	Elongate, with a substantial lumen, cells are not stacked end to end but overlapping	No
Vessel tube elements (vessel tube members)	Secondary wall deposited in a variety of patterns or sometimes uniformly	Elongate with large lumen; multiple cells are stacked on top of each other to form vessels	no
Sieve tube elements	Primary only	Elongate with large lumen; multiple cells are stacked on top of each other to form sieve tubes	Yes
Sieve cells	Primary only	Elongate, with relatively large lumen, overlapping cells, not stacked	yes

(cabbage) or below ground (onions). Gardeners are familiar with such structures: corms are enlarged stems, bulbs are stems with enlarged leaves, tubers are below ground stems. Several of these features are discussed in the Chapter 10 on vascular plant form and also in the organism fact sheets on potato, clubmosses and horsetails.

Protective structures (thorns and spines) may be produced as specialized stems or specialized branch systems.



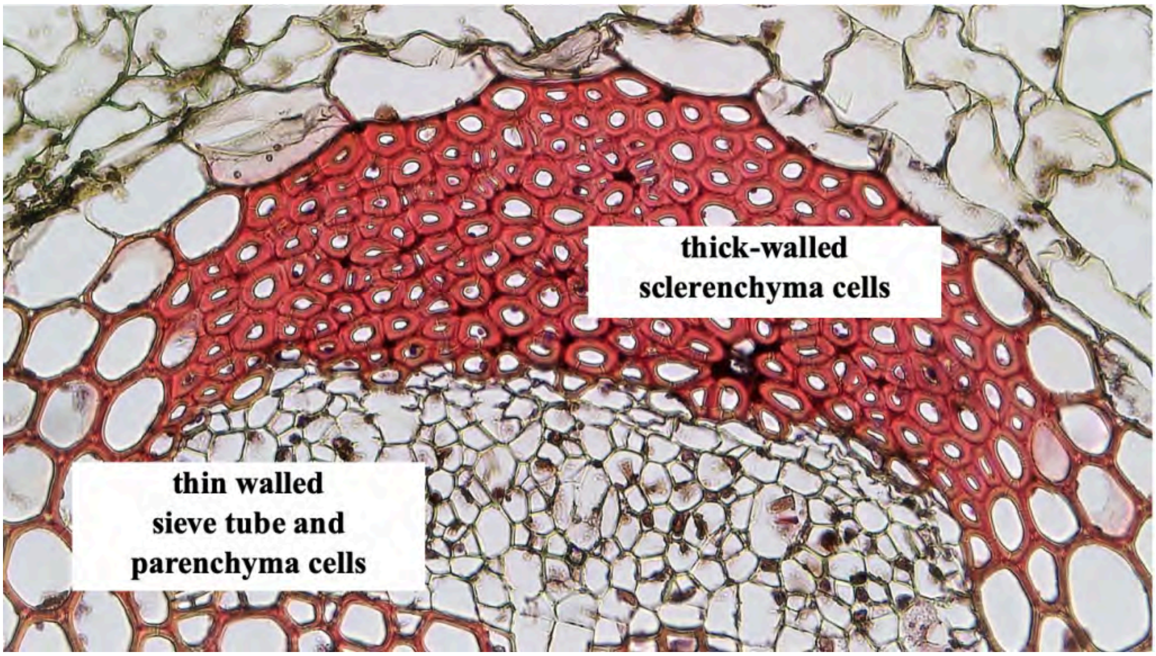


Fig. 10 Cross sections of stem tissue showing a variety of cell types

On the left: Tracheids are elongate cells with a secondary wall and large lumen. The cells overlap each other along the long axis of the plant. Individual cells are not lined up in stacks

On the right: Vessels tube members are also an elongate cell with a secondary wall but they stacked on top of each other, the top of one cell directly underneath the bottom of the next cell. The junction between cells has holes, forming a 'perforation plate'. The name for the stack of cells is a vessel. The individual cells of a vessel are called vessel tube members or vessel tube elements. By and large, vessel tube members are shorter and have a bigger diameter than tracheid cells.

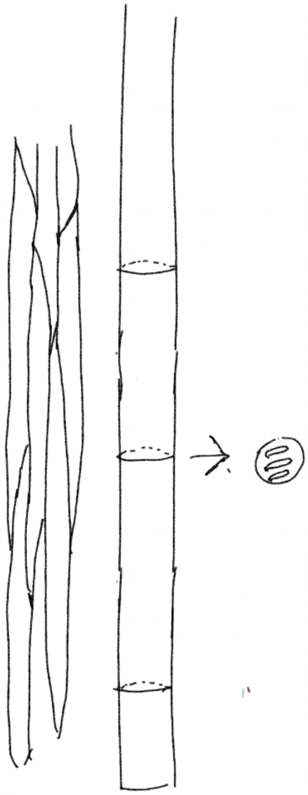


Fig. 11 Comparison of two xylem cell types, tracheas on the left and vessel tube members on the right.

Both vessel tube members and trachieds have thick cell walls but differ in diameter (vessel tube members are larger). It is difficult to distinguish the two cell types in cross-section. However, in a longitudinal section, vessel tube members are recognizable because of their stacking,. Additional distinctions will be considered when discussing water transport.

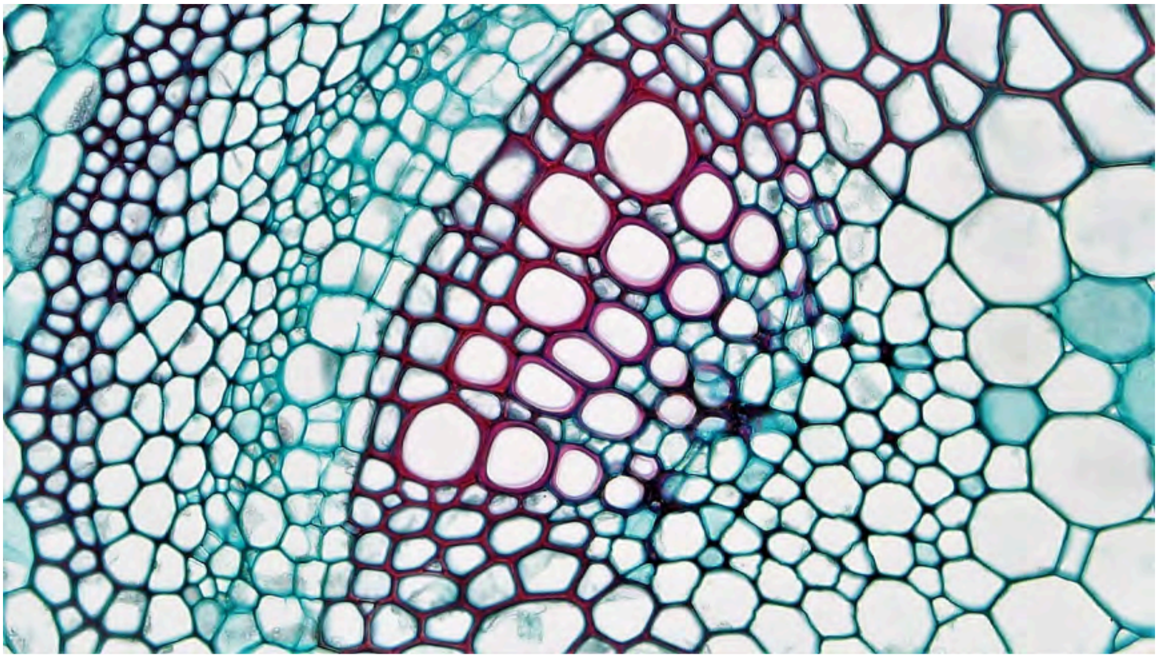


Fig. 12 Cross sections of stem tissue showing a variety of cell types.

A Few Other Types of Cells

Guard cells

Guard cells are special cells found in pairs in the epidermis of leaves of vascular plants. Guard cells operate to open pores called **stomata** in the leaf that allow carbon dioxide to enter. Guard cells change shape as they take up (or lose) water and pressurize or depressurize. The changes in shape cause an opening to appear or disappear in the space between the pair of guard cells (discussed in Chapter 22)

Spores, sperm and egg

As introduced in the previous chapter, these cells are associated with sex and reproduction. Sometimes they have special structural features, but most significant are their abilities and potentials. They are found in most of the groups considered here and are considered further in Chapter 11 and other chapters dealing with reproduction and also in the organism fact sheets.

Further Reading and Viewing

Images of non-vascular plants ("bryophytes"):

- Excellent site with many images of bryophytes:
    - https://digitalcommons.mtu.edu/bryophyte-ecology/
- Australian site on bryophytes:
    - https://www.anbg.gov.au/bryophyte/index.html
- Good discussion and images of liverworts:
    - https://www.anbg.gov.au/bryophyte/what-is-liverwort.html
- Images of Ohio mosses and lichens:
    - https://ohiomosslichen.org/MossID4.html
- Images of the mosses and liverworts of Illinois:
    - https://www.illinoiswildflowers.info/mosses/moss_index.html#snk_liverwort
- Remarkable story of an ancient fossil, prototaxites, that may be a liverwort silurian fossil:
    - http://coo.fieldofscience.com/2010/02/prototaxites-giant-that-never-was.html

Websites with excellent pictures of seed plant cells and tissues:

- University of Texas Austin Mauseth Lab Table of Contents
- University of Wisconsin Botany Resources
- "See the Plant Kingdom's Hidden Microscopic Wonders" by Michael Greshko. Nice plant cell (and some algal) pictures.
    - https://www.nationalgeographic.com/science/article/photography-plants-cells-diatoms-xylem-phloem-microscope
- Plant Tissues and Organs by the Berkshire Community College Bioscience Image Library. Plant anatomy slides.
    - http://blogs.berkshirecc.edu/bccoer/plants/
- Plant Anatomy Charts by BibliOdyssey. Botanical charts.

    - http://bibliodyssey.blogspot.com/2012/12/plant-anatomy-charts.html

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CHAPTER 7: PRODUCING FORM: DEVELOPMENT

A feature of living things, and not just organisms, is that they are dynamic, they change, and they do so in a predictable way that can be described and observed over and over again in a variety of biological entities. This pattern of change through time is termed development and while the term is mostly associated with organisms, it is significant to realize that organized (i.e., controlled in some manner) change through time is seen in cells (e.g., the cell cycle, apoptosis), populations (e.g., logistic and exponential population growth) and communities (e.g., succession).

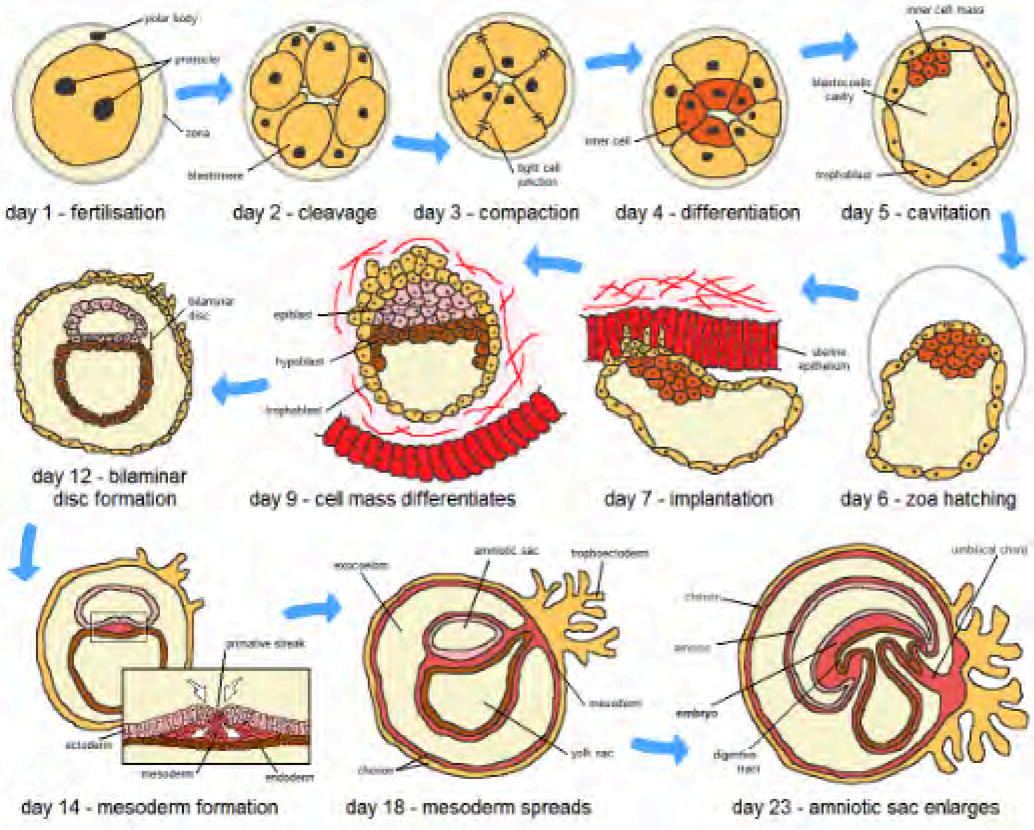

Fig. 1 Early human development (you started out this way!), an example of development of organisms.

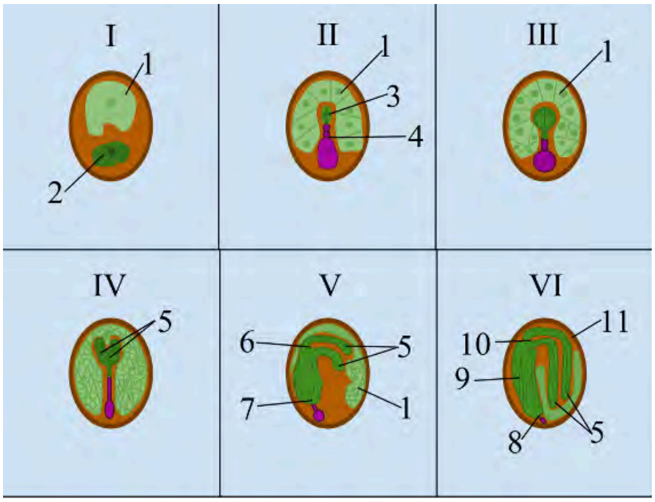

Fig. 2 Early development of a seed, which we will see in Chapter 14 is a composite structure where three ‘things’ are developing simultaneously.

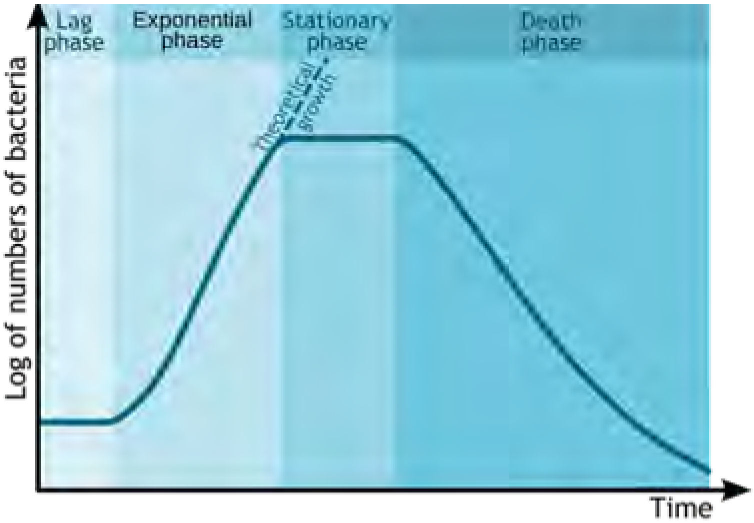

Fig. 3 Another example of biological development, this illustrates the changes through time (i.e., development) in bacterial populations

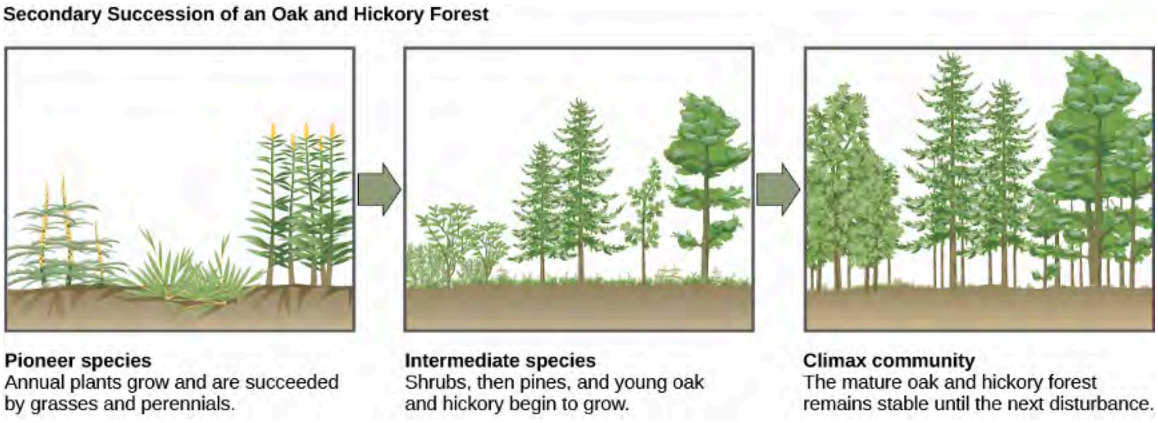

Fig. 4 Changes in communities through time is called succession.

TOPICS

- Organism development
- Development in unicellular organisms
- Development of cell shape
- Development in colonial organisms
- Development in coenocytic/siphonaceous organisms
- Development in multicellular organisms
- Development in plants

Organism development

Fig. 5 Organism development does not just include process that 'enlarge' an organism, it usually also involves processes that diminish parts of the organism (e.g., leaves) and sometimes the organism as a whole.

While development may include changes in a variety of aspects of an organism, from structure to physiology to behavior, we will focus here on how development produces and changes the structure and form of an organism throughout its lifetime. We have defined organisms as being distinct in time and space with a starting point and an ending point. And aspects of development are seen in the alterations in size, form and structure occurring during the organism's lifespan. For most familiar organisms the starting point is a special cell that has the ability to proliferate, develop a complex structure, and grow to produce an 'end point', a specific form that characterizes that particular creature. Many might think that this is the end of development, but for many organisms there are changes in the adult with time. Sometimes these changes in the 'adult' organism are dramatic and end its existence. That is, some organisms 'self-destruct' as part of its developmental process, just as some cells do. Salmon die after spawning, as do wheat plants. In both cases the endpoint of the developmental process is death. A corollary to this is that development does not just include growth and increases in complexity, it may also include, and in fact it often ends with, decreases in size and complexity and ultimately the end of the organism (Fig. 6).

Fig. 6 Harvesting wheat in Washington state. The wheat has died 'of its own accord' as part of its organismal development process.

The field of development has exploded in recent years and is being examined from molecular and evolutionary perspectives in great detail. We are focused at a very different level, considering the very basic developmental features that bring about the form and structure of the biological entities we describe as organisms. We have described several different forms of organisms: unicellular, simple multicellular (filamentous, sheets), coenocytic, complex multicellular. We will briefly consider how each of these forms develops. An important aspect of development for many organisms is the process of sex, involving the combining the genetic information of two organisms and subsequently halving it. Sex and reproduction are considered in Chapter 11.

Development in organisms that are unicellular

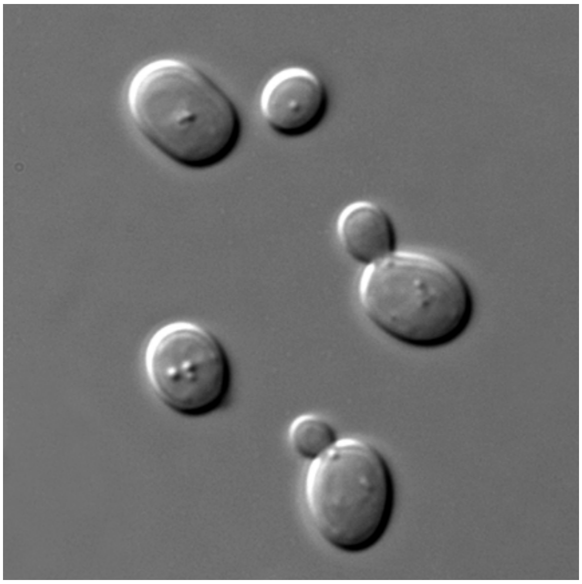

Fig. 7 Development in yeast, a unicellular organism, involves changes that bring about reproduction (cell division) by budding.

A number of organisms under consideration here (e.g., many bacteria, archaea, diatoms, dinoflagellates, and many green algae) are unicellular and, while their devel opment is quite different than for multicellular organisms, they do change over time and show definite patterns of development. Universally, development in unicellular organisms has two visible manifestations (there are many more developmental events that are not visible): cell division (Fig. 7) and cell growth. These processes are components of the 'cell cycle', a repeating series where cells acquire materials, synthesize molecules from them, and partition these materials into two daughter cells in the process of mitosis. While the most obvious molecule that needs to be made is DNA, there are a host of others: molecules for membranes, ribosomes and (for eukaryotic cells) for mitochondria and plastids. The construction of these materials requires that the cell obtain the elements that they are made of: carbon, nitrogen, phosphorus, etc. (Chapter 22), and part of the cell cycle involves the acquisition of these materials and the construction of the requisite molecules.

The relationship between cell division and cell growth is not the same in all organisms. Cells may divide repeatedly without any growth (e.g., in the early development of many animals). In this situation the original cell has plenty of 'materials' and the cell ular divisions simply partition these materials into daughter cells resulting in a multicellular organism that is basically the same size as the original fertilized egg. But this cannot go on forever, eventually there has to be material acquisition, reflected in an increase in mass and size (i.e., growth), to allow for continued cell division.

The main component of all cells is water and its acquisition is generally what drives cellular growth (i.e., expansion in size). For organisms with cell walls, water entry into the cell is effected one of two ways: by weakening the cell wall strength or by increasing the concentration of solutes, leading to an increase in internal pressure. This is discussed more in Chapter 24, but for now one should appreciate that both these processes can be controlled by cellular activity. Consequently water absorption and cellular growth may occur as a distinct phase that occurs before or after other materials are obtained, or it can occur gradually. That is, the cell can: (1) grow steadily as both water and other materials are obtained; (2) divide, acquire materials other than water while remaining about the same size, and once enough materials other than water have been obtained then rapidly acquire water and grow or (3) divide, grow quickly by absorbing water and show little growth as it acquires materials other than water, and then divide again. In the first case there are a range of cell sizes will be observed and the age of a cell is correlated with its size. In the second case, cells that are about to divide are recognizable because of their large size. In the third, case a population of cells would all be the same size except for some small cells that have just been produced by cell division.

The pattern shown by certain unicellular diatoms illustrates additional diverse possibilities. All diatoms are enclosed in a silica shell with two halves; some are structured like a petri dish with a circular top half having a diameter slightly larger than that of the bottom half, allowing it to serve as a cover the bottom. When the cytosol divides (cytokinesis) the top half produces one daughter cell by grow ing a new bottom half and this newly produced cell is 'fully grown' at its inception, i.e., it shows no growth. This cell, like all cells, goes through the G1 and G2 stages and during these stages' materials are acquired and put together into biomolecules that can subsequently be partitioned between two daughter cells, but these phases, although often described as 'growth 1' and 'growth 2' do not involve an increase in cell size. Now consider the second daughter cell, the one that is associated with the old 'bottom dish', the smaller dish. This bottom dish becomes a 'top dish' as the cell generates a new bottom half. Like its sister cell it does not grow and it ends up slightly smaller than the parent cell because the bottom half of the original cell has become the top half of the daughter cell; consequently, this cell is slightly smaller than its parent (remember the bottom shell has to fit inside the top shell and hence must be smaller). Thus, after cell division, two cells are produced; one is the same size as the original cell and one is slightly smaller. Growth of individual cells is not occurring. Through time, the mean cell size of the diatom population becomes smaller and smaller until some critical minimum size is reached when sexual reproduction is triggered and results, among other things, in cells that are the same size as the original.

Exactly what triggers a cell to divide is a tightly controlled process that has been extensively studied because of its connection to cancer. But the phenomenon is important in other situations as well. For example, in 'algal blooms', where a population of algae starts reproducing rapidly, producing very large populations whose existence often has very significant consequences. In both cancer and algal blooms, the importance of control mechanisms, other than nutrients, is indicated by the fact that nutrients alone may not trigger population/cancer growth: nutrients are necessary but not sufficient for growth and the control of the process is not simply that cells divide when they acquire enough materials to form a second cell.

Development of cell shape

Part of the development process, for both unicellular organisms and the cells of multicellular organisms, involves the acquisition of a characteristic shape. For some cells, growth proceeds equally in all dimensions and small cells have a very similar shape to large ones, but for many cells, growth is decidedly different in different directions and this produces 'adult' cells with characteristic shapes, distinct from the typically spherical/cuboidal shape of the newly produced cells. The attainment of this shape is an important feature of their development. For organisms with cell walls the shape of cells is determined by the relative strength of the cell wall in different directions. The cells grow by having an internal pressure that exceeds the cohesive strength of the cell wall. The wall yields and cellular growth occurs. If the strength of the cell wall is uniform then the cell expands uniformly (think of a typical balloon). But if the wall has less strength in a particular direction, then the expansion will occur in that direction, think of the specialty balloons that become long and skinny, this is a result of the balloon being much more resistant (higher cohesive strength) to radial expansion than to extension. The strength of cell walls is determined by the orientation of the cellulose microfibrils (Chapter 3) and this orientation is determined as they are deposited.

Development in organisms that are colonial

An essential aspect to unicellular development is that the daughter cells separate, a result of the fact that the junction between the 'new' cell and the 'old' one is weak and can be broken by forces in the environment or by forces that accompany the expansion of one or both of the daughter cells. If this does not happen cell division brings about an accumulation of cells that can drastically affect the functioning of each by changing the environment that they are exposed to and by changing organism form. Clusters of cells are considered colonies exhibiting 'simple multicellularity'. They are biological structures that do not nicely fit into the organism category, being somewhere between an organism and a population. Often colonies have characteristic shapes that develop as a consequence of patterns of cell division. Three basic patterns, filaments, sheets and spherical colonies, were described in Chapter 4 and result from the control of the plane of cell division. Each of these patterns has consequences for individual cells and their interaction with the environment. Spherical colonies result in some cells (those in the interior) that have very little contact with their environment, sheets and filaments represent situations where the colony of cells has more interaction with their environment although never as much as would be the case if the cells had separated from their parent. While most colonial organisms are described as indeterminate, producing no specific final endpoint but instead growing to sizes that are dictated by biotic and abiotic conditions, there are some colonies that are determinate, producing a colony with a set number of cells and usually with a specific form.

Development in organisms that are coenocytic/siphonaceous

Fig. 8 Complex form in coenocytic organisms. This one is a green algae that produces a complex form up to 10 cm in height.

The vast majority of organisms that are large (a mm or more in length) are made of cells that are organized in a particular, repeatable way to produce form, i.e., they are multicellular and their development from a single cell involves the creation of cells in particular places to create a form. But there are a few of 'large' organisms whose form is not a consequence of an accumulation of cells but rather they are a single large cell that has developed to considerable size. A remarkable example of this type of growth is *Acetabularia*, a green algae that ranges up to several cm in size and is shaped like a parasol. *Acetabularia*, and most organisms that are coenocytic/ siphonaceous, possess a cell wall and have internal pressures that develop as a result of osmotic forces. The shape that such cells produce are a result of the pattern of cellular expansion, which, as discussed above, is a consequence of relative strength of the wall in different directions. Bread mold produces parts (stolons, rhizoids, sporangiophores) that are all outgrowths of a single cell and there are developmental controls that direct where and when outgrowths are produced and what structure is to be formed. Similarly, some siphonaceous green algae (e.g. *Caulerpa*) are capable of producing complex and large forms by controlling the form and direction of extensions off of a single cell (Fig. 8). Some siphonaceous colonial forms are partly cellular in their construction: in *Hydrodictyon* individual cells are large (up to a centimeter) and multinucleate but are joined together into rings, commonly five or six-membered, to form a polygonal network.

Development in the coenocytic plasmodial slime molds are particularly dramatic. Within a period of 20 hours a giant, multinucleate cell flowing in a network of channels and moving at rates of up to 1 cm per hour can transform into a rigid structure bounded with a cell wall and in the form of a miniature forest (~ 1-2 mm tall) of stalked structures that bear sporangia at their summit (Fig. 10).

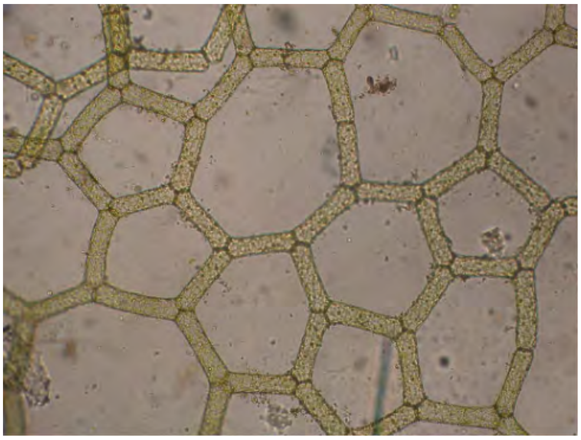

Fig. 9 Another coenocytic green algae, Hydrodictyon (water net) with individual cells up to 1 cm in length

Fig. 10 Fruiting bodies of a plasmodial slime mold. The orange spore-producing structures are about 2 mm tall and form in response to specific triggers that cause the coenocytic sheet of cytosol into distinct structures that will eventually split open to release spores.

Development in multicellular organisms

Development in multicellular organisms is a much more complicated process. Multicellularity requires that an organism produce more than one type of cell. Except in the unusual case of cellular slime molds (*Dictyostelium*), all the cells of multicellular organisms have the same genetic makeup. This means that there must be control processes that dictate that some cells follow one set of instructions while other cells follow different instructions. Unicellular and colonial organisms may have the ability to do this to a limited extent. Although the majority of cells of these organisms are all the same, they may produce specialized cells to effect the sexual process, to carry specialized metabolic functions (e.g., the akinetes of cyanobacteria), or to accomplish dispersal. Complex multicellularity requires an additional significant feature besides the ability to produce different types of cells: the ability to organize multiple cell types in a three-dimensional pattern to form tissues, with tissues organized to form organs, and with the organs organized to form organisms. This organization requires a developmental process that dictates what types of cells are produced, where they are produced, and to what extent and in what direction each cell expands.

A significant developmental distinction between animals and most of the organisms covered here results from the presence of the cell wall. Animal development includes the possibility of cell migration, with the movement of cells allowing for particular arrangements and forms to be produced. Outside of the animal kingdom, cell migration occasionally occurs but only in organisms that lack cell walls. Cells of cellular slime molds must migrate in order to aggregate and subsequently move relative to each other, and cellular slime mold development involves a physical rearrangement of cells. However, when a 'final' form of a cellular slime mold is produced the individual cells are no longer capable of moving because they have developed cell walls and are stuck to neighboring cells. Almost all of the multicellular organisms dealt with in this book possess cell walls and a newly produced cell is 'stuck' to the cell that produced it. Moreover, for all plants, cell division occurs in a region called a meristem, a region that produces new cells with a three-dimensional organization. The new cells that are produced are not only attached to their parental cell, but are also attached to multiple cells that are being simultaneously produced around them. In contrast, as discussed previously, fungi and some red, green and brown algae produce three-dimensional multicellular structures in ways that do not involve a meristem, generally by having individual filaments (one-dimensional structures) glued together in ways to create a three-dimensional form.

Development in plants

Plants (mosses, liverworts, hornworts and vascular plants) have several developmental features that are not found in familiar animals:

1. Plant growth is generally indeterminate, i.e., without a defined endpoint
2. Plants possess meristems, embryonic regions, throughout their life.
3. Plants exhibit modular growth, a pattern also found in some less-familiar animals (e.g., hydroids, corals, sponges), but not in familiar animals.
4. Plants show alternation of generations, meaning that there are two forms of the organism, one haploid and one diploid. Alternation of generations (Chapter 11) is also present in some green algae, brown algae, red algae and a few chytrids (fungi).

The first three points are considered below with the final point considered in a later section of the book.

Determinate and indeterminate growth and the growth of plants

By far the most familiar pattern of organismal development is that shown by mammals who grow for a short period of time (relative to the entire life of the organism) and then spend most of their life as an adult form. This type of development can be termed 'determinate' because the final form is 'determined', there is an endpoint (an adult) to the development process. While some of the organisms covered in this course, in particular many of the unicellular forms, show this type of development, most 'non-animals', and in particular plants and fungi, show a very different patterns of development, one that is described as indeterminate, where there is no endpoint and the organism is, in essence, everlasting. The key to its everlasting nature comes from the fact that that plants retain portions of their body that are **permanently embryonic**. In the familiar mammalian pattern of development an organism is an embryo for a portion of its life and then transforms into a juvenile and eventually an adult. An embryo is often defined as a 'young organism' but what makes it special is not its age but the fact that it cells are capable of cell division, cell differentiation and cellular growth. In animals these cellular abilities are for the most part only found for a short period of time. The whole animal is basically the same age and through time it transforms from an embryo into an adult. In order to observe development in animals one observes an embryo through time. While the adult does replace cells, in terms of development it is not changing in form. In contrast, plants always have regions that are embryonic and capable of dividing, differentiating and growing; and at any one point in time one can see the developmental process by moving from the embryonic parts of the plant to the older parts of the plant, i.e., the entire plant is NOT all the same age. If you planted an acorn ten years ago you might consider the structure that you now see is 'ten-years old', but most of it is considerably younger and one can even find parts in the embryonic regions that were 'born yesterday'. At any point in time one can observe the entire developmental process, from embryo to 'adult', by moving distally, from the embryonic regions, located at the tips of roots and shoots, to progressively older tissues further from the tips.

The embryonic regions of plants are called meristems. There are two basic features that distinguish embryonic regions: (1) cells are dividing and thereby producing more cells, (2) cells are small, undifferentiated and not yet committed to a final cell type. The activity of meristems may vary seasonally, it often has periods of quiescence or dormancy, but its ability to produce more cells that develop into a variety of cells is intrinsic to the meristem region. Very early in the life of the plant the entire plant is embryonic but soon some of the cells become developmentally programmed to mature into particular types of cells and, along with this, lose their ability to divide. In seed plants this transformation takes place within the seed and a mature seed has within it a small plant with two embryonic regions on opposite ends of a very short root/shoot axis. Throughout the life of the plant this axis will extend because of the expansion of the cells produced at the two ends. The meristems produce more and more cells and the expansion of these cells pushes the two meristems further away from each other and elongates the root and shoot. The se embryonic regions are called **primary meristems** (they are the first ones formed) and also **apical meristems** (they are located at the tips, apices, of roots and shoots). Root apical meristems divide to produce cells that extend the root axis. Shoot apical meristems serve a similar function for shoots but while producing new shoot material they are also producing leaves. Growth from apical meristems is called **primary growth**. In general, the oldest part of the plant is at the soil surface and one encounters younger and younger tissues as one moves towards the tips of shoots or tips of roots. The actual region of growth is generally restricted to a small portion, typically a centimeter or less, just behind the meristematic regions.

Plant growth is modular

In addition to being indeterminate, plant growth is modular, producing structures that are fundamentally self-similar and recursive. There are two basic modules to a vascular plant: roots and shoots, and both can produce new modules, branch roots and branch shoots, that are replicas of the original shoot axis and root axis. With time, a seemingly complex entity is produced, yet the rules governing its construction are very simple: the shoot can generate branches and these can generate more branches and these can generate even more branches. The same thing is true for roots. The growth of all the modules results from the activities of apical meristems and all such growth is considered primary growth.

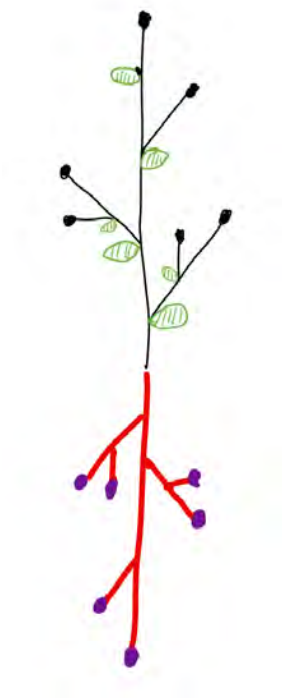

Fig. 11 Modular plant growth: Plants grow in a modular fashion with two basic modules: shoots (which bear leaves) and roots. Both of these modules have at their tip a meristematic zone (shoot apical meristem and root apical meristem). These modules are capable of producing additional modules, branch roots and branch shoots and these in turn can produce more branches, i.e., the branches have branches. It is a recursive structure. The original root and shoot meristems are created in the seed. Branch shoots originate in specific places, adjacent to where the leaf was or is attached to the stem. A group of meristematic cells, called a bud (branch) primordium is left behind by the apical meristem each time that it produces a leaf. These generally do not develop immediately and although a potential branch is produced at every leaf junction, many of them never develop. The production of branch roots is not as rigidly determined. The growth produced by apical meristems is considered 'primary growth' whether it occurs on the original root or shoot or occurs on branch roots or shoots.

Leaf development

In contrast to the roots and shoots, whose growth is indeterminate, leaves are determinate, producing a defined form, the product of a structure with a defined (determined) development process. The shoot apical meristem produces mounds of embryonic tissue, called leaf primordia, that divide for a period of time, grow for a period of time and then exist in a static form until the process of senescence is triggered that culminates with the leaf becoming detached from the rest of the plant.

Origin of new modules

To create a new module, one needs to create a new apical meristem. These originate differently in roots and shoots. In roots, new apical meristems form as the result of the activity of certain cells in the outermost layer of the central core of root vascular tissue (more details in the next chapter). Some of these cells are stimulated to start dividing and become organized to form a root apical meristem. Growth of cells produced by this meristem pushes the branch root apical meristem out of the original root and into the soil, where it continues to grow in a fashion similar to the original root.

Branch shoots are created in a differently and originate from a shoot apical meristem. In addition to extending the shoot and producing embryonic leaves, the shoot apical meristem also produces a new shoot apical meristems in the 'axil' of each leaf. These are new shoot apical meristems and are called bud primordia. They are produced in a dormant state and need to be stimulated to start dividing and produce new cells that will allow the branch to elongate. Most bud primordia are never stimulated to grow; if they all were stimulated a very 'branchy' structure would result, with a branch being produced at every position where there was or is a leaf. Often, but certainly not always, branch shoots are only stimulated to grow after the leaf they are adjacent to has fallen off the plant.

Plants are also capable of producing new modules in non-standard ways. Roots and shoots thus produced are termed 'adventitious'. Sometimes roots are produced from stem tissues and these would be described as adventitious roots because all 'standard' roots are formed off existing roots. Similarly, sometimes root tissues can develop shoots; obviously these are not originating in the axil of a leaf, thus these would be termed adventitious shoots. The ability of some plants to produce adventitious roots or shoots allows for the vegetative propagation of plants: if detached stems can be stimulated to produce roots then one can propagate plants from 'cuttings'; similarly, roots can be used to propagate plants. And for some plants leaf tissue can be stimulated to produce adventitious roots and shoots; thus, propagation is sometimes possible from leaves. In all of these situations, certain cells, called parenchyma cells, are stimulated to start dividing and organize to form an apical meristem. Once one module (a root or a shoot) is started, new modules can be formed from it. A unique feature of parenchyma cells is their ability to 'de-differentiate' and resume an embryonic condition, capable of dividing and producing a variety of cell types, even after they have differentiated to become parenchyma cells.

Cell types of vascular plants were introduced in the previous chapter but will be considered further in the next chapter, considering the anatomy of roots, stems and leaves.

Further Reading and Viewing

Some interesting sites related to plant development.

- "Plant embryogenesis" by Sacco C.de Vries et al.
  - https://www.sciencedirect.com/science/article/pii/S0960982217305626
- "Xylem cell death: emerging understanding of regulation and function" by Benjamin Bollhöner et al
  - https://academic.oup.com/jxb/article/63/3/1081/475758
- "Programmed cell death: A way of life for plants" by Jean T. Greenberg
  - https://www.pnas.org/doi/pdf/10.1073/pnas.93.22.12094

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CHAPTER 8: VASCULAR PLANT ANATOMY: PRIMARY GROWTH

As described in Chapter 6 the three organs of vascular plants (roots, stems and leaves) have the same basic structure: a boundary of dermal tissue enclosing ground tissue that has one to many strands of vascular tissue running through it. The three organs differ in the distribution of vascular tissue: in roots it occurs as a single central strand; in stems, the vascular tissue occurs as multiple bundles imbedded in ground tissue; and in leaves the vascular tissue often occurs as a reticulate network of veins or as parallel strands of vascular tissue. In both cases there is ground tissue filling the space between vascular strands and dermal tissue. This basic anatomy is easily seen in asparagus if one trims the base and looks at the cut end. The dermal tissue is the tougher outside, the vascular bundles are seen as small circles scattered in the outer portion of the stem, and ground tissue makes up the rest.

Roots and shoots show two polarities, a radial polarity, meaning that tissues and cells differ as one moves outward from the center (along a radius), and a proximate/distal polarity, meaning that cells at the tips of organs, where they are produced, differ from cells away from the tip, cells which are older. Leaves have a tip to base polarity and often have a top/bottom polarity.

In this chapter, we describe in more detail the plant anatomy of flowering plants resulting from primary growth (growth derived from root or shoot apical meristems), and consider the developmental changes and consequently the patterns shown with age (distance from the apex).

TOPICS

- Root development
- Mature root anatomy
- Shoot development

Fig. 1 Germinating sunflower seeds. The tip of the shoot is between the two leaves (cotyledons). The junction between the root and stem is at the soil surface. Note that the root of the seedling in the foreground is (atypically) running horizontally. and showing numerous root hairs

- Mature shoot anatomy
- Leaf development
- Leaf anatomy

Root Development

If a root is sectioned along the long axis (i.e., a longitudinal section) its developmental pattern is readily apparent. Near the tip is the meristem, recognized by the small size of cells and by mitotic activity, often evidenced by the appearance of chromosomes. Moving back from the tip (proximally, towards the plant body) one encounters older and more mature cells, recognizable because they are larger, no longer dividing, and possess features that distinguish different cell types, e.g., secondary cell walls of tracheids and vessel tube members. Because there is no more cell division or expansion after one moves a short distance from the root apex, the diameter of a root showing only primary growth is generally constant along its length, except for the terminal few millimeters. (Roots exhibiting secondary growth do increase in diameter and are discussed in the next chapter). Cells that are produced by the root apical meristem expand the most in a distal/proximal direction (up/down, assuming the root is vertical) and produce cells that are elongate in this direction. There is much less expansion radially, hence roots primarily grow longer, not wider, and this growth occurs near the root tip. Even more significant than the expansion of individual cells is the fact that most cell divisions in the meristematic zone divide cells, so that most of the additional cells that are produced are in the longitudinal (distal/proximal) plane. This is similar to how a unicellular filament divides to extend itself, with cell divisions that are perpendicular to the long axis of the filament. Cell divisions in the root apical meristem adds cells in the distal direction and only to a limited extent do roots add cells radially. Most roots are roughly 20 to 100 cells wide (assuming only primary growth) but roots are often millions or trillions of cells long.

Assuming a cell division that adds to the number of cells in the distal/proximal plane, a second key consideration following cell division is whether the cell that remains meristematic (and does not grow) is distal (towards the tip) or proximal (towards the rest of the plant). In the vast majority of cell divisions of root meristematic cells, the cell that remains meristematic is distal, and the expansion of the other cell pushes the meristematic region into the soil. However, in a small portion of cells it is the proximal cell that remains meristematic and the distal cell matures and becomes part of the protective root cap, located at the extreme distal end of the root. The cells of this root cap are continually sloughed off as the root extends through the soil, and the root cap ensures that meristematic cells themselves are not sloughed off.

Developmental changes in primary root growth

Proceeding proximally from the root tip one encounters the following regions which transition gradually and overlap:

- zone of cell division, the embryonic region, often less than one millimeter
- zone of cell expansion, generally only a few millimeters in extent, a region where cells are elongating, and to a much lesser extent, getting bigger in diameter; .
- zone of cell maturation, a region where cells develop characteristic features. This

zone extends from less than a cm to several cm in length. In the youngest part of this zone root hairs are produced but they soon senesce and are lost from the plant

Significant aspects of cell maturation zone include (in order from the tip as one moves proximally):

- conducting elements of the phloem become functional
- the waterproof compound suberin is deposited as a **casparian strip**
- conducting elements of the xylem become functional
- root hair appearance and disappearance. Root hairs are extensions off of dermal cells. They are produced after these cells have stopped elongating but are present for only a short time before senescing. Hence, root hairs are only present in a relatively small section of the root.

The significance of the casparian strip

These hydrophobic deposits initially occur as a band that blocks water movement through the wall from the outside to the inside. Eventually the entire endodermal cell wall is coated. The casparian strip forces water and any minerals dissolved in water to enter the cytosol at some point in their journey between the soil and the xylem tissue. Before the casparian strip is deposited, i.e., in the youngest part of the root, water can move from the soil to the center of the root through the '**apoplast**', a term that describes the collective space of cell walls and any water filled spaces between cells, which typically includes at least 10% of the tissue volume. Because the endodermal cells are tightly bound to each other, once the casparian strip is deposited water is forced to move through the **symplast** in order to cross the endodermis and get to the interior of the root. The symplast is a term that describes the collective volume of the cytosols of all cells, collective because all cells are interconnected by plasmodesmata, membrane bordered cytoplasmic threads that run between cells.

The casparian strip of the endodermis, once deposited:

1. allows the plant to regulate, by virtue of the selective permeability of cell membranes, what minerals do and do not enter the xylem tissue, the conduit to the top of the plant
2. allows the plant to, under certain conditions, concentrate solutes in the root xylem

because the apoplast solution inside the endodermis (and connected to the xylem tissue) is separated by a two membranes (one providing entry into the symplast, one providing exit from the symplast) from the apoplast solution outside the endodermis. Note that the apoplast outside the endodermis is continuous with the soil.

3. **decreases** the ease with which water can move from the soil to the root xylem.

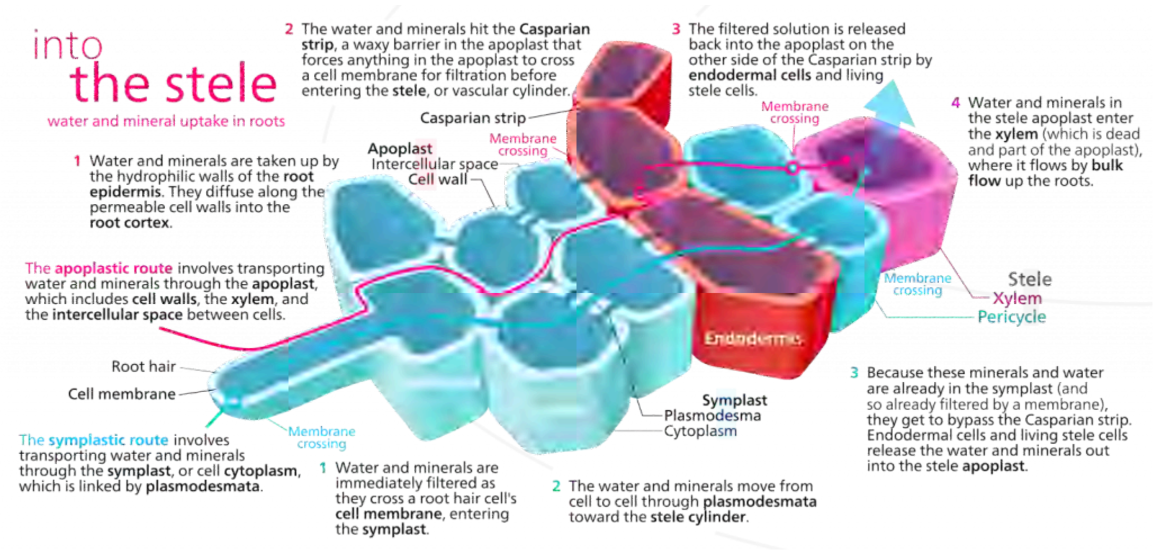

Fig. 2 Diagram of a root showing root hair, epidermis, cortex, endodermis and stele (central core of vascular tissue). Traced in blue is a symplastic route for water to move from the soil to the stele. Traced in red is an apoplastic route except for where the casparian strip of the endodermis forces water to enter the symplast.

Role of root hairs

Root hairs appear when of the epidermal cells produce a thin outgrowth, called a root hair, that extends perpendicularly from the root into the soil. The root hair is thin (~ 10 um) but may extend several mm into the soil. As discussed earlier, although root hairs greatly increase the area available for water and nutrient absorption, their more significant effect might be in increasing the volume of soil within certain distance to the root. Considering root hairs, water/nutrients may:

- enter the cytosol of the root hair and then proceed inwards through the symplast
- enter the cell wall of the root hair and move through the apoplast to the interior of the root (note that once the casparian strip is deposited in the endodermal cell walls, this root is blocked)

- by-pass the root hair and move through the soil to the root proper

For moist soils water may move most quickly through the soil rather than using the routes through the root hairs and it is possible that root hairs may be most significant in nutrient absorption rather than water absorption

Mature root anatomy

A typical root cross section shows dermal tissue on the outside, surrounding a region of ground tissue (the cortex) which surrounds the endodermis, recognizable because the suberized layer of the cell wall picks up stain. Just inside the endodermis is the pericycle, a ring of parenchyma cells which can be stimulated to form root apical meristems that grow out of the root to form lateral roots. Inside the pericycle is the vascular tissue which is arranged differently in different roots. Some roots have a central pith of parenchyma cells while most roots have a central, solid core of vascular tissue.

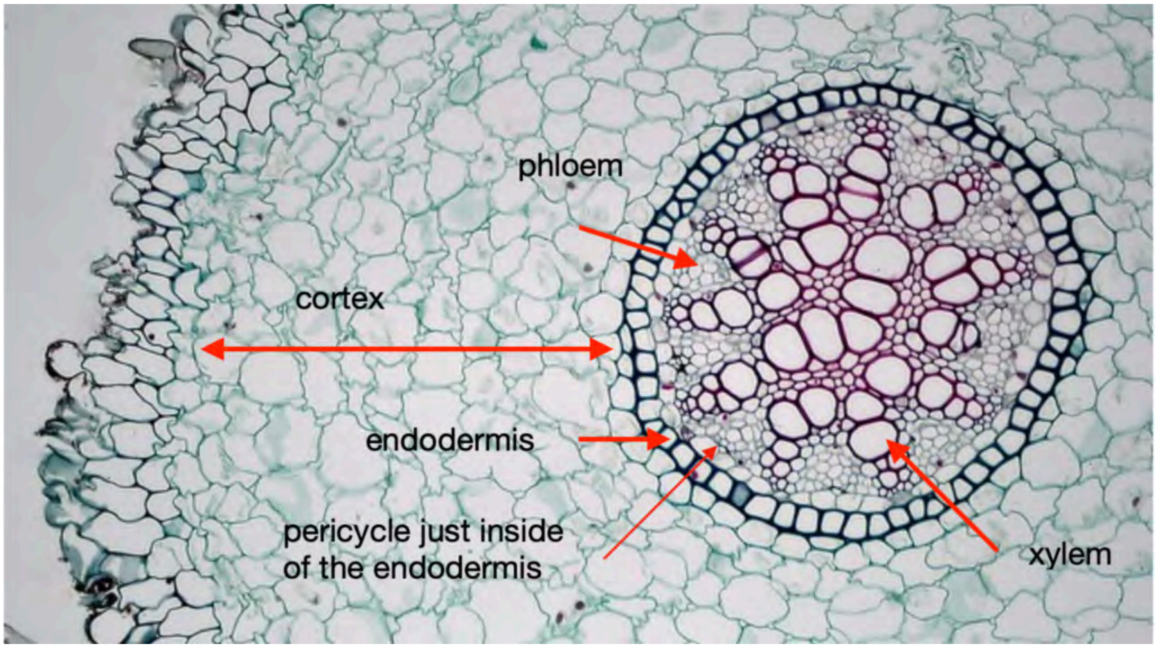

Fig. 3 Cross section of a mature root.

Shoot Development

The basic pattern of development for shoots is the same as that for roots: a terminal region of cell division above a region of cell growth above a region of cell maturation. But shoot growth is more complicated than root growth in several ways, one is the fact that shoot apical meristem not only extends the stem but it also produces embryonic leaves (leaf primordia) and branch shoots (bud primordia) positioned just above the leaves. The presence of these structures divides the stem into nodes, the places where leaves connect with the stem, and internodes, the spaces between nodes. Both of leaf and bud primordia develop vascular tissue that needs to be connected with the vascular tissue of the main stem. If one were to follow the vascular tissue in a leaf or a branch back to the main stem, one would observe one or more bundles of vascular tissue extending from the leaf/branch to the stem. This accounts for the presence of 'vascular bundles' in the stems of flowering plants: fundamentally they represent the traces of vascular tissue running to the leaves and branches. At the nodes one can see vascular traces diverging from the stem to enter leaf and branch primordia. Ferns, horsetails, clubmosses and a number of fossil plant groups have different patterns of vascular tissue distribution within the stem (described as 'stelar structure') and, because vascular tissue is often represented in fossils, its distribution has been useful in classifying fossilized vascular plants.

Leaf primordia are produced in a characteristic pattern that depends upon the species of plants. The most easily described pattern is one where leaves are produced in pairs on opposite sides of the stem. Sequentially, leaves are produced in pairs occur ring with a 90^o rotation from the previous pair of leaves, i.e., if you were viewing a stem from the top and the first pair of leaves were north and south the next set of leaves would be east and west. The next set of leaves produced would be back to the original north-south orientation. Most plants have a more complicated **phyllotaxy**, i.e., arrangement of leaves, that can be described by counting the number of new leaves and the number of rotations around the stem before you end up with a leaf directly under another leaf.

While the elongation of roots, brought about the expansion of newly produced cells, is generally consistent in time and space, occurring soon after cells are produced and very close to the root apical meristem, elongation of stems is not as consistent. Elongation of shoots results from extension of the internodes. In some plants, internode growth occurs close to the shoot tip, resulting in a stem with leaves that separate from each near the tip of the shoot and at a pace consistent with the production of new leaf primordia. In other plants internodal growth is delayed or absent, producing very short stems with multiple leaves very close together (rosettes). Such a structure may be permanent or may be temporary until a particular cue is received and the stem 'bolts', rapidly elongating by increasing the space between leaves, e.g., in lettuce or spinach. Some monocots (see below), in particular grasses, have meristematic zones at the nodes of stems and at the base of the blade of the grass leaf. These meristems are activated if the stem or leaf above them is damaged (usually from grazing).

In contrast to roots, there is no maturation of cells on the distal side of the shoot apical meristem, i.e., there is no 'shoot cap' (cf. the root cap) derived from the shoot apical meristem. Generally, the this apical meristem is not being pushed through the soil so the function that the root cap provides is not generally required. However, the shoot apical meristem is covered by young leaves that grow very close to the tip of the shoot and are able to cover it. Some stems, called rhizomes, do grow through the soil and they are protected by modified leaves called cataphylls that protect the shoot apical meristem and form a pointed structure that can more easily be pushed by growth through the soil. Similar modified leaves, called bud scales, cover the shoot apical meristem of woody plants during the extended periods when they are not growing. While most roots often are actively growing most of the year including during the growing season, shoot growth for plants in seasonal habitats is often of much duration. Many plants, especially trees, exhibit growth (extension of stems) for only a short period, often less than 30 days in the spring. However shoot cell division occurs much earlier than cell growth, often as much as eight months earlier, that is some new cells expanding in the spring were produced in late summer of the previous year.

Mature shoot anatomy

Traditionally, flowering plants were separated into two groups, monocots and dicots, based on a number of features, one of which was stem anatomy. While the monocot group is still considered to be a valid phylogenetic entity, most workers consider 'dicots' to be an artificial grouping, and have separated dicots into 'eudicots' and several other groups. The vast majority of the former dicot group are eudicots and in the discussion below we will use the term dicots.

Dicot stems have vascular bundles arranged in a ring close to the margin of the stem. The tissues running from the outside to the inside are: epidermis, cortex, vascular bundles (in a ring), with variable amounts of ground tissue in between the bundles), pith.

Monocot stems differ from dicot stems in having vascular bundles scattered throughout the stem.

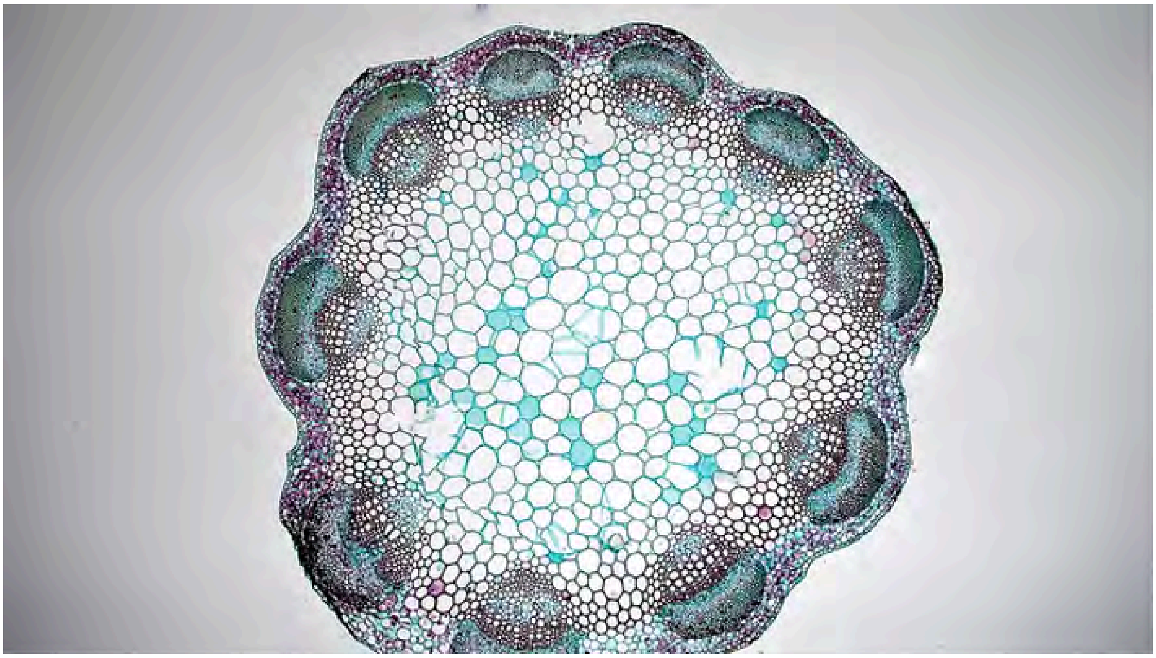

Fig. 4 Clover (Trifolium), a dicot, stem, showing vascular bundles arranged in a ring with a large central pith. Vascular bundles have sclerenchyma cells to the outside and phloem and xylem tissues as one moves inward.

Leaf development

Unlike roots and shoots, leaves are determinate structures whose developmental pattern is comparable to humans and frogs. They start as an embryo called a leaf primordium, whose cells divide and subsequently grow for a defined period of time to produce a three-dimensional form that is often substantially more complex than the cylindrical structure of roots and stems. Moreover, the diversity in leaf form found in vascular plants, especially for flowering plants, far exceeds that found in roots or stems. After cellular division and growth cease, the leaf remains in an 'adult' form for a (generally) defined period of time before it undergoes its final developmental process of senescence that ultimately results in the leaf's separation from the plant (abscission). Leaf senescence and abscission will be

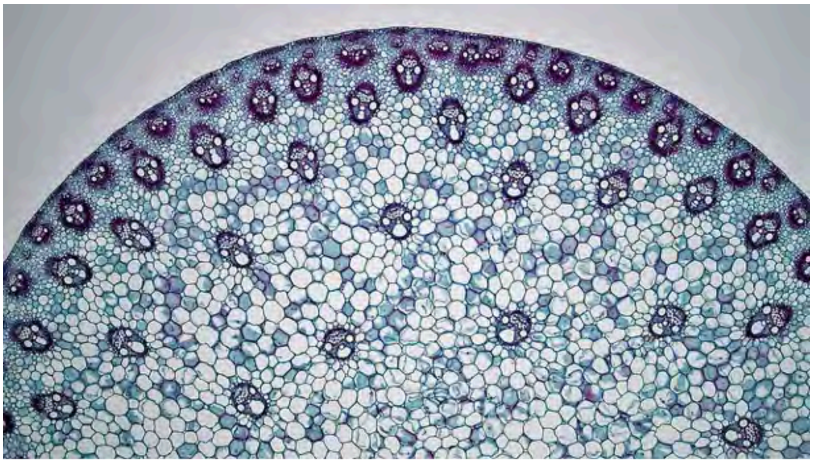

Fig. 5 Zea (corn, a monocot), stem cross section showing numerous vascular bundles embedded in ground tissue.

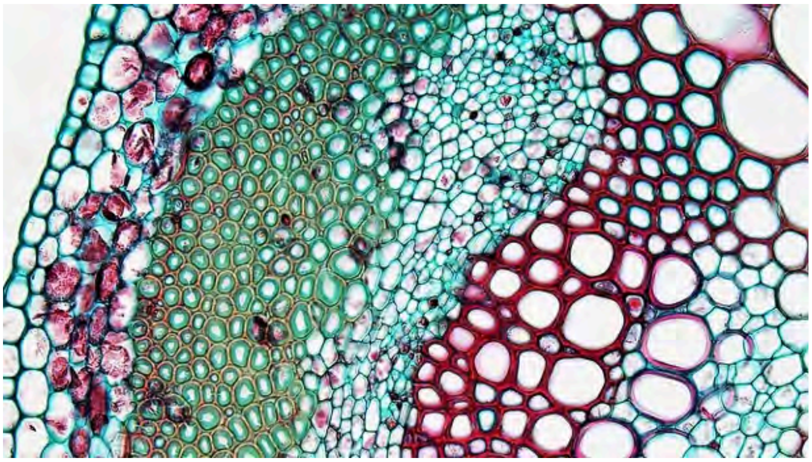

Fig. 6 Cross section of a dicot stem showing a vascular bundle. Moving from the outside: dermal tissue, cortex, sclerenchyma (stained green with thick walls), phloem tissue (stained blue), xylem tissue (stained red with thick cell walls)

discussed later but it is important to emphasize here that these developmental processes are highly significant to the life of the plant.

Intercalary meristems are present in some leaves, in particular grass leaves, and allow a leaf whose tip (distal portion) has been grazed to resume growth and replace lost photosynthetic area. The ability to grow in this manner has been particularly important to the success of grasses.

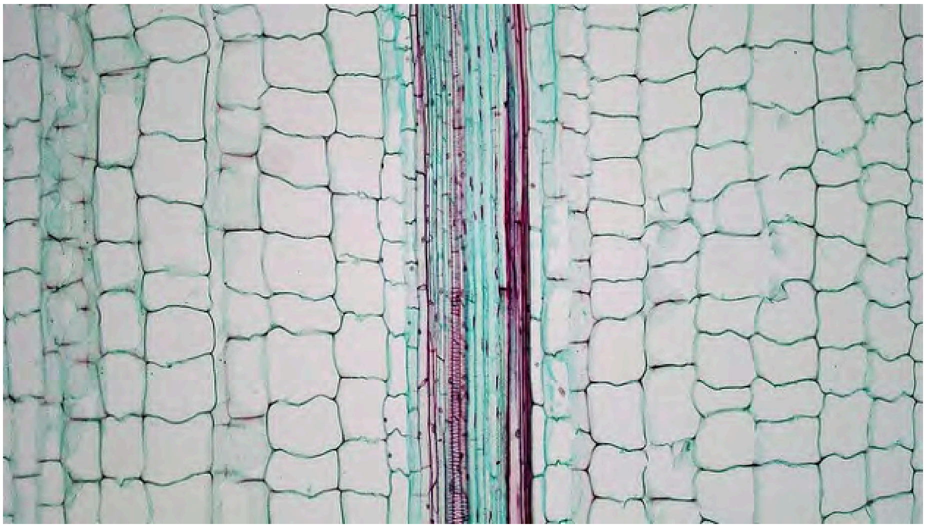

Fig. 7 longitudinal section of stem showing vascular bundle with red stained cells. This in enlarged below.

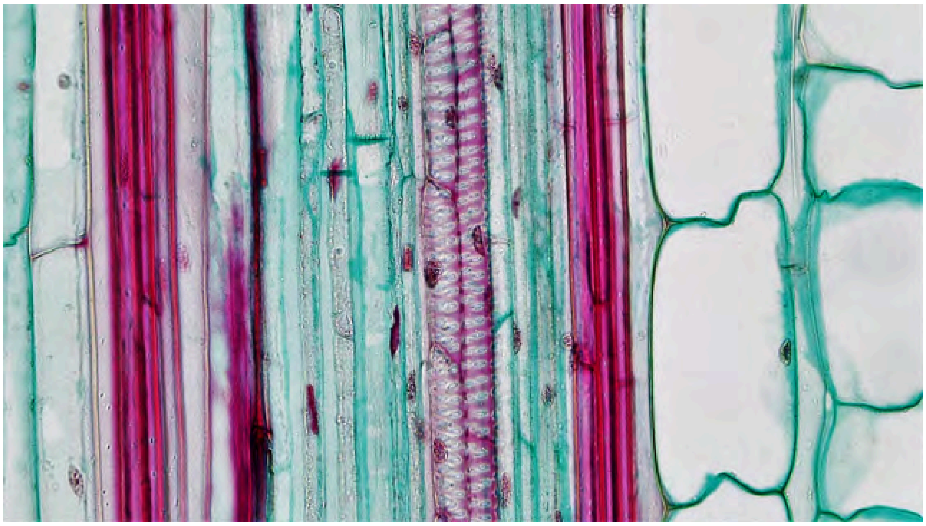

Fig. 8 Longitudinal section showing vessels Note that typically the secondary cell wall of vessel tube members is not laid down continuously and often occurs as rings, or spirals. Also stained red are sclerenchyma fibers whose secondary walls are laid down continuously.

Leaf structure

Many leaves show a polarity between the upper surface and the lower, with the lower epidermis having regulated pores, stomata, while the upper surface does not. Additionally, the ground tissue of the upper part of the leaf is layered with cells that are oriented parallel to each other (this region is called the palisade mesophyll) while the mesophyll cells of the lower part of the leaf (called the spongy mesophyll) has cells that are not oriented in a consistent way relative to each other and have much larger air spaces between individual cells. Many monocot leaves have veins that run parallel to each other and this means that if you cross section the leaf you are likely to see cross sections of all the vascular bundles. In most dicot leaves the veins run at various angles and a cross section through the leaf is unlikely to show cross sections through any other bundle except the main central vein.

Fig. 9 Lilac leaf showing upper and lower epidermis, the central vein in cross section with red stained vascular tissue, a palisade layer that is general two rows of cells and a spongy mesophyll layer.

Further Reading and Viewing

See the following sites that were also listed in Chapter 6.

Websites with excellent pictures of seed plant cells and tissues:

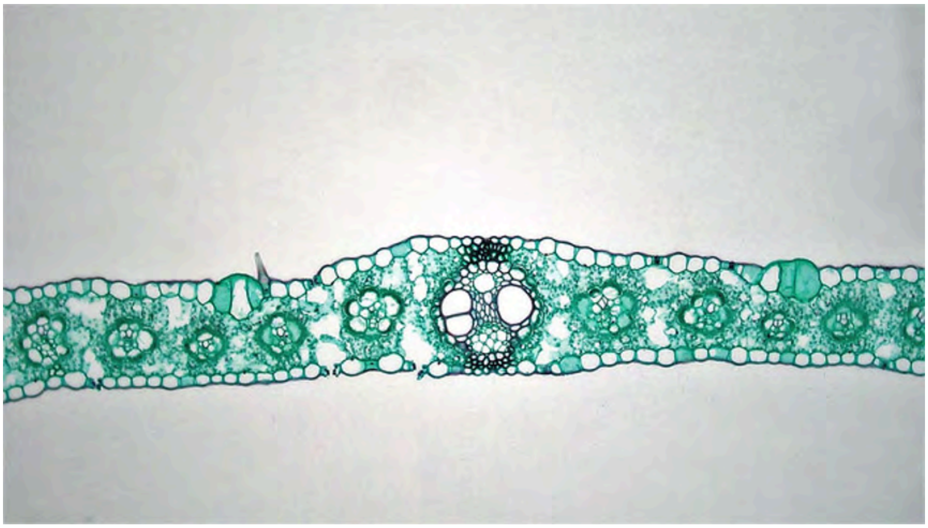

Fig. 10 Cross section of corn leaf showing multiple vascular bundles and a mesophyll that is not split into palisade and spongy components. Also visible are enlarged cells surrounding the vascular bundles (bundle sheath cells) that are significant to their photosynthetic pathway (C4).

- University of Texas Austin Mauseth Lab Table of Contents
- University of Wisconsin Botany Resources
- "See the Plant Kingdom's Hidden Microscopic Wonders" by Michael Greshko. Nice plant cell (and some algal) pictures.
    - https://www.nationalgeographic.com/science/article/photography-plants-cells-diatoms-xylem-phloem-microscope
- Plant Tissues and Organs by the Berkshire Community College Bioscience Image Library. Plant anatomy slides.
    - http://blogs.berkshirecc.edu/bccoer/plants/
- Plant Anatomy Charts by BibliOdyssey. Botanical charts.
    - http://bibliodyssey.blogspot.com/2012/12/plant-anatomy-charts.html

Media Attributions

CHAPTER 9: SECONDARY GROWTH

Fig. 1 Secondary growth makes trees and forests possible. Paleobotanists think that the first forests appeared over 300 million years ago when plants developed the ability to grow wider and, because of this, taller. The first forest plants were members of groups that have no living descendants.

Primary growth extends the root/shoot axis and produces branch roots and shoots. Recall that the width of a root or shoot produced by primary growth is limited because most cells do not expand much in the radial direction. And for most plants cell division in the apical meristem is almost exclusively in a direction that causes more cells in the long axis, with very few divisions that would increase the number of cells across the diameter of the root or shoot. Primary growth allows the plant to get longer and 'bushier' (because of the added branches) but in general it does not allow the roots and shoots to get very wide. This lack of radial growth limits the height of the plant—without thicker stems to resist the combined efforts of wind and gravity, it is hard for a plant to become tall. At the same time, competition for light gives a clear advantage to taller plants. Another problem with only having primary growth is that the source of water (the youngest parts of roots) keeps getting further from the place that needs water, the shoot tips where the leaves are and where new growth occurs. While branch roots, or adventitious roots may be created to shorten the route, the fact still remains that primary growth separates water sources from parts that need water. Additionally, both the conducting cells of the xylem and those of the phloem can fail for a variety of reasons. Because repair of existing cells is often not possible and because primary growth does not allow for the production of replacement conducting cells, the ability to make stems wider, and in particular make them wider with the addition of transport cells and structural support cells, provides some clear advantages, including but not limited to longevity.

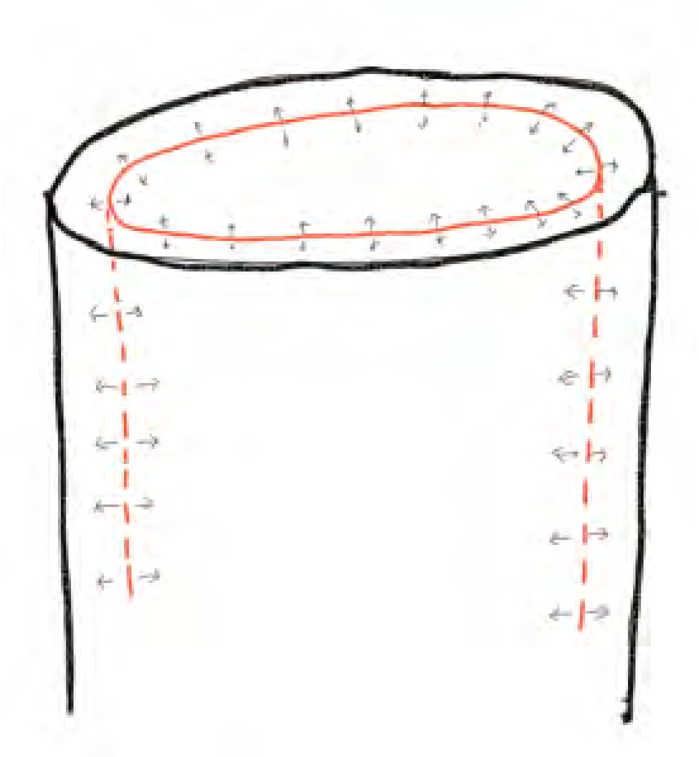

Fig. 2 Lateral meristems appear as circles in cross section but actually exist as cylinders within stems and roots. They produce cells that expand in a radial direction, increasing the girth of the stem/root. There are two lateral meristems, the vascular cambium, shown here, and the cork cambium, which occurs outside of the vascular cambium.

Radial growth is possible in plants that produce what are known as lateral meristems. These meristems are capable of increasing the girth of roots and shoots beyond what is produced by primary growth. Lateral meristems are cylinders of embryonic cells running the entire length of the root/shoot axis. Cell division in these embryonic regions, followed by expansion of the new cells, allows stems and roots to increase in girth in a type of growth defined as secondary growth. Because any radial expansion will rupture the tissues outside of where the growth occurs, the dermal tissue produced in primary growth is going to be split open and a new 'skin' needs to be produced. Consequently, radial growth in roots and stems requires two lateral meristems, one, the vascular cambium, responsible for most of the increase in girth, and one, the cork cambium, responsible for making a new skin. In contrast to the new cells produced by the apical meristems, the cell divisions of the lateral meristems are generally parallel to the surface of the root or shoot and the new cells expand in a radial (inside/outside) direction, thereby increasing the diameter of the stem or root but not changing its length.

TOPICS

- Vascular cambium
    - Secondary xylem and secondary phloem
    - Rays
- Cork cambium
- Evolutionary origins of secondary growth
- Wide and woody monocots

Vascular cambium

The vascular cambium produces new vascular tissue and is responsible for most of the radial expansion of stems and roots. In a cross section of a stem or root the vascular cambium exists as a circle of cells, only a few cells in width. In three dimensions the vascular cambium is a cylinder. Developmentally the vascular cambium originates from undifferentiated cells produced by the apical meristem, located between the xylem and phloem. Recall that the primary growth of stems produces xylem and phloem in bundles that, for all groups other than monocots (which do not exhibit secondary growth), occur in a ring within the stem. To make the vascular cambium a continuous ring requires that cells between the vascular bundles be stimulated to become meristematic and start dividing.

The vascular cambium also develops in roots, again originating from cells located between the xylem and phloem plus additional cells to form a continuous ring.

Secondary xylem and secondary phloem

Cell divisions of the vascular cambium produce xylem and phloem that is called 'secondary' to distinguish it from the primary xylem and phloem produced by the apical meristems. Whether any particular cell produced by the action of the vascular cambium differentiates into secondary phloem or secondary xylem depends on its position, a common factor controlling cellular differentiation. In the simplest case, when a vascular cambium cell divides it produces one cell that remains embryonic (does not expand or differentiate) and one cell that is destined to expand radially and differentiate. If the maturing cell is to the outside of the cell that remains meristematic it is destined to become a phloem cell: a sieve tube member, a parenchyma cell, or a fiber. If the maturing cell is produced to the inside of the cell that remains meristematic it is destined to become a xylem cell: a vessel tube element or a tracheid or a fiber or a parenchyma cell. Most of the new cells produced by the vascular cambium are on the inside thus more secondary xylem is produced than secondary phloem.

The vast majority of the cells produced by the vascular cambium are elongate along the long axis of the stem (in the phloem: fibers, sieve tube elements, and sieve cells; in the xylem: fibers, tracheids, vessel tube members). This elongate shape is not the result of the growth of these cells; any elongation of these cells in the up/down direction is impossible: a woody stem cannot elongate in the middle, only from the tip. The elongate shape of these cells is the result of shape of the cell that divided to produced them. The vascular cambium consists primarily of cells, called fusiform initials, that are elongate and which, after dividing, produce daughter cells that are also elongate. These cells only expand in a radial direction, i.e., they get fatter, not longer, producing a stem that is wider, not taller.

Rays

There are, however, a few cells of the vascular cambium, called ray initials, that are not elongate but are roughly cubical and they produce parenchyma cells that are not elongate in up/down direction but are slightly elongate in a radial direction. The rectangular parenchyma cells produced by ray initials are found in clusters (i.e., a ray initial is likely to have a ray initial above and/or below it in the vascular cambium), and they form struc-

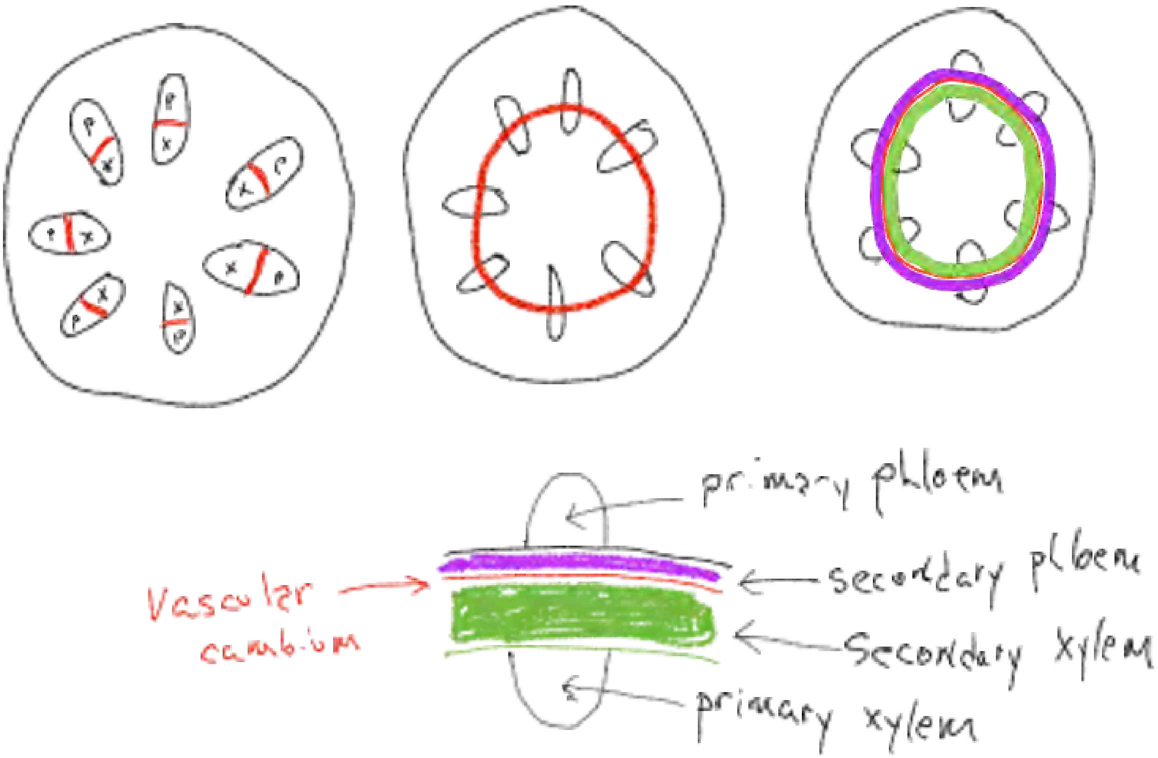

Fig. 3 The development of vascular cambium in stems: upper series: left, embryonic regions (red) appear between primary xylem and primary phloem; center, a complete meristematic ring is formed; right, cell divisions of the vascular cambium produce secondary phloem on the outside and secondary xylem on the inside. Bottom figure, close up of the vascular cambium expanding the region between the primary xylem and primary phloem

tures called rays that run radially from the inside to the outside of the stem. Rays range from one cell in thickness and less than 10 cells in height (i.e., along the longitudinal axis of the root/stem) and invisible with the naked eye, to rays that are hundreds of cells in height and tens of cells in thickness and easily visible with the unaided eye. Rays are produced in both the secondary xylem and secondary phloem and are particularly significant for carbohydrate storage. Carbohydrates transported by the phloem are stored in rays and then can be mobilized when needed. In secondary xylem rays are also significant as being the only living cells present because the other secondary xylem cells (fibers, trachieds and vessel tube elements) all die very shortly after being produced. While the ray cells do not live forever they do live for multiple years, and in addition to carbohydrate storage can respond to pathogens. When they do die, they produce anti-bacterial/anti-fungal compounds that permeate the surrounding tissues, usually darkening it and producing what

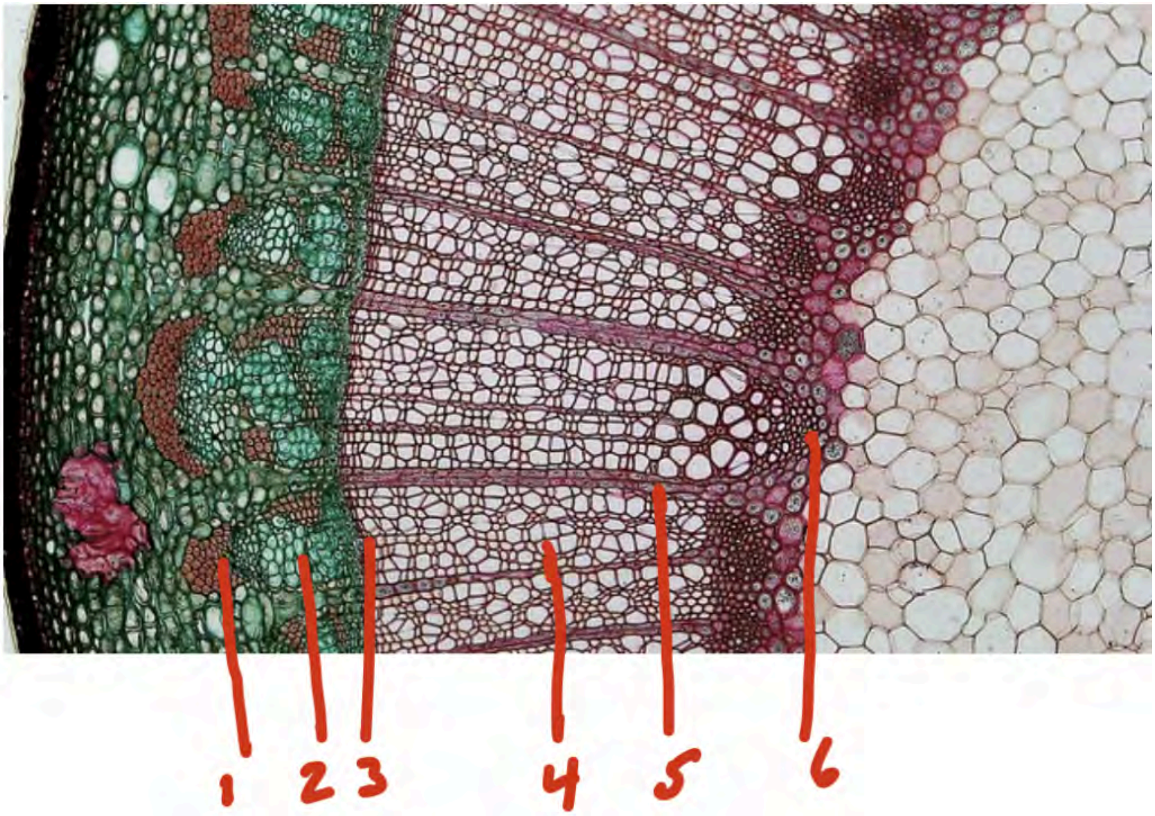

Fig. 4 Cross section of Liriodendron (tulip poplar) stem after one year of growth. 1= primary phloem fibers, 2= primary phloem, 3= vascular cambium, 4= secondary xylem (stained red), 5= secondary xylem ray, 6= primary xylem. Secondary growth (mostly secondary xylem) has separated the primary phloem from the primary xylem. Secondary phloem occurs in a thin band outside the vascular cambium. In this species, rays are produced in between vascular bundles

is described as heartwood in the central part of a woody stem. The cylinder of secondary xylem still with living parenchyma cells is termed sapwood and it generally is lighter in color.

Wood

In almost all plants, the xylem cells that are produced by the vascular cambium, termed secondary xylem, have a substantial secondary cell wall containing lignin and are strongly attached to adjacent cells. Thus, this secondary growth is a tissue that is structurally strong and rigid and we know it as wood, a material that is of much utility because of its mechanical characteristics and also its beauty.

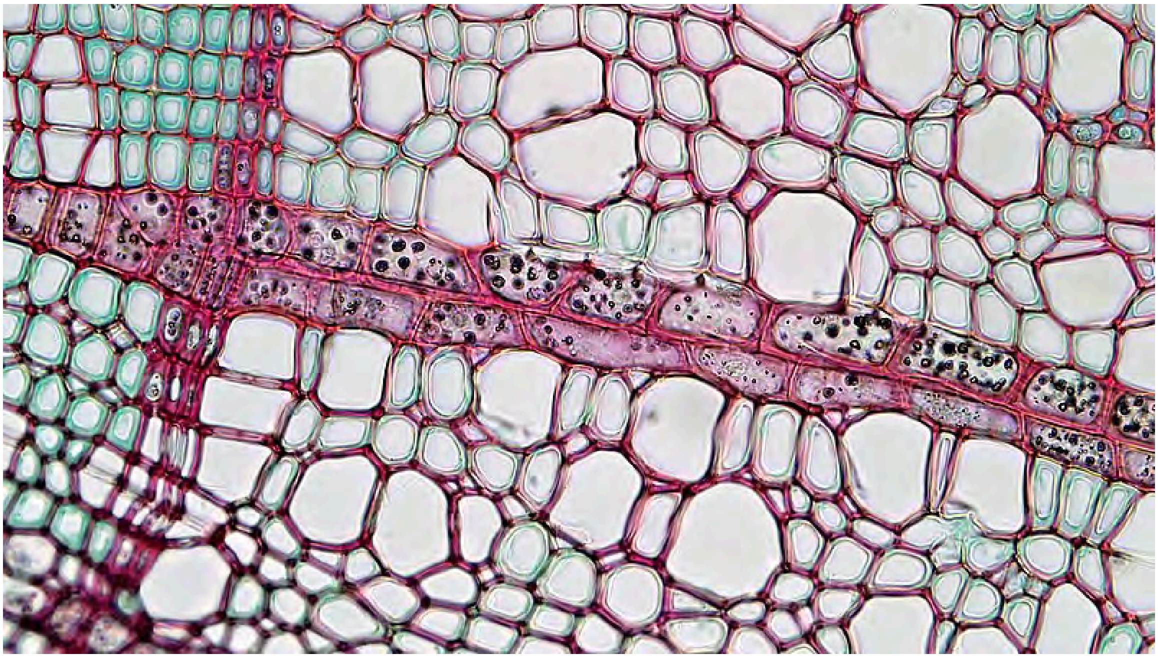

Fig. 5 Xylem ray of secondary xylem seen in cross section. Ray cells are oriented radially (long axis runs inside to outside). Ray cells are parenchyma cells with a secondary cell wall and live for several years after being produced, unlike the fibers, vessels and trachieds, which die soon after being produced.

Annual rings

In many regions of the globe the action of the vascular cambium is seasonal, e.g., only occurring in the spring and early summer. Within the period of cambial activity, often the nature of the xylem cells produced varies in a characteristic way. For instance, it is quite common that the cells produced late in the growth season have smaller lumens and proportionately thicker cell walls than cells produced in the early spring. Another common pattern results from vessel tube elements only being produced in the early spring, so that each spring's growth is easily identified by the presence of large vessel tube elements. Because of such changes, there is generally a substantial contrast between the last cells formed at the end of the growing season and the first cells formed the following spring. This results in a pattern known as 'annual rings' when wood is viewed in cross section. In a radial longitudinal section the growth 'rings' are present as parallel lines.

Fig. 6 Wood, seen in a cross-section (top of block) and a longitudinal radial section (side with tape). In cross section the annual pattern of changing cell characteristics creates 'annual rings'. Seen in longitudinal sections the yearly pattern is visible as parallel lines.

Periderm

As the new cells produced from the vascular cambium expand, the strength of the secondary xylem is enough to prevent the older xylem to the inside from being crushed. Instead, the expansion of new xylem cells pushes outward and crushes most of the cells to the outside of the vascular cambium. Newly produced secondary phloem cells, as long as they are alive, can resist being crushed, as can highly lignified fiber cells which often are present, but most other cells are crushed by the outward expansion caused by growth of the cells produced by the vascular cambium. Additionally, this outward growth, ruptures the epidermis, the original 'skin' of the stem that was produced by the apical meristem.

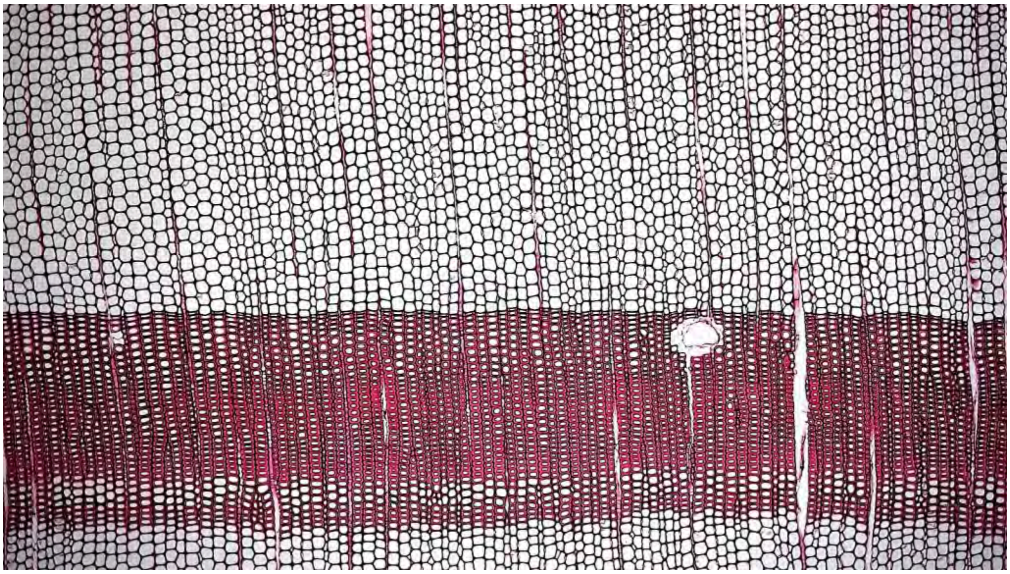

Fig. 7 Growth ring seen in cross section in pine. Almost all the cells that are visible are tracheids but the cells formed late in the growing season have much thicker cell walls, creating a darker band (seen here because of staining, but also visible without staining). Rays, made of parenchyma cells, are visible as horizontal lines running from top to bottom on the slide, that is radially (outside/inside) in the actual stem. Also visible are one large and one small resin duct.

Plants with secondary growth produce a lateral meristem called the cork cambium that produces cells that form a new skin that is called the periderm.

Unlike the vascular cambium, the cork cambium usually is not a continuous cylinder. Instead, it generally exists as a series of arcs that collectively form a ring. Like the vascular cambium, the cork cambium produces different cells to the inside and outside; the cells produced to the outside are short-lived and have cells walls that are impregnated with suberin, a waxy waterproof compound. The cells that are produced to the inside are parenchyma cells and live for a longer time, usually several years. This is significant because the cells of the cork cambium, unlike those of the vascular cambium and apical meristems, are not long-lived; they die within a few years. And a new cork cambium forms to the interior, originating in the parenchyma cells that were formed to the inside of the older cork cambium. In shoots, the initial cork cambium originates within the cortex and subsequent cork cambia originate from derivatives of earlier ones. In roots, the cork cambium originates from activity of the pericycle and again reforms inward from parenchyma cells produced by earlier cork cambia. Thus, through time the cork cambium

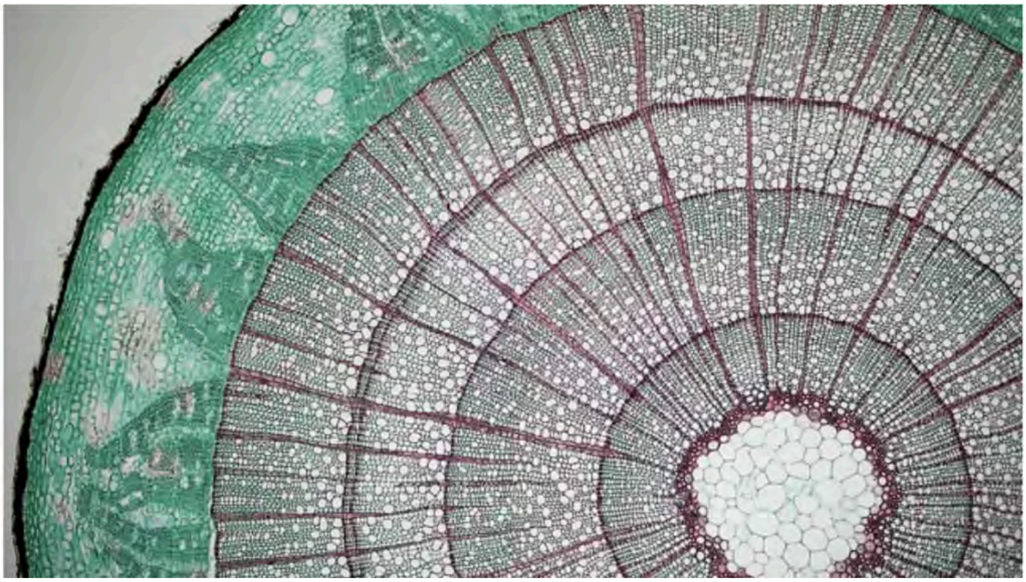

Fig. 8 Tulip poplar (Liriodendron) after 4 years of growth. Annual growth rings are visible and in this species, as in pine, are the result of smaller diameter/ thicker walled cells being produced late in the growth season and larger diameter cells being produced early in a growth season. Large diameter vessel tube members are common in the xylem. Xylem rays are obvious and note that more rays are present in the outer rings than the inner growth rings.

moves inward while the whole stem is growing outward because of the action of the vascular cambium. The cells that the cork cambium produces, as well as the secondary phloem cells, are continually being compressed by expansion from within; these tissues are also being split apart as the trunk's girth increases.

In general, the cells produced to the outside by the cork cambium are closely packed and have no cracks or air spaces, as was the case for the original epidermis. But the cork cambium regularly produces areas called lenticels where there are cracks and fissures. It is thought that lenticels are significant in allowing oxygen penetration into the stem. At the same time, lenticels provide a space to allow water to escape and pathogens to enter. This again highlights the fact that while some aspects of life are favored by isolation from the outside environment, other aspects of life require connection with the outside environment.

In woody stems the material to the inside of the vascular cambium (all of it secondary xylem, ignoring the tiny bit of primary xylem and pith that may remain in the center of the stem) is called wood. All the material outside of the vascular cambium–secondary

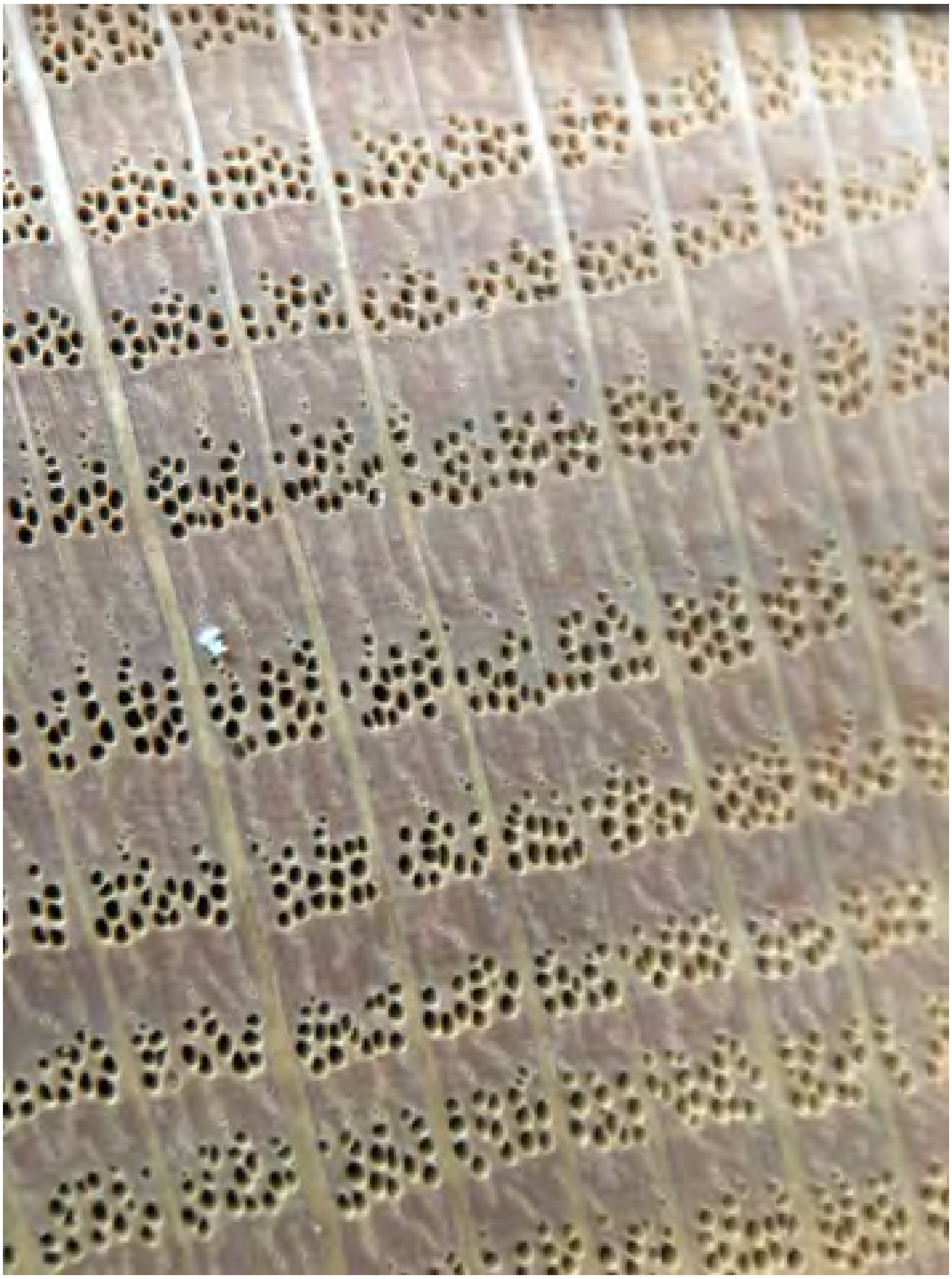

Fig. 9 Cross section of red oak showing growth rings, in this species defined by the springtime production of large diameter vessels contrasting with the late spring production of vessel-free wood. Also visible are extremely large rays, composed of parenchyma cells.

Fig. 10 White ash bark, a new skin created by the actions of the cork cambium, a lateral meristem that occurs to the outside of the vascular cambium

phloem, the cork cambium and the products of the activity of one-to-many cork cambia, plus tiny bits of primary phloem, cortex and epidermis, are collectively called bark. The look of bark varies tremendously due to differences in behavior of the cork cambium.

Fig. 11 Jeffrey pine bark

Evolutionary origins of secondary growth

Secondary growth and along with it, woody, tree-like plants has apparently originated multiple times: once in a group containing present day clubmosses, once in a group containing present day horsetails; at least once and probably several times in extinct groups of plants ('seed ferns') that are not grouped with any of the existing plants with seeds, and once in the group that produced all extant seed plants (flowering plants, conifers, cycads, ginkgo and gnetophytes). Although secondary growth appeared several times, it has also

Fig. 12 While many trees have furrowed bark, as illustrated by the white ash shown above, others produce bark of scales or plates as illustrated by Jeffery Pine and American Sycamore, shown above. For most trees, the 'look' of bark often changes as trees older and larger

disappeared multiple times: no extant clubmosses or horsetails show secondary growth and many seed plants, in particular many flowering plants, show no secondary growth. The extinct woody forms were highly significant in the past, in particular in the late Paleozoic (350-250 million years ago) when they formed extensive forests whose productivity is utilized still through coal and gas deposits.

Wide and woody monocots!

If wood is defined as secondary xylem and monocots have no secondary growth then monocots have no wood—but this does not prevent some monocots from being woody, that is possessing lignified tissues. Primary growth often does produce lignified cells, but usually not extensive tissues that are lignified. In most primary growth there are relatively few woody cells, but in some monocots (e.g., bamboo, which is a grass) primary tissues can be quite woody. Also, because monocots lack secondary growth and because primary growth is generally limited in a radial direction, monocots are generally narrow. However, some monocots (e.g., palms, joshua tree) show prolonged radial expansion in primary growth and consequently can produce stems of substantial girth.

Fig. 13 Joshua tree—a woody monocot that grows in parts of Southern California (visit Joshua Tree National Monument!), Arizona, Nevada and Utah.

Further Reading and Viewing

- The Structure of Tree Bark by NatureTech. Bark anatomy images.
    - https://cronodon.com/NatureTech/Bark.html
- “Botany Within Your Reach – 1. Corks” by The Phytophactor. Cork.

Fig. 14 Date palms. Palms are a large monocot family and most members are woody. Dates are one of the oldest cultivated plants, going back to at least 5000 B.C.

    - http://phytophactor.fieldofscience.com/2015/10/botany-within-your-reach-1-corks.html
- *Arnoldia*, The Magazine of the Arnold Arboretum. Cork (go to page 74).
    - http://arnoldia.arboretum.harvard.edu/pdf/issues/2016-74-1-Arnoldia.pdf
- "Modifications to Cactus Wood" by Mauseth Research: Cacti. Xylem modification for water storage in cacti.
    - http://www.sbs.utexas.edu/mauseth/researchoncacti/Wood.htm
- "The first forests" by Sedeer el-Showk. Carboniferous forests 300-400 million years ago.

    - https://www.nature.com/scitable/blog/accumulating-glitches/the_first_forests/
- "Plants Are Cool, Too! Episode 2: Fossilized Forests!" by PlantsAreCoolToo. Cretaceous forests 15 million years ago.
    - https://www.youtube.com/watch?v=YfRXDbtkEio

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CHAPTER 10: VASCULAR PLANT FORM

One of the striking features of plants is their diversity in form. This is nicely demonstrated with a visit to a greenhouse but can also be seen by looking at outdoor plants, both in native habitats and in gardens. At the same time, all seed plants are fundamentally the same in form and follow a pattern depicted in the Fig. 1 and described as being 'modular' and 'recursive'. What accounts for the apparent diversity in plant form when they are basically put together the same way? There are six key areas of variation that influence the above-ground form of flowering plants and these are listed below and are main sections of this chapter. While the bulk of the chapter deals with flowering plants the form of non-flowering seed plants and vascular plants without seeds is also discussed.

TOPICS

- Flowering plants
    - Factors affecting above ground form
        - Internode length
        - Branching frequency
        - Variation in the size, shape and orientation of leaves
        - Direction of growth of stems and branches
        - Presence or lack of secondary growth
        - Loss of parts (leaves and branches)
    - Below-ground form
- Form of non-flowering seed plants
- Form of vascular plants without seeds

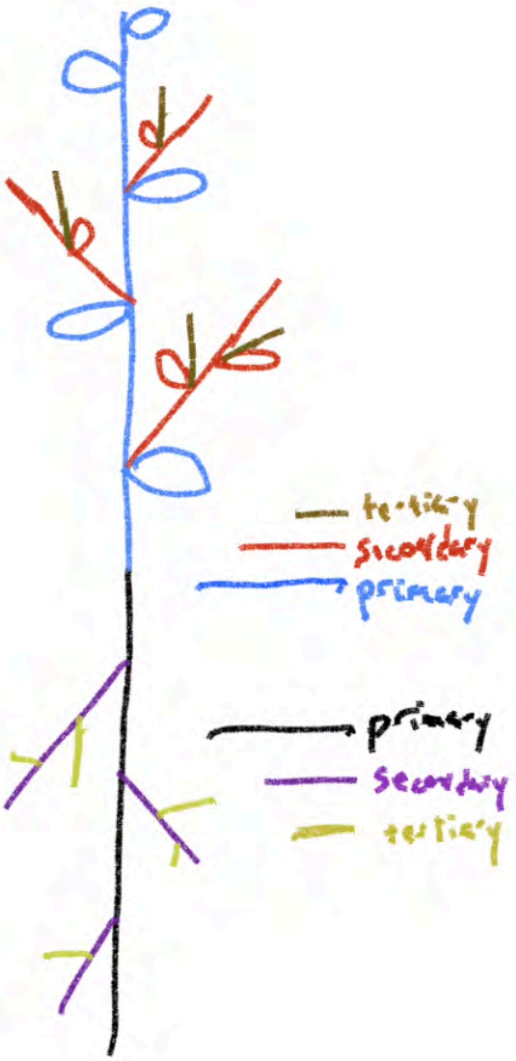

Fig. 1 The modular and recursive nature of plant form

Factors affecting flowering plant form I: Internode length

Fig. 2a Dandelion rosette. All the leaves are connected to a very short stem.

Fig. 2b Amaryllis has a similar growth pattern although its leaves are more erect

Do dandelions have stems (Fig. 2a)? They must, because they have leaves and leaves are always attached to stems, but dandelion stems certainly are not very evident because they are so very short. You could say that dandelions are 'vertically challenged' and as a result, their leaves are very closely clustered, forming what is known as a rosette. Rosettes are a common plant life form and result from the fact that the distance between individual leaves is extremely short, making it appear that there is no stem. While the leaves of dandelion typically run horizontally, parallel to the ground, some plants, like Amaryllis (Fig. 2b) also have very short stems but with leaves that are oriented more vertically. Dandelions live for a number of years and never produce a recognizable stem, although they do produce branches that are flowering stalks. Other plants, including both agricultural crops (e.g., carrots, beets, cabbage, turnip) and common weeds (e.g., mullen, burdock, 'wild' carrot, garlic mustard) are biennials. They form a rosette in their first growth season (Fig. 3) and in their second year of growth they 'bolt' as the stem produces much longer internodes to produces a more 'normal-looking', elongate stem, upon which are born flowers (Fig. 4). A small number of plants, including the one used to make tequila, are a rosette for multiple years, maybe 7-10, before the stem 'bolts.'

Fig. 3 Mullen, a common weed, showing its rosette form after one year of growth

What determines internode length?

Recall that leaves and stem material are produced in the embryonic region called the apical meristem at the very tip of stems. In this region new cells are produced by mitosis and the cells are organized as new stem material and as leaf primordia, outgrowths from the stem that grow and produce the structures that we know of as leaves. In dandelions and other rosette plants, the distance between leaves is very short. As mentioned above, internode length may vary with age, or more specifically vary with environmental factors that coordinate with age, in which case plant form may drastically change with age (see images of mullen, above). Internodes produced in the first season of growth are very short, those in the second season of growth, after the plant has been exposed to a cold period, are a great deal longer.

Fig. 4 Mullen, showing its form after a second year of growth—the stem has bolted an the internode length (the distance between leaves) if much greater than in the first year of growth

Fig. 5 Many root crops, including turnip, are biennials harvested at the end of the summer after planting. If allowed to overwinter they will bolt, producing flowers and seeds but reducing the amount and quality of the root material.

What are the consequences of producing rosettes as opposed to stems with leaves more widely spaced (Fig. 4, 6)? One factor is microclimate, rosette leaves, if they are close to the ground, may be in a very different environment that leaves that are elevated. A second factor is self-shading of leaves, although this is influenced by several other factors including the size of the leaves and their distribution on the stem. Also, plants with short stems and clustered leaves are also more likely to be shaded from above because the stem is not carrying leaves upwards and potentially above the neighboring plants. At the same time, growing upward exposes the plant to a number of problems that are not present if it stays low to the ground. One is mechanical. Growing upward requires stems to be able to resist the combined effects of gravity and wind. Another problem is that an elevated shoot apical meristem becomes more apparent and vulnerable, at least to some herbivores. The loss of the terminal apical meristem is particularly damaging because it eliminates the source of growth, although growth may continue by the activation/stimulation of lateral buds. The accessibility of the stem tip depends on the herbivore—something big, and especially something big with a big nose (think deer!) might have a hard time nipping the tip of a dandelion, but have no difficulty nipping the tip of a tomato plant. But for smaller herbivores like insects, stem tips are available for both short and tall plants.

Factors affecting flowering plant form II: Branching frequency

Note the images of Diffenbachia and cabbage (Fig 6). Like dandelion, they have no branches. 'Typical' plants with modular growth and a dendritic form have branches and the branches have branches. This repetitive pattern is one of the familiar aspects of plant form that makes them so appealing as an artistic model. However, some plants, like dandelion, Diffenbachia and cabbage, have no branches, there is just one axis to the plant, and this gives them, and other plants, a distinct look.

Fig. 6 Impact of internode distance. The top image of a Diffenbachia stem shows the widely spaced-out leaf scars about 3 cm apart. The bottom image of cabbage shows a very distinctive rosette form.

Recall that branches result from the fact that as the shoot apical meristem elongates and produces embryonic leaves it also produces a potential branch, called a branch primordium or bud primordium in the 'axil' of each leaf, placed just above where the leaf attaches to the stem. A branch primordium is a replica of the shoot apex, an embryonic shoot capable of elongating and producing a shoot with leaves upon it. All that needs to happen to produce a branch is that the branch primordium be stimulated to start growing. Branch upon branch upon branch can be produced as each shoot in turn produces leaves that have branch shoots appear from their base. This does not happen in dandelion and in many other plants, both rosette and non-rosette. In such plants, growth occurs solely from the original shoot, although many of them will form branches if the original shoot apical meristem is removed. In dandelion, although branch primordia are produced, they are only activated to grow after being transformed into flower primodia (technically inflorescence primordia). Thus, when activated, they produce not a branch but a leafless dandelion 'flower' (technically it is an inflorescence, a cluster of flowers, not a single flower). This type of growth pattern is also seen in Aloe and a number of other rosette plants.

Frequently one may see a cluster of dandelion plants together, which might appear like a group of branches. However, these are usually formed when the root of a dandelion is broken off (usually as the result of someone trying to pull it up). The root that remains is stimulated to form new (adventitious) shoots. Often what happens is that multiple shoots are produced by a single root, forming in a cluster of stems. Each of them originated separately from the root tissue, so what you see is not a cluster of branches but instead a cluster of adventitious shoots.

Often branches don't look like branches

In grasses and many other plants, the branches often aren't recognized as such. Branches often appear at the base of the plant when branch (bud) primordia of the lowest leaves are stimulated to grow in one of three ways (Fig. 7 and 8): (1) extending vertically, producing a leafy stem called a tiller in grasses (on non-grasses this sometimes called a 'sucker' or a 'pup') that is basically the same in structure and function as the original stem; (2) extending horizontally and above-ground, producing only rudimentary leaves with very reduced blades and elongate sheaths. These horizontal stems (branches) are called stolons; (3) extending horizontally but below ground, again producing only rudimentary leaves. These horizontal underground stems (branches) are called rhizomes. Stolons and rhizomes are sometimes considered a means of reproduction; they can also be thought of as providing mobility. Eventually both produce vertical, photosynthetic stems that originate from the bud primordia associated with the rudimentary leaves. A number of plants (e.g., goldenrods, asters) that appear to exist as vertical stems are actually a group of vertical branches all connected to a below-ground stem (rhizome).

Fig. 7 Rhizomes (horizontal below-ground stems) of goldenrod.

Factors affecting flowering plant form III: Variation in the size, shape and orientation of leaves

In contrast to dandelions, which look like they don't have a stem when they actually do, grasses (and a number of other plants, including bananas) possess something that looks like a stem but actually isn't. The 'trunk' of a banana plant is actually a cluster of leaf bases tightly wound (Fig. 9) around each other and called a 'pseudostem' because it has the appearance of a stem. Bananas and grasses are monocots, a group that includes orchids and a number of other flowering plants. One feature commonly found in monocots, and specifically in banana and grasses, is a leaf with two main parts (Fig. 10). One part is called the blade; this is typically flattened and extends outward from the plant and is often roughly horizontal to the ground. This is the part that most people recognize as a leaf. If you follow the blade back to the rest of the plant, it abruptly narrows (a great deal in banana, less so in grasses) to a section of the leaf that is vertically oriented and cylindric. This part of the leaf is called the sheath. Early in the growth of both grasses and bananas the structure that looks like a stem is actually just multiple leaf sheaths extending upward from a very short stem, like a dandelion stem.

While dandelion leaves are generally horizontally displayed, in grasses the bases of the leaves (i.e., the sheaths) are vertical. The more recently produced leaf sheaths are located inside of older ones and they collectively form a structure that seems like a stem. In grasses

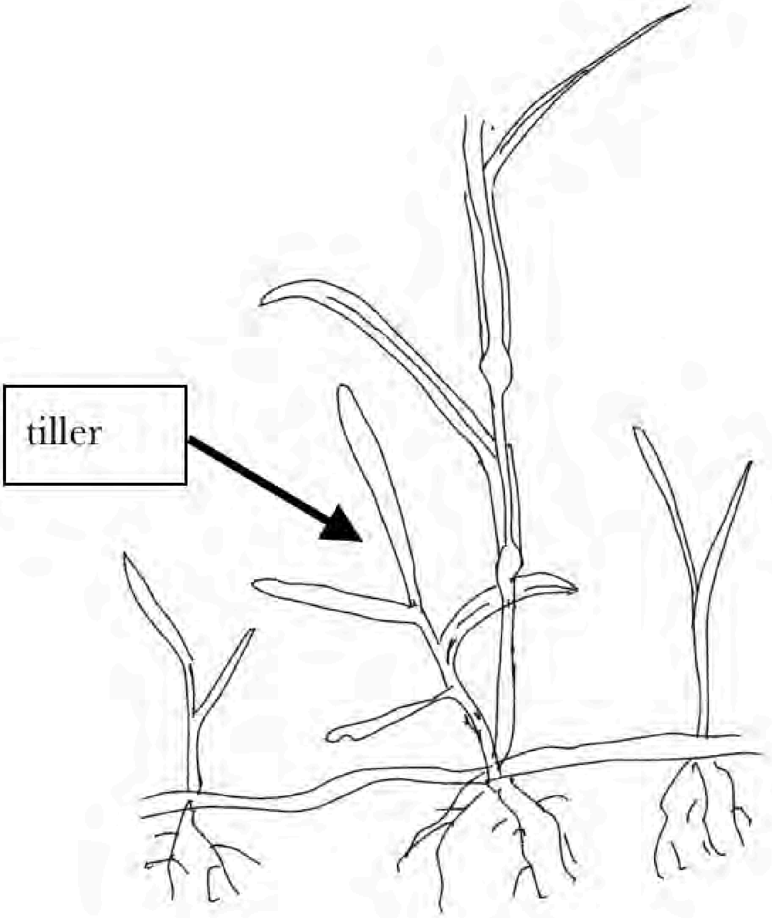

Fig. 8 Grass plants commonly produce branches that are called tillers and generally originate from the branch primordia produced along with the earliest leaves. Grasses also produce horizontal running branches that are called stolons if they are above-ground and rhizomes if they are below-ground

and bananas, the stem eventually elongates, the result of very large increase internode length of the youngest leaves. If one were to measure the internode lengths of the first 10 leaves of a grass they might be (in mm and starting with the first leaf produced): 1, 1, 1, 1, 1, 10, 50, 100, 150, 200. After producing six leaves the stem is 6 mm in height, after producing four more leaves it is 506 mm in height. The stem 'telescopes' upward inside of the sheaths, and often exposes the uppermost nodes, the actual point attachment of leaves to the stem. When the stem of a grass or a banana elongates, it signals the end of the life of that stem and its associated leaves. An inflorescence is produced at the end of the stem, with flowers that develop into fruits. Nutrients are mobilized from the leaves to

Fig. 9 Banana plant. The vertical structure is not a stem but instead a cylindrical group of leaf sheaths oriented vertically.

the developing seeds and fruits. As noted above, many grasses and bananas branch from the base and this may perpetuate the organism even if the original stem flowers, senesces and dies.

Dandelion, grass and banana leaves just scratch the surface of variation in leaf form. Palm leaves may be up to 25 m in length and duckweed leaves are about 3 mm (Fig. 11, 12). Most leaves are flat but some are thick (succulent) and may be round and bead like (Fig. 13). Some leaves are appressed to the stem (Fig. 14). Leaves can be lobed and toothed in a variety of ways. Many leaves are dissected into parts sometimes in such ways that it isn't obvious whether one is looking at a leaf or a leaflet (Fig. 15).

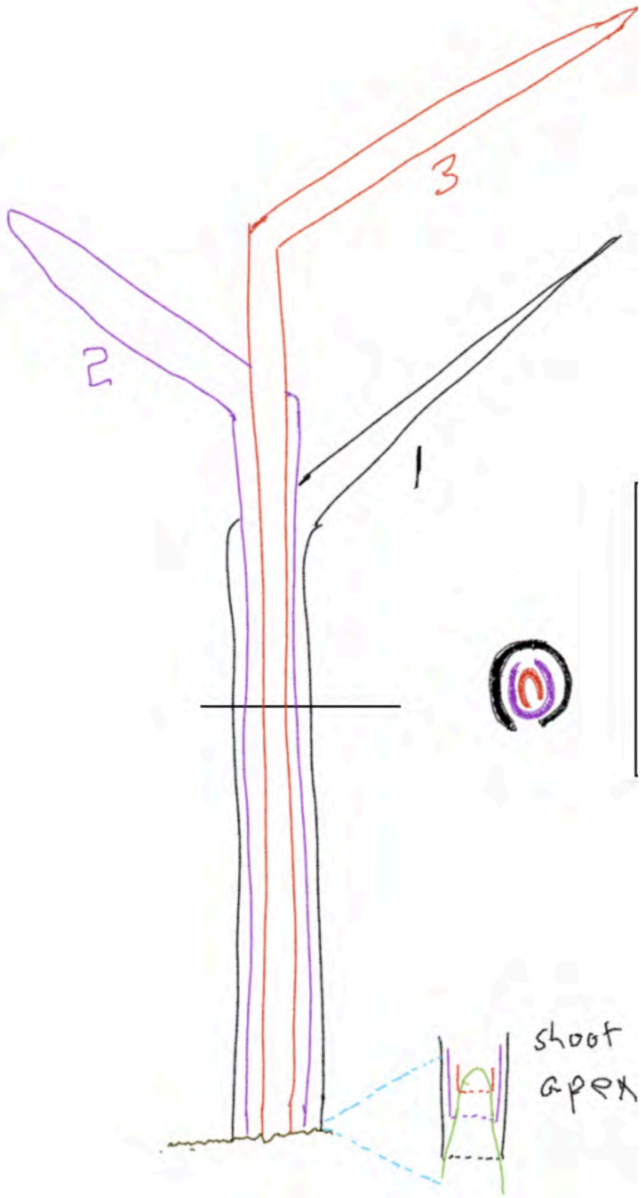

Fig. 10 Longitudinal view of a grass pseudostem, showing three grass leaves elongating from a very short stem, shown in expanded view in the bottom right. Each leaf has a vertically oriented sheath and a more horizontal blade. Newer leaves occur inside of older ones.

Fig. 11 Duckweed, one of the smallest flowering plants, with leaves less than 3 mm. It floats on the surface of ponds and streams.

Factors affecting flowering plant form IV: The direction of growth of stems and branches: vertical, horizontal or something in between

Although most familiar plants have a main stem and branches that grow upwards, this is not always the case. As mentioned earlier, branches may be hidden below ground because they do not grow vertically but instead extend horizontally below the ground. As a result, multiple stems rising from the ground may not be separate plants but actually be branches that extend vertically from a main stem that is running horizontally below ground. While most familiar plants have stems that grow upwards, the exact angles vary and some run horizontally, producing what is known a 'prostrate' growth form seen in partridge berry and strawberry below (Fig. 16-17)

Some plants (pin oak) have branches that extend roughly 90 degrees from a vertically oriented stem, i.e., they extend horizontally. Other plants have branches that run more vertically, perhaps at an angle of 45 degrees from the main stem.

Fig. 12 Coconut palm has leaves that typically are several meters long; some palms have leaves over 20 m long.

It is also quite common that orientation changes, generally in a controlled manner. In the example of grasses or banana described above the original stem is vertical but 1st order branches may run horizontally (if they are rhizomes or stolons) and third order branches (i.e., branches off of the stolon/rhizome) again run vertically. Thus plants vary in the way that the original stem and its branches are oriented, both within a plant and between different species.

Fig. 13 An example of leaf variation: string of pearl leaves are almost spherical.

Factors affecting flowering plant form V: whether or not the stems and branches exhibit secondary (generally woody) growth

Secondary growth allows plants to become wider and taller. While most people associate woodiness with trees, two other plant forms are woody: ‘Shrubs’ have no rigid definition but are tree-like but show limited growth in height but abundant branching (Fig. 18). Most vines (lianas) are woody and have an interesting cellular nature that lacks scle-

Fig. 14 The leaves of tamarix are small and scale-like, forming what looks to be a photosynthetic stem. A similar form is found in junipers.

renchyma fibers and consists almost entirely of water conducting cells with relatively thin secondary walls. This is possible because they utilize the structure of other plants to provide support. Consequently vine wood has a low density and rigidity when compared to tree wood.

Factors affecting flowering plant form VI: shedding of plant parts

A final factor that impacts the 'look' of plants is the shedding of plant parts. Most plants discard pieces as they grow. Generally, the discarded parts are leaves but branches may also be shed (Fig. 19-20). The loss of parts may be synchronous, as it is with most deciduous trees, but other plants may shed parts continuously. Plant structure is dynamic and

Fig. 15 A single leaf of a box elder tree with five leaflets. Where the leaf attaches to the stem there is an axillary bud but the individual leaflets have none.

parts are not solely being added, they are generally also being removed. These changes are often not noticed, except by gardeners/landscapers, because the changes are relatively slow, the new growth looks just like the old growth and the pieces shed are matched by pieces added. For most plants both the growth and the shedding are usually sporadic, occurring in spurts with inactivity between them.

Below-ground form

Root systems also have a variety of forms but, obviously, it is harder to see the form of root systems. One distinction that is often cited is the distinction between a taproot system, where the embryonic root (the one formed in the seed) persists and becomes the main trunk of the root system that connects with the stem. Note that a carrot is perhaps not the best example of this, even though it is often used, because in carrot the root is performing a carbohydrate storage function, something that does not have to be the case for plants with taproots. In contrast to taproots, many plants have a root system that forms from adventitious roots that are produced off of stem/rhizome/stolon and do not have

Fig. 16 Partridge berry

a dominant, primary root. Fibrous root systems may only have a few levels of branching whereas taproots typically have more, especially as they age. The primary function of roots is to acquire water and the pattern of water distribution is significant to root system form, specifically lateral spread vs. vertical spread. Alfalfa roots are known to penetrate 15 meters down in order to obtain water. On the other hand, most cactus roots spread extensively but do not penetrate deep in the soil. Cactus also commonly produce roots quickly after a rain and then rapidly loose them (i.e., they senesce and die) as the soil dries. All plants, not just cactus, shed root structure; similar to the situation aboveground, root structure is dynamic, with pieces continually being added and shed.

Form of seed plants without flowers

There are four groups of seed plants that lack flowers. Representatives of most of these groups are present in the 'Organisms to Know' section and are highly in blue.

Fig. 17 Strawberry plants

The ginkgophyte group only has a single species, ginkgo, which in form is typical of a deciduous (angiosperm) tree (Fig. 21), except that the leaves are unusual, being fan shaped with bifurcating parallel veins. Ginkgo also has ‘spur shoots’ (‘short shoots’), branches with a very short internode distance and consequently leaves clustered very close together. Spur shoots make identification of ginkgo easy during the winter months.

Fig. 18 Sagebrush, a common shrub of the western US.

Fig. 19 Note that in most forests branches are not present close to the ground. There had been branches but they have been shed.

Fig. 20 This is what is known as a 'wolf tree' one that initially grew in an open area and did not shed its lower branches.

A second group are the conifers, including pines, hemlock, redwoods and juniper. For most, but not all, conifers the leaves are present on the plant for more than a year, making the tree 'evergreen'. Many conifers have needle-like leaves although some have small, scale-like leaves that overlap each other, producing what are essentially photosynthetic twigs which are shed as a unit after senescence. Most conifers have tree-like forms (Fig. 22) with a fairly rigid branching pattern that produces the characteristic 'Christmas tree' shape. There are a few conifers that are shrubs, primarily in the yew-family and some in the cedar family.

Fig. 21 Until one looks closely at the leaves, ginkgo trees appear like typical angiosperm trees. They are widely planted, often in urban areas where they do well but they do not reproduce in the wild.

A third group of non-flowering seed plants are the cycads, most of whom have a distinct form, generally with an unbranched, short stem axis and relatively long pinnately compound leaves (Fig. 23). These stem and leaf features are found in two other groups with which cycads may be confused: tree ferns (see below) and palms (a group of flowering plants). Distinguishing between the three groups is easy if reproductive structures are present: palms produce flowers and seeds; cycads have no flowers but produce seeds in a type of cone; and tree ferns produce no seeds but have clusters of spores visible on the leaves).

The fourth group of seed plants lacking flowers, the Gnetum group, has only three genera, each with a very distinctive forms *Welwitchia* (there is only one species and it lives in southern Africa) is by far the most bizarre of the group (Fig. 24). It produces only two leaves which grow from the base and elongate to form long, strap-like leaves that often shred longitudinally so it appears that there are more than two leaves. The apical meristem dies after these two leaves are produced and hence there is no stem. Reproductive

Fig. 22 These are Blue Spruce showing a typical conifer form. Conifers do particularly well in montane habitats and also at high latitudes (the boreal zone).

Fig. 23 Cycads showing their typical elongate pinnately compound leaf. Sometimes the trunk can grow to a meter or two. There is limited secondary growth and branching is rare.

structures are produced by the ‘crown’ at the base of the leaves and plants are either male or female.

Fig. 24 Welwtichia mirabilis. The specific epithet (mirabilis) expresses the wonder of its discoverer who is quoted as saying "[I] could do nothing but kneel down and gaze at it, half in fear lest a touch should prove it a figment of the imagination."

A second genus in the Gnetophyta groups is *Ephedra* (roughly 70 species), whose members are highly branched shrubs with photosynthetic stems and small leaves that are soon shed (Fig. 25).

Fig. 25 Ephedra is a leaf-less, many branched shrub that grows primarily in arid regions. As can be seen the stems are green and photosynthetic.

The final Gnetophyte genus is *Gnetum* (roughly 40 species) which has species that look the most 'normal' (i.e., like many flowering plants) of the Gnetophyte group, with 'normal' leaves (determinate structures with a petiole and a flattened blade) occurring on forms that could be described as small trees, shrubs or vines.

Form of vascular plants without seeds

We will consider three groups of plants that possess vascular tissue but do not produce seeds. Again, note that representatives of these groups are described in the 'organisms to know' section.

The least diverse and easiest to identify are the horsetails (*Equisetum*). There are less than 20 species and all look similar and have a distinctive form (Fig. 26-27). They have below-ground rhizomes that produce erect ribbed and 'jointed' stems with whorls of minute, scale-like leaves occurring at the joints. Some species vary from forms with and without whorls of branches, while other species are strictly unbranched or strictly branched. Aall living species show no secondary growth bit relatives in the Paleozoic era, 300 million years ago, had tree-like forms with secondary growth and stems up to 30 m high.

Fig. 26 Horsetail— three stems showing the small, yellow scale-like leaves.

Most members of the clubmoss group have a typical plant 'stem with leaves' structure. The stems and roots are vascularized and the leaves have a single vascular trace (vein). Probably because of this, leaves are small and often appressed to the stem, giving the plants a 'moss' look, although the plants and leaves are bigger than almost all mosses. Although representatives of the group used to possess secondary growth and tree-like forms, all forms present now are small, usually less than 20 cm tall, and non-woody (Fig.

Fig. 27 A branched form of horsetail emerging from a rhizome.

28-29). Most species have stolons or rhizomes from which vertical branches appear. These may or may not branch. One genus in the group (*Isoetes*, the quillworts) has a very different form. It is an aquatic, unbranched plant with very short internodes, forming rosettes with awl-shaped leaves that may be 10 cm or more in length (Fig. 30).

Fig. 28 A common forest clubmoss in northeastern forests. The yellow cylindrical structure (the 'club') is where it produces spores.

Fig. 29 The clubmoss species shown above is sometimes called 'ground cedar' because its small, scale-like leaves are appressed to the stem, comparable to many cedars, trees in the conifer group.

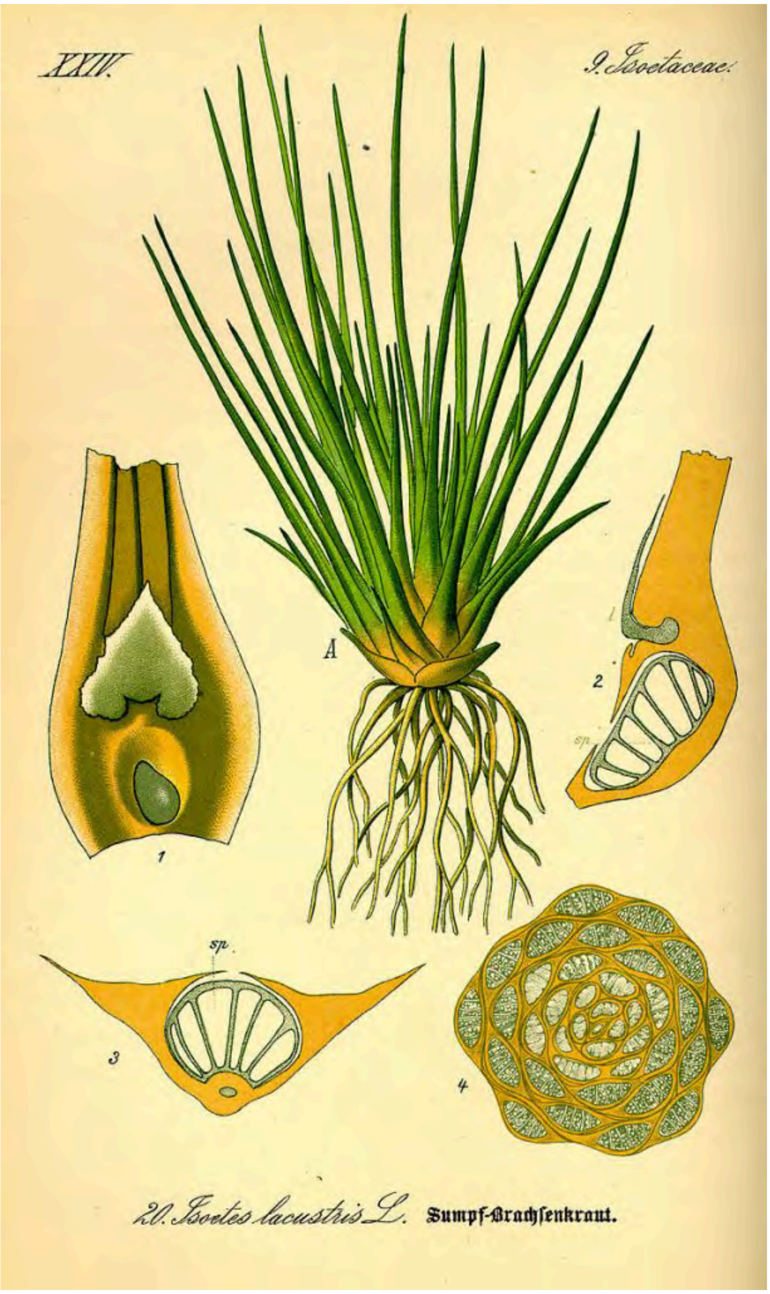

Fig. 30 A quillwort, an aquatic genus in the clubmoss group with a very different structure.

The fern group is by far the largest group of vascular plants without seeds and it is the group with the most diversity in form, although the majority of ferns seen in north temperate habits are generally uniform in structure with an underground, woody (i.e. showing secondary growth) rhizome from which leaves arise (see sensitive fern, wood fern). Thus, when you see a fern you are generally seeing a group of leaves (fronds) that originate in a below-ground woody rhizome. Some species have rhizomes that are short and vertical and produce a circular cluster of leaves resulting in an urn-shaped display (Fig. 31). Other species have rhizomes that run strictly horizontally and producing a more uniform 'patch' of ferns (Fig. 32). the leaves can be more or less dense depending upon the pattern of leaf production along the rhizome.

Fig. 31 A cinnamon fern, showing an urn-shaped cluster of leaves

Fig. 32 Hay-scented ferns typically have leaves thet are not clustered.

In the tropics there are some ferns that are tree-like with an above ground stem vertically oriented stem that may be 2 m in height producing plants that superficially resemble palms and cycads. There also are aquatic ferns that are small and float on the surface of water (Fig. 33), comparable to growth of duckweed, which is a flowering plant. A final example of the diversity in fern form is *Marsilea*, a fern that resembles four-leaf clovers (Fig. 34) and has a very interesting pattern of sex discussed in Chapter 13.

Fig. 33 An aquatic fern, Azolla, which floats on the water surface and has leaves about 1 mm in size that sometimes house nitrogen fixing cyanobacteria.

Fig. 34 Two ferns that commonly grown in aquatic habitats, sometimes with leaves floating on the surface.

Further Reading and Viewing

- Fern Structure by the U.S. Forest Service. An excellent description of fern form.
    - https://www.fs.usda.gov/wildflowers/beauty/ferns/structure.shtml
- "Intriguing Lime-Green Blobs Appear In The Andes Mountains. Are They Alive?" by Robert Krulwich. Llareta, an amazing plant.
    - https://www.npr.org/sections/krulwich/2014/05/16/313122134/intriguing-lime-green-blobs-appear-in-the-andes-mountains-are-they-alive
- "Maximum rooting depth of vegetation types at the global scale" by J. Canadell et al.
    - https://link.springer.com/article/10.1007/BF00329030

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CHAPTER 11: REPRODUCTION AND SEX

Reproduction is an essential component of organisms—organisms are 'living things' that can replicate themselves, i.e., reproduce. While some other 'living things' (e.g., cells, some organelles) can reproduce, many forms of life cannot (e.g., tissues, organs (usually) , many communities). We have defined organisms as biological entities that are discrete in time, i.e., they have a beginning and ending; organisms originate as the result of a reproduction event carried out by some already existing organism(s). Although sex is often associated with reproduction, it is a distinct phenomenon. And many organisms, especially non-animal organisms, usually reproduce in ways that do not involve sex and some have no sexual process at all.

TOPICS

- Reproduction — single celled organisms
- Reproduction —multi-cellular organisms
- Reproduction and dispersal in space
- Sex
- Examples from the green, red and brown algae
    - *Chlamydomonas*
    - *Oedogonium*
    - *Fucus*
    - *Saprolegnia*
    - *Lamanaria*
    - *Ulva*
    - *Porphyra*
    - *Polysiphonia*

Reproduction—single celled organisms

For single celled organisms, reproduction is a familiar and conceptually simple process (although the cellular details are far from simple!)—cell division. The original cell is partitioned by the synthesis and deposition of a new boundary (Fig. 1). For all cells, the boundary includes two plasma membranes (one for each cell) and for organisms with a cell wall the new boundary also has wall material between the two membranes. Note that for cell division to be a means of reproduction the daughter cell needs to detach from its parent cell either immediately following cell division or at some point in the future. Otherwise the new cell is simply increasing the size of the existing organism.

Fig. 1 Reproduction by budding in brewer's yeast. The nucleus spans both parent cell and daughter as chromosomes are being delivered to the daughter cell. The daughter cell has already received a mitochondrion and other cellular organelles. Yeast reproduction can involve sex but rarely does.

The original cell need not be divided equally, but both cells must be provisioned with whatever is required for the cell to maintain itself, in particular it needs genetic information in the form of DNA. Consequently, before the cell divides it needs to replicate its DNA and give each daughter cell a copy. For eukaryotic organisms, the DNA is packaged in units, chromosomes, that replicate before division, with one copy going to each daughter cell, i.e. the process of mitosis. Also present in eukaryotic cells are organelles (e.g. mitochondria) that need to replicate before cell division, with at least one ending up in each daughter cell. For photosynthetic organisms the same would be true for plastids that develop into chloroplasts. Remember that most biologists consider mitochondria and plastids to be remnants of unicellular organisms and their ability to divide is support for this idea.

Reproduction has to involve growth at some point but, as discussed in Chapter 7, growth might come after cell division (a cell is cut in half and then each half grows to full size) or before (a cell grows to twice its normal size and divides); ultimately reproduction requires that the organism acquire material, but this does not need to be a direct part of reproduction.

Although basically simple in outline, cell division, and the reproduction that it brings about in unicellular organisms, involves a myriad of details, some of which are unique to particular groups and are used to unite (classify) organisms.

Reproduction—multi-cellular organisms

Fig. 2 Bryophyllum crenatodaigremontianum. Note the plantlets at the margin of the leaf. These are easily dislodged and will fall to the ground, root and continue growing.

Reproduction in multicellular organisms involves another level of complexity because it requires the coordinated production of multiple cell types positioned in time and space in ways that achieve a functional organism (i.e., a developmental process, see Chapter 7). The information to direct this development is present in the DNA, and since most, or all, of the cells of an organism possess the same DNA, any of these potentially could develop into a new, multicellular organism. However, most cells are unable to express the required information to direct the production of a new organism and thus are NOT able to proliferate and develop a new organism. The developmental potential that can transform a single cell into a multicellular organism generally only finds expression under very limited circumstances. For most familiar organisms (mammals) this potential is only revealed in a single cell, the **zygote** (defined and discussed below). In these organisms, in spite of the fact that all cells have the same genetic information, only the zygote uses it to develop into a new organism as it undergoes embryogenesis and transforms into an embryo. However, in many of the organisms studied in this course, this developmental potential is encountered more frequently, and cells that aren't zygotes can develop into new multicellular organisms in a process described as somatic embryogenesis. This may occur spontaneously or may be induced to occur. *Bryophyllum*, or mother plant (Fig. 2), nicely illustrates this. On the margins of its leaves new plants develop. This is possible because certain leaf cells behave like a zygote, using their potential to develop into a new organism (at least they will be new organisms when they detach from the parent plant). Another plant exhibiting the same ability is bulb-bearing fern (Fig. 3) which also produces structures on its leaves that detach and grow into new plants.

Fig. 3 Cystopteris bulbifera, bulb bearing fern. The roundish green structures are easily dislodged. The small brown dots produce spores, another means of reproduction

New multicellular organisms do not necessarily have to originate from the proliferation of a single cell. Reproduction can be achieved by the cleaving of an existing organism into two or more parts, as long as the resultant pieces of an organism are capable of regenerating the missing parts, or if the organism is so simple that it doesn't have parts, e.g., a filamentous algae or a fungus. Such a pattern of reproduction is very common for many of the organisms covered in this book. Since a new organism can be produced by breaking a piece off an existing organism, a means of enhancing reproduction would be to have pieces that easily break off. This happens in *Bryophyllum* and in bulb-bearing ferns and in many other organisms as well. Both mosses and liverworts commonly produce 'splash cups', cup shaped organs (Fig. 4) that have at their bottom clusters of cells packaged into disk-shaped gemmae (singular gemma) that are easily dislodged and can be thrown out of the cup by a water droplet whose force is focused by the shape of the cup.

Reproduction and dispersal in space

Fig. 4 Splash cups in Marchantia, a complex thalloid liverwort. The small pieces of tissue visible inside the cup are the gemmae.

The phenomenon of splash cups points out that reproduction isn't just about making new organisms, it is also about moving organisms around, i.e., dispersal. For many of the organisms dispersal may be the most significant aspect of reproduction, far more important than the making of a new individual. For familiar (determinate) organisms like mammals, reproduction is the only way to be perpetuated through time. In contrast, organisms that are indeterminate can potentially live forever, so continuation through time may not be a significant consequence of reproduction, but dispersal often is. Environments are dynamic both in their physical conditions and their biotic conditions, thus the fact that an organism can survive at a particular time in a particular place does not ensure that it will be able to do so in the future. Particularly for the organisms covered in this book, most of whom are immobile, it is often the case that reproduction is less about making new individuals and more about getting to new areas. 'Pando', the clone of aspen growing in Utah (see Populus), apparently has perpetuated itself for 80,000 years just by growing. Although in the past 80,000 years it has spread to new areas, it is not moving around very quickly. And, significantly, it is growing in an area where seedling establishment is impossible (i.e., conditions are less hospitable now than they used to be).

Getting to new areas involves the production of propagules, a unit that not only makes new organisms (reproduction), it also can put them in a new place. A fungus that produces a million spores may seem impressive but the consequences in its immediate area may be trivial. Similarly, a pine tree that produces thousands of seeds may be doing nothing to its functional population size at that site and at that time; the more significant effect of producing propagules is enhancing the possibility of establishing a population at some distant site or this site at some time in the future. Common propagules are spores and seeds but certainly the 'bulbs' of bulb-bearing ferns and the gemmae of mosses and liverworts should be considered propagules as well.

Probably the most significant feature that most propagules possess that enhances their dispersal ability is the fact that they are generally inactive, 'dormant'. A general feature of cells and organisms is that the less active they are the less sensitive they are to a variety of 'insults', in particular desiccation and adverse temperatures. Cells and tissues that are in an inactive state, e.g., most spores, seeds, tree buds in the winter, can withstand conditions that active tissues cannot. The changes that accompany inactivity include changes in membrane and protein structure. An indicator of inactivity is a low metabolic (respiratory) rate associated with a general lack of any cellular activity such as protein synthesis or cytoplasmic streaming. Because of their inactivity, many spores can survive prolonged periods without the basic requirements that most organism require: moisture, matter and energy availability, temperatures within a particular range. This aids in dispersal simply because the propagule can travel longer distances while still being viable. Becoming dormant is a physiological process that may be triggered by specific environmental conditions or may simply be an aspect of a developmental pattern, e.g., a cell is programmed to become inactive soon after being created. What triggers the resumption of activity in a propagule varies from the return to 'favorable conditions', e.g., warmth and moisture, to more specific environmental cues, e.g., photoperiod. Some of these are discussed in Chapter 16.

The two common propagules found in the organisms covered here are spores and seeds. Seeds are only found in some plants and will be discussed in depth later. For now, simply appreciate that seeds function both in dispersal and reproduction. Spores are found in almost all of the organisms covered here (Bacteria, Archaea, Fungi, most protists, all plants (including those that have seeds). Their function varies considerably, from being a structure primarily associated with perpetuation in time (endospores of bacteria, akinites of cyanobacteria, zygospores of bread molds) to functioning primarily for reproduction and dispersal (zoospores of water molds and *Oedegonium*) or primarily for sex (considered later in this chapter and in Chapter 14).

Many organisms produce multiple types of spores which may differ in their structure and function, e.g., degree of dormancy, specific requirements required for resumption of growth (see bread molds, *Oedogonium*). A common type of spore is called a zoospore, a flagellated spore found in many of the green algae, most of the water molds, many brown algae, and many of the chytrids (the only fungi that possess flagellated cells).

Zoospores reflect the costs and benefits tied to mobility: their flagella provide them with the mobility that unflagellated cells lack, but flagella require metabolic activity and consequently zoospores have limited lifespans and this limits their mobility and dispersal ability. Another trade-off relates to size. Spores are single cells and generally very small. This enhances mobility by allowing for dispersal by wind. However, any spore benefits by storing material that will be utilized in establishing the new growth following spore germination. The more material saved the heavier the spore is and the more limited its dispersal. These same considerations are significant to seeds, which are multicellular propagules considered in a Chapter 14.

Although reproduction is obviously of significance to the organism(s) that are produced, one final general point about reproduction concerns its impact on the 'parent' organism. Because reproduction utilizes material and energy that might otherwise be used to perpetuate the life of the parent organism, reproduction generally diminishes the likelihood that the parent will be perpetuated through time. The magnitude of this detrimental effect varies from highly significant, when reproduction insures the death of the parent (salmon, wheat plants) to extremely trivial, when reproduction has virtually no effect on the survival of the parent. Because of this impact on the reproducing organisms, reproductive effort is evolutionarily modified and often controlled by specific environmental cues (Chapter 16). Besides the impact at the individual level, reproduction also has potential consequences at the population/species level, increasing the population size and perpetuating the species through time. This effect is strongly dependent upon on other conditions.

Sex

Most students equate sex and reproduction, but they really are two separate processes that happen to be combined in the organisms that we are most familiar with. Reproduction is about making new organisms; sex is about mixing the genetic information of two organisms. Bacteria and Archaea exchange genetic information by several different processes (conjugation, transformation, transduction) but none of these are considered to be sex. Sex is defined as a particular type of genetic exchange that can only happen in organisms with chromosomes (eukaryotic organisms). Sex requires the fusion of two cells (syngamy), producing a cell with twice the number of chromosomes as either of the parent cells. Generally, both of the fusing cells have one copy of each chromosome and are described as being haploid, while the fused cell has two copies of each chromosome and is described as being diploid. Sex also requires a mechanism that can produce haploid cells from diploid cells. This process is meiosis, unfortunately often described as a 'type of cell division,' but is more aptly described as a process involving two cell divisions that produces haploid cells from diploid cells. Keep in mind that the haploid cells that are produced don't simply separate the chromosomes of a diploid cell into two groups, the two groups each have one copy of each 'type of chromosome'. Consider *Arabidopsis* ('Mouse-ear cress'), the most studied plant in the world. If one looks at the chromosomes of a diploid cell, one sees ten chromosomes. But closer examination of the chromosomes reveals that there are actually five distinct types of chromosomes present, and their are two chromosomes of each type. (A chromosome can be recognized by its size and shape. And genetic analysis reveals that they are also distinct in the genes that they possess.) In *Arabidopsis,* meiosis produces cells with five chromosomes not ten, moreover, it produces cells that have one of each type of chromosome, i.e., a complete set.

Sex is a process that allows genetic material (genes) from two different organisms to be mixed. It almost always involves producing new individuals (reproduction). However, the unicellular organism *Paramecium* demonstrates that sex can happen with no reproduction: two cells, each with a diploid nucleus join temporarily. The diploid nucleus of each cell undergoes meiosis to form four haploid nuclei, three of these disintegrate and the remaining one divides mitotically to produce two haploid nuclei in each of the joined cells. Each cell sends one of these two nuclei to the other cell so that both cells have two nuclei, its 'original' one and one that came from its partner. Finally, in each cell, the two nuclei fuse to form a diploid nucleus, the original condition. Thus, the cells have undergone the sexual cycle but have not reproduced: there were two cells at the beginning and there are two cells at the end. Although sex and reproduction are different processes, they often (especially in familiar organisms) occur simultaneously.

Specifically, sex requires:

- Fusion of two cells and the subsequent fusion of the two nuclei in a process called syngamy, combining the genetic information of each. A ssuming that the original cells had one copy of each gene (i.e., the cells were haploid), the product of fusion will have two copies of each gene, i.e., will be diploid. Only special cells have the ability to fuse with one another and these cells are called **gametes**.
- A process (meiosis) that starts with a diploid cell and produces haploid cells, each with one copy of each chromosome. This process is feasible in eukaryotes because

> they have genes that are packaged into structures (chromosomes) that can be sorted and moved. Describing a cell as 'having two copies of each gene' is the same as saying that the cell has 'two copies of each chromosome'(in fact it is more accurate since it is commonly the case that genes often get replicated, i.e. a haploid cell commonly has multiple copies of a gene, sometimes all copies are on one chromosom e, other times it has copies of a gene on several chromosomes.)

Most students consider sex to be related to the fusion process, but it is important to appreciate that meiosis is also an essential part. The essential components of sex (syngamy and meiosis) are sometimes distantly separated in time and may be separated between organisms. We will study a number of situations where two types of organisms are produced, both associated with the same species; one organism develops from a diploid cell (zygote) produced by syngamy and is diploid; the other develops from a haploid cell (spore) and is haploid. However, there are other organisms where the cell created by syngamy immediately undergoes meiosis, i.e., both steps of sex, syngamy and meiosis, occur in the same cell. As we will see there are lots of variations on the basic sexual cycle.

Sex is not universal. Many organisms, including some very successful groups (Archaea and Bacteria, the endomycorhizal forming Glomeromycota, most dinoflagellates, many fungi) have no sexual process. While sex is generally considered to be significant to the process of evolution because it promotes the variation that natural selection can act upon, it is important to realize that variation and evolution can occur without sex and that the success of a group of organisms at one point in time, and through time, is possible even if that group has no sex.

For multicellular or colonial organisms, reproduction, unless occurring by fragmentation of an already existing colony/organism, requires a cell that will proliferate and form the colony/organism. In the familiar case of humans, that cell is the zygote. But in many organisms it is a haploid cell produced by meiosis, generally called a spore, that has the developmental potential to proliferate and form a multicellular organism. And for all plants and many of the macroalgae, multicellular/colony development can proceed both from a zygote and from a haploid spore produced by meiosis. Such organisms will have both a haploid stage, derived from the spore, and a diploid stage, derived from the zygote.

The rest of this chapter will illustrate several examples of sex and reproduction, showing a diversity of patterns from several different groups. It is important to realize that for many of the larger groups (generally phyla) that we study, in particular for the macroalgae (green, red and brown algae), sex and reproduction are NOT consistent across the group, i.e. there is no single, standard pattern of sex and reproduction. In separate chapters we will consider groups that do show some consistency: with several of the fungal phyla (Chapter 12), with non-seed plants (Chapter 13), with seed plants (Chapters 14 and 15).

Chlamydomonas

Chlamydomonas is a unicellular green alga that primarily reproduces asexually (left side of diagram below), i.e,. most new cells are not the product of a sexual process. On the right side of the diagram is shown the sexual process which is trivial in terms of reproductive effort but significant for the variation that it creates and also because the thick-walled 'zygospore' (so named because it develops from a zygote) is able to withstand hostile conditions (dispersal in time). The sexual process is 'triggered' by conditions that make normally asexual cells behave like gametes, with the ability to fuse with other cells. The only diploid cell is the zygospore.

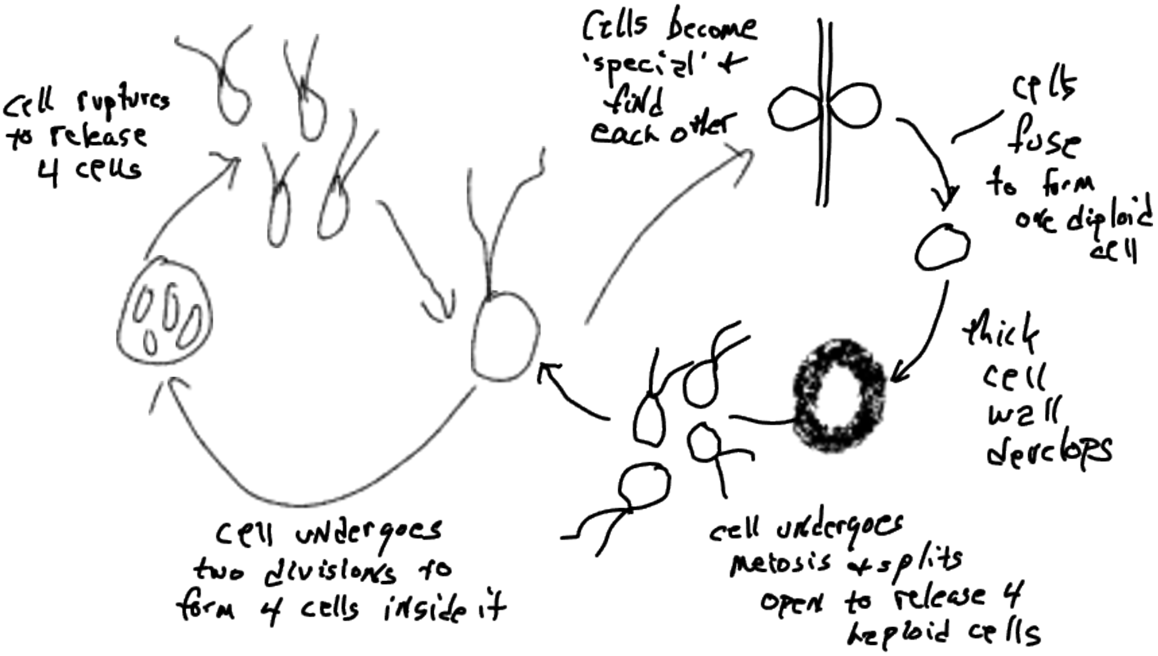

Fig. 5 Sexual (on the right) and asexual (on the left) reproduction in Chlamydomonas.

Oedogonium

Oedogonium, a filamentous green algae, shows the same basic patter as *Chlamydomonas* except that: (1) it is colonial, not unicellular, (2) in the sexual cycle the gametes do not look alike but are structurally very different with one (called the egg) being large and immobile and the other (called sperm) being much smaller and mobile. Sperm are released from the colonial filament to swim to and join with the egg (syngamy). Both the egg cell and cell producing sperm need to develop a hole in the cell wall in order for the sperm to escape and enter the egg cell. The zygote develops into a zygospore that is released from the filament and eventually undergoes meiosis and releases flagellated zoospores that, like the asexual zoospores, are capable of attaching to a substrate and developing into a filament, i.e., the cell that initiates a colonial organism is not a diploid zygote, rather it is haploid zoospore.

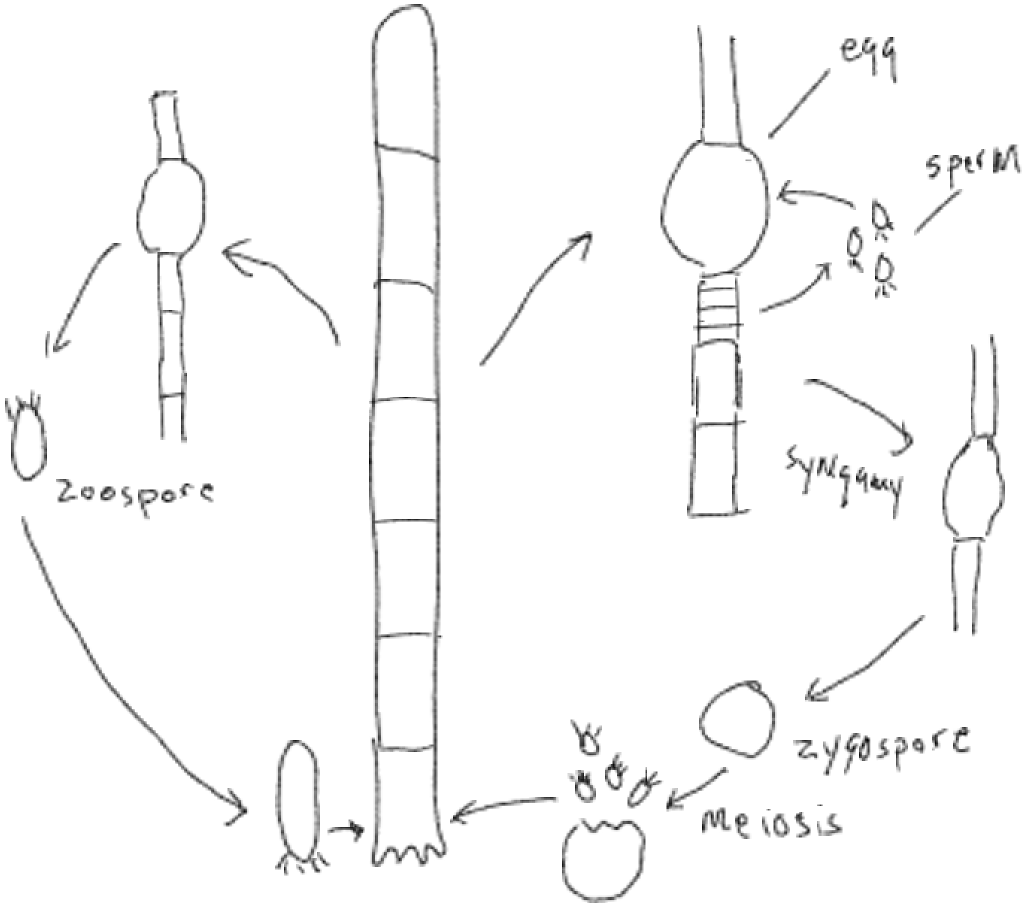

Fig. 6 Sexual (on the right) and asexual (on the left) reproduction in the filamentous green algae Oedogonium.

Fucus

Fig. 7 Fucus (rockweed), a diploid individual. Note the swollen branch tips. These contain multiple structures called conceptacles (see figures below) with openings to the outside, visible as dots.

Fucus is a multicellular brown algae with a life cycle comparable to humans (Fig. 7-9). The organism is diploid and the only haploid cells are gametes, which come in two varieties: a large, unflagellated egg and a small, flagellated sperm. Unlike in humans, gametes are released to the environment and syngamy occurs there. The zygote is formed outside of a parental gamete-forming organism. The zygote develops into a new diploid organism, which, unlike humans, generally can produce both male and female gametes. Note that, in contrast to the two previous examples, the zygote divides mitotically and does not undergo meiosis, hence there is a diploid organism, not simply a single diploid cell.

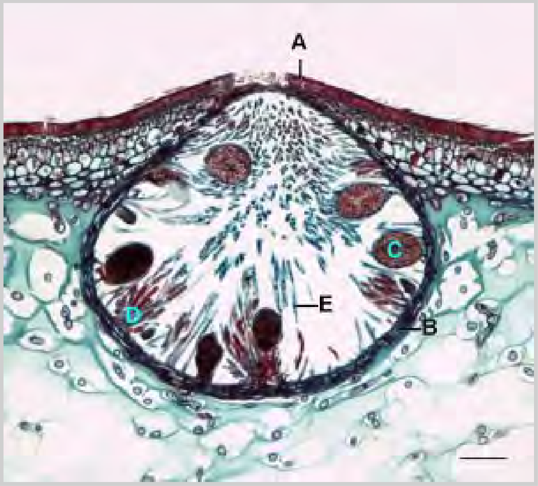

Fig. 8 Cross section of a conceptacle, showing the opening to the outside (to the left of A) and the structures that produce eggs (C) and sperm (D).

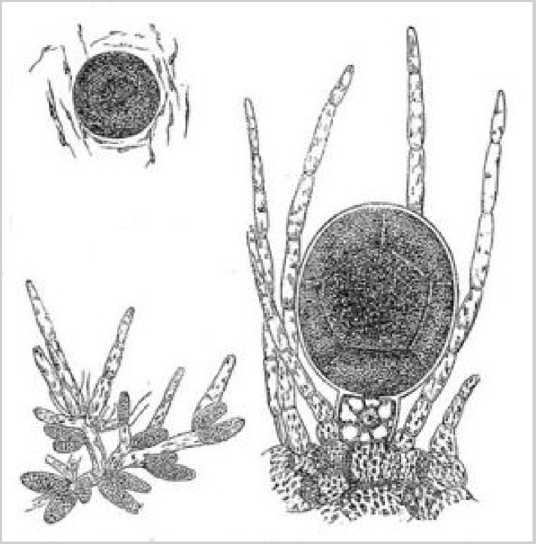

Fig. 9 Diagrams of the egg and sperm producing structures. Eggs are produced when a diploid cell undergoes meiosis with the four haploid products dividing mitotically to produce eight eggs that are

released; sperm are produced when a cell undergoes meiosis followed by four rounds of mitosis to produce 64 flagellated sperm that are also released.

Saprolegnia

Saprolegnia, a water mold in the same group as *Phytophthora*, also has a life cycle that is primarily diploid, like humans. The organism is filamentous and siphonaceous, with no cross walls. The nuclei found in the hyphae are diploid and the the diploid organism is capable of reproducing asexually by producing structures that produce diploid, flagellated zoospores that are mobile and capable of germinating to produce more diploid organisms. This is the primary way that the organism reproduces. The zoospores may also develop into cysts, dormant cells, capable of surviving conditions that the zoospores and hyphae cannot. The diploid hyphae may also be induced to form enlarged spherical structures at their tips that contain a single diploid nucleus that undergoes meiosis. After a few additional divisions the structure now contains several haploid eggs. Chemically attracted to the egg containing structures are hyphae that develop enlarged hyphal ends that attach to the egg producing structure and whose diploid nuclei to undergo meiosis to produce sperm. The structure also produces fertilization tubes that penetrate the egg containing structure and allow the haploid nuclei ('sperm') to enter and fertilize eggs. These zygotes develop substantial cell walls and are termed oospores. These remain dormant and are capable of dispersal and survival under adverse conditions. When they germinate they produce diploid hyphae.

Laminaria

Laminaria is an extremely large multicellular brown algae with a life cycle that departs slightly from that of humans and *Fucus* in that the products of meiosis (called meiospores) are not gametes and are not capable of fusing with each other. Instead they are a type of 'spore', a cell that, like some zygotes, is capable of developing, in this case developing into a microscopic filamentous colonies that do produce gametes. This is similar to what happens in *Oedogonium*. In *Laminaria* there are two types of meiospores that develop into two different types of filamentous gamete-producing colonies. These are not distinguishable by form but one produces eggs and the other produces sperm. The sperm are released to the environment and are attracted to and fertilize the eggs, which may or may not have been released (if it has not been released then the filament that produces it deteriorates soon after fertilization). The zygote attaches to a substrate and grows into the large kelp that is typical of the species.

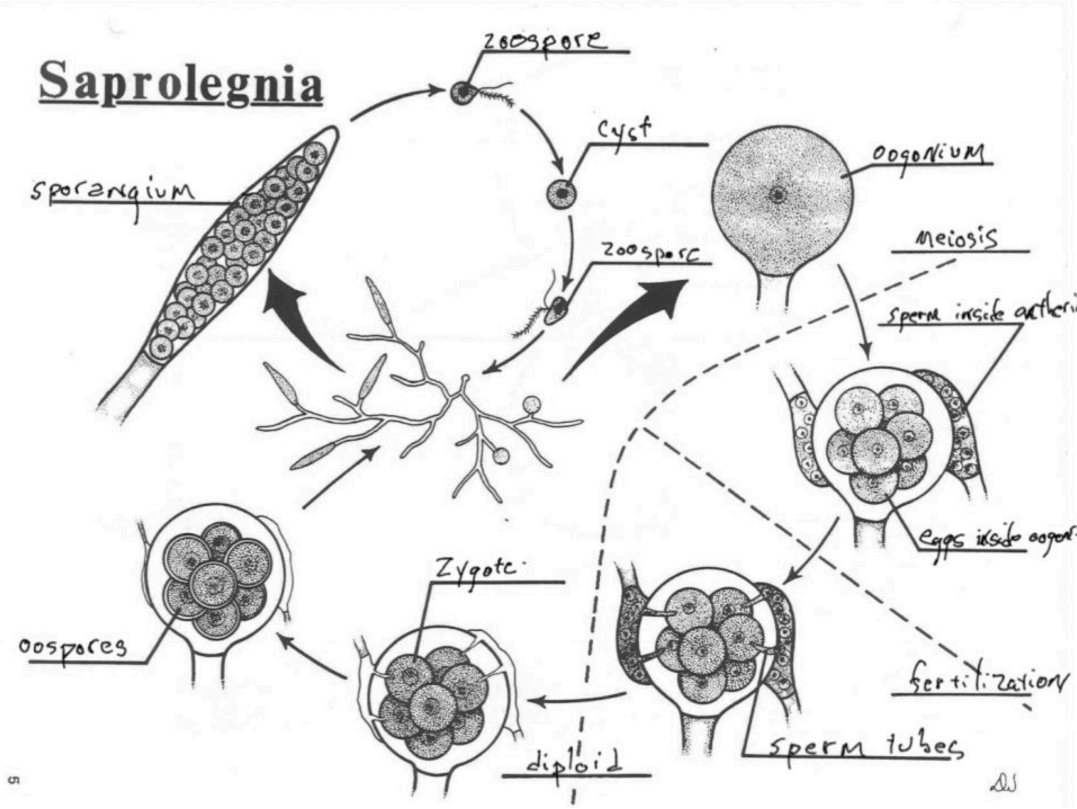

Fig. 10 The life cycle of the water mold Saprolegnia, a coenocytic organism that is diploid (left side of diagram). Parts of the organism become haploid when cells in the oogonium and antheridium undergo meiosis to form egg and sperm. The sperm grow to the structure containing eggs to fertilize them.

Laminaria exhibits what is called alternation of generations, (Fig. 11) producing two different organisms, one diploid, one haploid. The haploid form produces gametes and is called a gametophyte. The diploid organism produces spores and is called a sporophyte. Note that both spores and zygotes show 'developmental potential'. Spores divide and produce a haploid colonial filament (the gametophyte). Zygotes divide and produce a diploid multicellular kelp that is initiated in the female gametophyte that has produced the egg. Since the haploid and diploid forms are very different, *Laminaria's* life cycle is described as 'heteromorphic alternation of generations' with hetero- referring to different and -morphic referring to forms.

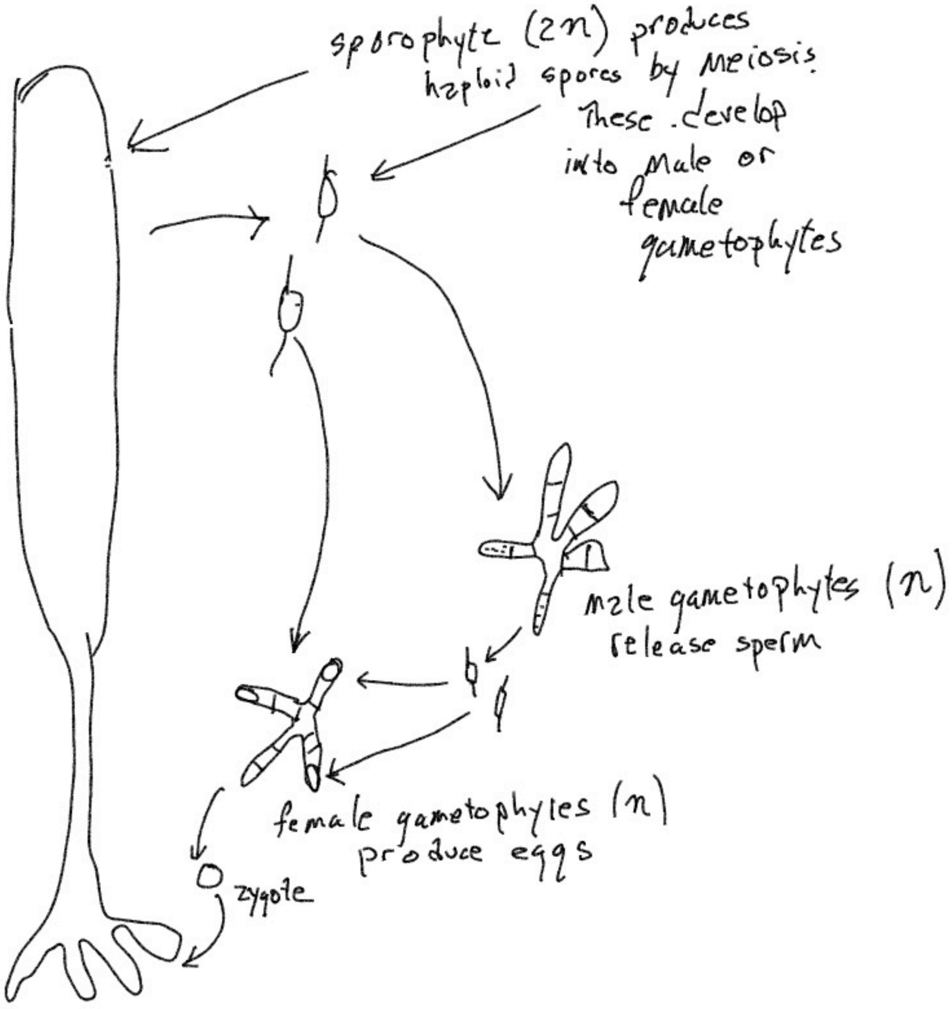

Fig. 11 Life cycle of the brown algae Laminaria. The large kelp that grows more than 15 m in length is a diploid sporophyte. The haploid gametophytes are much smaller and of two types, one producing sperm that are released and the other producing eggs that are fertilized on the gametophyte to form a zygote that grows and forms the sporophyte.

Ulva

Ulva is a colonial green algae, producing sheets that are two cells thick. It produces two forms, one haploid, one diploid, that are indistinguishable in form. Diploid organisms are produced from the growth of zygotes produced by the union of two gametes. The gametophytes (i.e. the haploid organisms that produce gametes are produced by the development and growth of haploid spores; these are products of meiosis that occurred in cells at the margins of the diploid plants, which are sporophytes. Diploid organisms are produced by the development of zygotes (note that, like *Laminaria*, both haploid spores and diploid zygotes show 'developmental potential'; they can develop into organisms). *Ulva* demonstrates what is known as 'isomorphic alternation of generations' (iso- referring to same); the gametophyte and sporophyte look the same.

Fig. 12 Ulva, a green alga composed of flattened sheets. Haploid and diploid forms look identical.

Porphyra

Porphyra is a red algae that, like *Laminaria,* has two forms that look very different. The haploid, gamete-producing form (i.e., the gametophyte) (Fig. 14) is a macroalgae and has long been harvested as food in both Ireland and Japan (nori). It is a sheet that may be one or two cells thick. The gametophyte form releases sperm that are unusual because they lack flagella (there are no flagellated cells in the red algae). The eggs are fertilized while still present on the gametophyte. The zygotes (called carpospores) are then released to the water column, settle and establish themselves by drilling into oyster shells or other substrates. They then grow into small, filamentous diploid, spore-producing organisms (sporophytes). The spores that are produced are diploid but undergo meiosis upon ger-

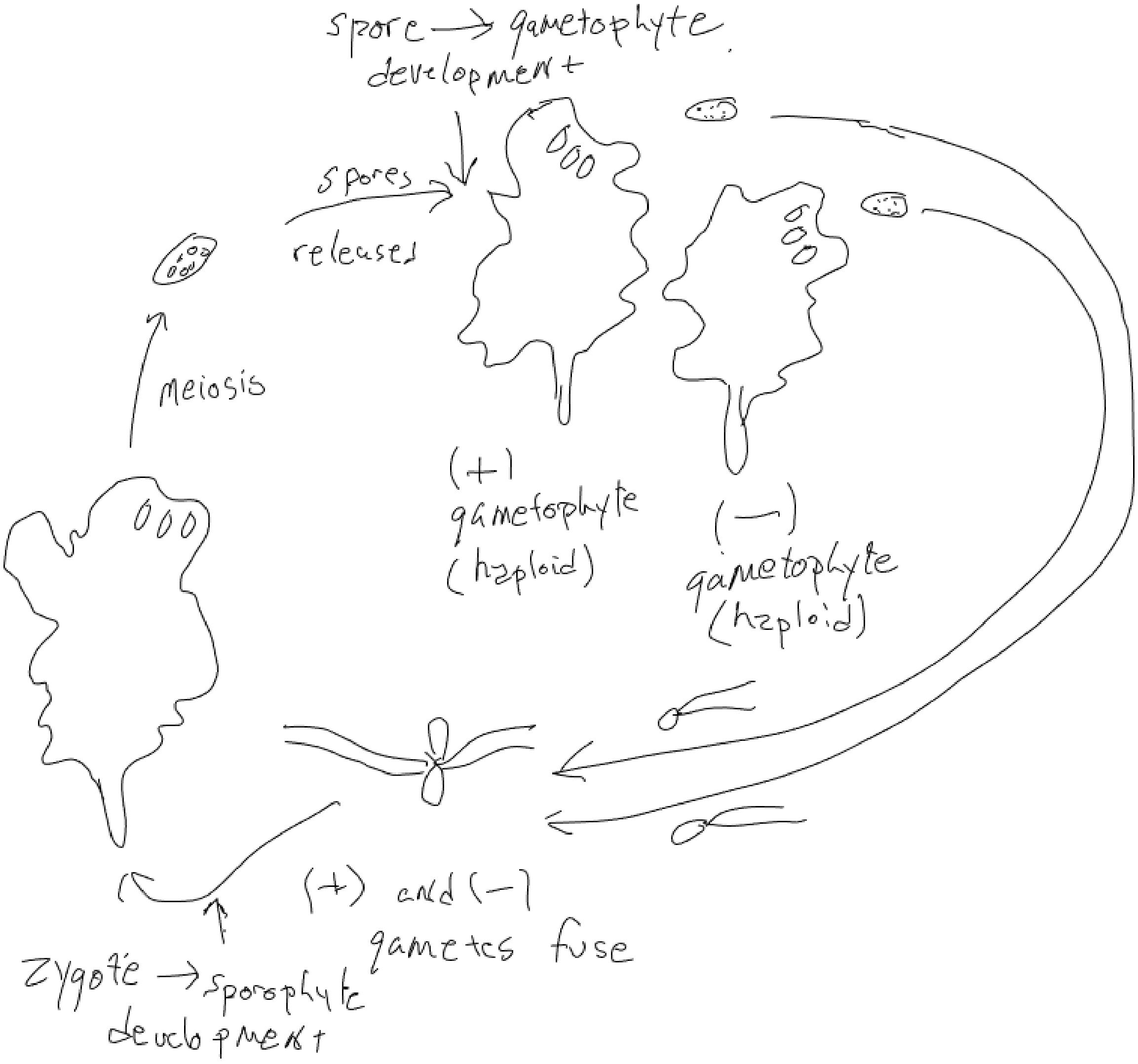

Fig. 13 Life cycle of the green algae, Ulva, which shows isomorphic alternation of generations with the sporophyte and gametophyte both of the same form.

mination and grow into the larger, blade-forming gametophytes. In general, this life cycle is like that *Laminaria*, there is a heteromorphic alternation of generations, but the larger, conspicuous form is haploid and the smaller, inconspicuous form is diploid. One interesting aspect of the *Porphyra* life cycle is that both the gametophyte and sporophyte are capable of reproducing asexually. Another interesting aspect is that until the studies of Kathleen Drew Baker, published in 1949, the diploid organism was described as a separate red algal species. Her work was fundamental to the development of commercial *Porphyra* cultivation.

Fig. 14 Porphora, the larger, sheet-forming sporophyte.

Polysiphonia

Polysiphonia is a red macroalgae with a finely branched form that looks identical as: 1) haploid, sperm-producing (male) gametophyte plants, 2) haploid egg-producing (female) gametophyte plants and 3) diploid spore-producing plants (sporophytes = tetrasporophytes). As in all the red algae, sperm do not swim but are carried by water currents after being released from the male gametophyte plant. If they are able to attach to a projection extending from the eggs, which are produced on the female gametophyte plants, then fertilization (syngamy) occurs. The zygote then develops on the female gametophyte plant, producing a very diminutive 'extra' diploid generation called a 'carposporophyte', that is found on the gametophyte plant. These produce diploid carpospores that are released and germinate to form what is called a tetrasporophyte plant. These look identical to the gametophytes but are diploid. The tetrasporophyte produces haploid spores as a result of meiosis and these germinate and grow into haploid gametophytes.

The basic pattern is an isomorphic alternation of generations but with an additional generation between the gametophyte and sporophyte (Fig. 14). Hence there are three 'generations', not two. Two of them are diploid and one is haploid. Several commonalities with other groups can also be pointed out, keeping in mind that none of these reflect phylogenetic relationships:

- the zygote is retained on the on the organism that produces the egg; an analogous situation is found in the life cycle of all plants and some green algae
- one generation, the carposporophyte, is very diminutive and completes its entire life as part of the organism that produced it; something comparable occurs in seed plants and some non-seed plants
- the egg produces a filamentous extension that facilitates receiving sperm; a similar structure is found in some of the basidiomycete (club) fungi, specifically the rusts, and, although they don't have 'typical' sperm, in the ascomycete fungi. Similarly, although it does not directly involve egg and sperm, but rather the structures that contain the egg and sperm, a comparable structure is found in the stigma of flowering plants.

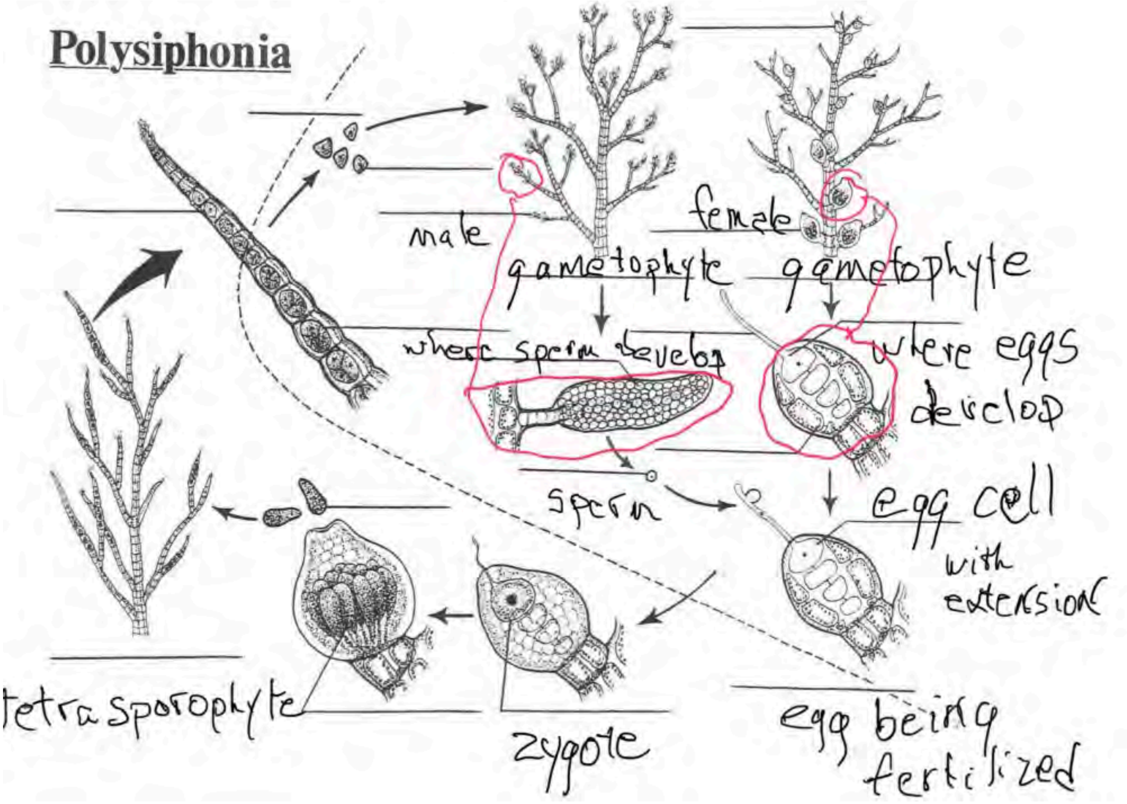

Fig. 15 The life cycle of Polysiphonia. The dotted line separates the diploid form on the left, from the haploid forms on the right. Sores, released from the tetrasporophyte, undergo meiosis, making haploid spores that grow into the gametophytes.

Further Reading and Viewing

- "Australian Bryophytes – Splash cups" by Heino Lepp. More on splash cups.
    - https://www.anbg.gov.au/bryophyte/splash-cups.html
- "Australian Bryophytes – Elaters in liverworts" by Heino Lepp. Elators in bryophytes.
    - https://www.anbg.gov.au/bryophyte/elaters-liverworts.html
- "Splash-cup plants accelerate raindrops to disperse seeds" by Guillermo J. Amador et al. Splash-cup plants accelerate raindrops.
    - https://royalsocietypublishing.org/doi/10.1098/rsif.2012.0880
- "Size matters for violent discharge height and settling speed of Sphagnum spores" by Sebastian Sundberg. Spore discharge in sphagnum.
    - https://academic.oup.com/aob/article/105/2/291/196099
- "The Seaweed Site: information on marine algae – Fucus" by M.D. Guiry. Good site on "seaweeds" including rockweed sex.
    - http://www.seaweed.ie/algae/fucus.php
- "Living together and living apart: the sexual lives of bryophytes" by David Haig. Bryophyte sex.
    - https://royalsocietypublishing.org/doi/10.1098/rstb.2015.0535

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- saprolegnia labelled
- laminaria new

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- polysiphonia labelled

CHAPTER 12: FUNGAL SEX AND FUNGAL GROUPS

Fig. 1 Although many fungi reproduce without sex, the sexual organ, if present, is the most visible structure of the organism and, until the advent of molecular techniques, it was the structure used to identify fungi. In many fungi the sexual organ is too small to be seen but in some, like this pale chanterelle, the 'fruiting body' is not only large, its also edible!

The 'vegetative' (i.e., not associated with sex and reproduction) structure of most fungi are generally very consistent: they are composed of branched filaments that explore the volume of material that they feed on (be it living or dead) and this structure provides for acquisition of materials that they need to grow and survive. The consistency of vegetative form makes it difficult to classify fungi because they mostly look alike, although some vary on the basis of whether or not the filaments on coenocytic or septate (with cross walls and therefore cellular). However, fungi do show variation, and can be grouped, based upon structures that are associated with sexual reproduction. The exceptions to this are the two groups where sex is either completely absent (Glomeromycota — the endomycorhizal forming fungi) or rare (Chytridomycota — the chytrids). The remaining three groups (bread molds = Zygomycota, cup fungi = Ascomycota, and club fungi = Basidiomycota usually exhibit specific features associated with sexual reproduction that are used define these groups (generally considered phyla). Fungi that show no sexual features used to be put into a group called the 'Fungi Imperfecti' (Deuteromycota), but molecular techniques now allow these fungi to be placed in one of the groups mentioned above.

Fungi have the following features associated with sex and reproduction that are different from most familiar sexual organisms:

- Reproduction often involves both sexual aspects and asexual aspects. Cells called **spores** — defined as cells with both dispersal capabilities (i.e., mobile cells) and reproductive capabilities (i.e., cells that can grow into new fungal organisms) are often important in both asexual and sexual reproduction.
- **Gametes** (cells that can fuse with other gametes) are quite different from what most would consider 'typical'; they are usually hyphal cells (part of the fungal filaments) that have the ability to fuse with other hyphae. Depending upon the group, these special hyphae may or may not have structural features that would distinguish them from the normal hyphae.
- **Syngamy** often involves two steps separated in time and often in space. This is a consequence of the fact that the fusion of the hyphae serving as gametes is generally not followed immediately by the fusion of nuclei. Cellular fusion is called plasmogamy and nuclear fusion is called karyogamy. Plasmogamy followed by a delayed karyogamy allows fungi to have a novel condition, the dikaryon state, where a cell has two nuclei ('dikaryon' means 'two nuclei'), one from each parent. This condition is often perpetuated: the dikaryon cell divides while both nuclei divide, thereby forming a new cell that is also dikaryon. This process can continue, producing multiple dikaryon cells and dikaryon hyphae. Note that although a dikaryon cell has two copies of each chromosome, it is not considered diploid because each nucleus is haploid, with only one copy of each chromosome.
- At some point, some of the dikaryon cells become diploid as a result of the fusion

of the two nuclei (karyogamy). The diploid cells are **NOT** perpetuated; they undergo meiosis to form haploid nuclei which develop walls to become haploid cells. Thus, the diploid state is very brief in extent (i.e., size and number of cells) and often brief in time as well — the diploid cells never divide mitotically to form more diploid cells, they only divide meiotically to form haploid cells. These haploid cells are, or soon become, spores that are dispersed from the parent fungus to a new location where they germinate and form haploid hyphae.

- 'Mating strains' are a common mechanism that ensures that fungi do not mate with themselves. Within a particular species there are two to many mating types. A particular mating type needs to find a different mating type in order to interact sexually (i.e., fuse hyphae). The simplest situation has two mating types: "+" and "-" and they need to find each other to mate, but there may be more than just two types, e.g., types A, B, C, D, E. And mating type A could mate with any of the others but not with another A. Generally, the interaction, or lack of it, involves chemical signals (pheromones) that are emitted by one mating type and sensed only by fungi of a different mating type. In response to the pheromone, hyphae grow and find each other, bringing about plasmogamy.

TOPICS

  - Zygomycetes (bread molds)
  - Ascomycetes (cup fungi)
  - Basidiomycetes (club fungi)

Zygomycetes, the bread molds

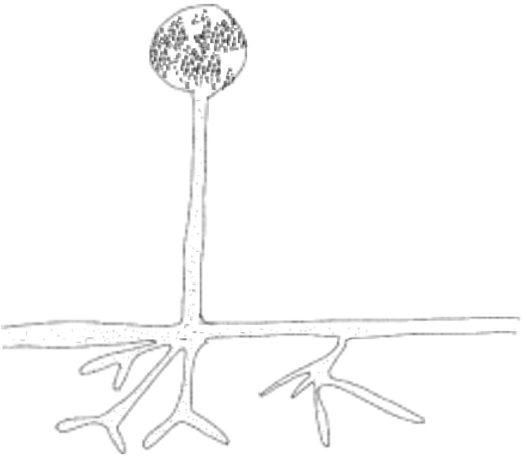

Fig. 2 Zygomycete organisms are coenocytic, with multinucleate cells except in the sporangium which has uninucleate spore cells.

In the zygomycetes (Fig. 2-3), most reproduction is asexual and results from the production of a stalked structure (sporangiophore) terminated with spherical sporangium. Inside the sporangium is the only cellular tissue produced by the group, meaning it is a structure where walls are present and individual nuclei are packaged one to a cell. These cells mature into spores that are dispersed when the sporangium disintegrates. Much less frequent is reproduction associated with a sexual process when a specific structure, the zygospore, is formed and from which the group gets its name. The process is initiated when two compatible hyphae sense each other's presence because of

Fig. 3 Bread molds can be significant pests of garden produce, but play many other significant roles including parasites and symbionts of animals

pheromones. This triggers hyphae grow towards each other with the production of specialized hyphal branches that are capable of fusing to each other. Since bread molds are coenocytic, the fusion of two hyphae (plasmogamy) allows multiple nuclei to come into proximity (Fig 4). Unusual for the group, two cross walls, one in each of the fusing hyphae, form near the point of fusion, creating a single coenocytic cell with nuclei derived from each of the two mating strains (Fig. 5-6). This is the only dikaryon cell produced by the bread molds and it develops into a structure called a zygospore (Fig. 7-8) by enlarging slightly and developing a thick wall. Inside the zygospore haploid nuclei of one type pair with nuclei of the other type and fuse (karyogamy) to form diploid nuclei, transforming the cell from being dikaryon to being diploid, but it is still multinucleate. The zygospore is generally dormant and generally has more specific germination requirements and a longer lifespan than the asexual spores. When the zygospore germinates it produces a sporangiophore comparable to those produced asexually with a sporangium at its tip. As this develops the diploid nuclei undergo meiosis and the haploid nuclei are individually packaged into spores as cell walls are produced. The spores are subsequently dispersed, and when they germinate they produce haploid, coenocytic hyphae. Note that the dikaryon state is limited to a single cell and has a very brief existence.

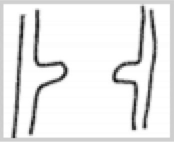

Fig. 4 When hyphae of different mating strains are in proximity, pheromones trigger hyphal branches of each strain to grow towards each other.

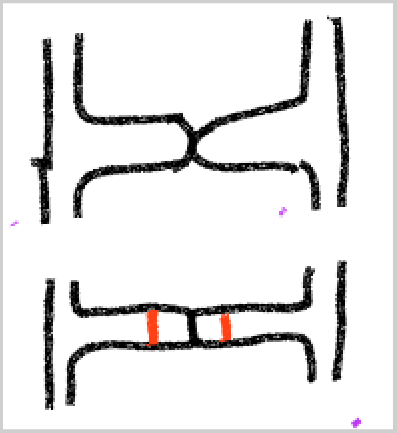

Fig. 5 When the two strains make contact, new cell walls (in red) form, producing two multinucleate cells at the tip of each branch other.

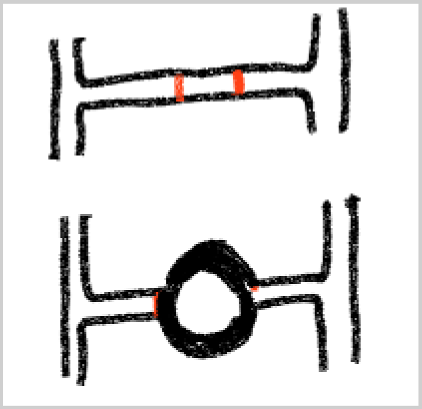

Fig. 6 The cell walls where the two hyphae made contact are broken down, plasmogamy occurs, creating a multinucleate cell that is dikaryon, with haploid nuclei from the two parents present. The haploid nuclei of the two types find each other, fuse and thus form a coenocytic cell with diploid nuclei (plus some unmatched haploid nuclei). At the same time the cell develops into a zygospore with a thick cell wall. It matures and becomes dormant.

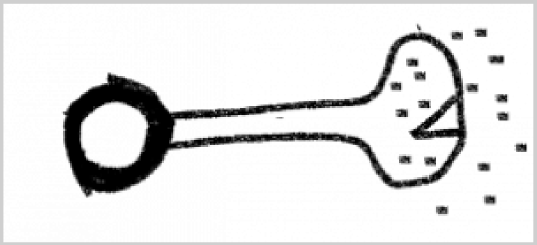

Fig. 7 When the zygospores germinate the diploid nuclei undergo meiosis and the zygospore produces a stalk with a sporangium containing haploid cells; these are dispersed.

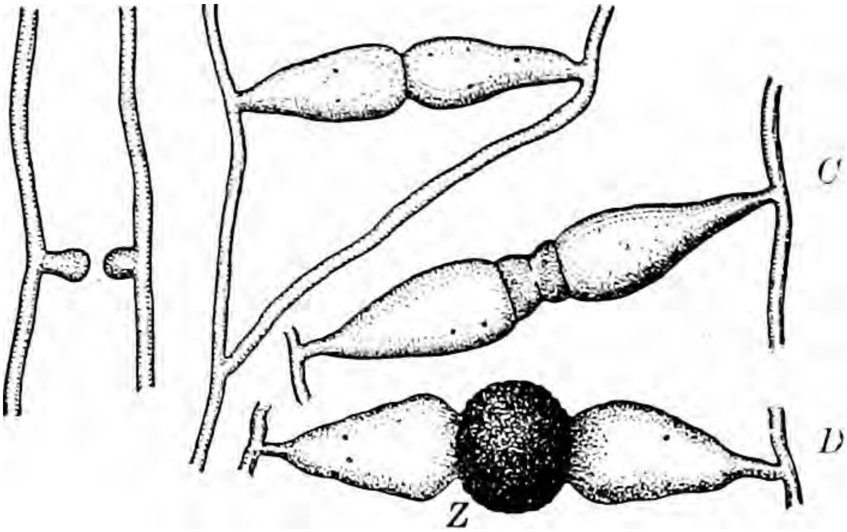

Fig. 8 When the zygospores germinate the diploid nuclei undergo meiosis and the zygospore produces a stalk with a sporangium containing haploid cells; these are dispersed.

Ascomycota — the cup fungi

Fig. 9 The cup fungi (Ascomycota) get their common name from the cup-shaped fruiting bodies that some species produce.

Unlike the bread molds, the cup fungi (**Ascomycetes**), are septate, i.e., they have cross walls and the 'feeding hyphae', the ones that acquire nutrients, are constructed of cells that have a single haploid nucleus. Many members of the group, reproduction is primarily to exclusively asexual, a consequence of the production of specialized hyphal branches that produce small cells (conidia) that are easily broken off to serve as propagules. Generally, these cells are dormant and have other cellular features, e.g., stored food, that promote their role in reproduction and dispersal. When and if sexual reproduction occurs, it is initiated when compatible mating strains are close to each other and communicate by pheromones. Inflated hyphal branches are produced, one on each strain, producing cells that are slightly different in form and are multinucleate. When they are close to each other one of the cells produces an extension that touches the expanded cell of the other mating type and fuses with it (plasmogamy occurs) and haploid nuclei move from one of the structures, termed the antheridium and considered male, to the other one, called an ascogonium and considered female. As a result of the migration of nuclei, the archegonium cell becomes dikaryon, with two types of nuclei, one from each parent. The ascogonium develops extensions and two nuclei (one from each mating type) associate and migrate into them. A cross wall is formed, producing the first cell of what is described as an ascogenous hypha. These hyphae grow from the tip and remain dikaryon, with two haploid nuclei per cell, a result of a coordination of tip expansion, two nuclear divisions (one for each nucleus), nucleus migration, and septum formation. Growth of the ascogneous hyphae plus growth of both (haploid) parental hyphae produce a fruiting body of densely intertwined hyphae. The size of the fruiting body ranges tremendously in size, from roughly 100 um to 10 cm or more, with most at the smaller end. The size and shape vary and can be used to identify species. The common name for the group ('cup fungi') relates to a cup shaped fruiting body. Cup fungi are found both living independently and also as the fungal partner of a number of lichens; many lichens produce ascocarps (Fig. 10) that are relatively large and visible to the naked eye. Other fruiting bodies are flask-shaped or completely closed and typically are less than a mm in extent.

Fig. 10 A lichen showing 'fairy cups', which are actually the cup-shaped ascocarps of the fungal component of this composite organism.

In a specific part of this fruiting body the sexual cycle is completed. The tips of the ascogenous hyphae form a hook, turning back on itself and the two nuclei fuse (karyogamy occurs) in the cell that has formed the hook (crozier), making it (briefly) a diploid cell. The only diploid cells found in the Ascomycota are these specific cells, eventually called asci (singular = ascus) situated at the ends of the ascogenous hyphae. These hyphae produce no additional cells after forming the hook. The diploid cell elongates and then undergoes meiosis to form an elongate cell with four haploid nuclei. Each of these then go through mitosis to produce an elongate cell called an ascus with eight haploid nuclei in a row. Each nucleus acquires a cell wall and develop into what is called an ascospore. Asci with eight ascospores are diagnostic for the Ascomycota.

Hydrostatic pressure within the ascus causes ascospores to be forcibly dispersed when the tip of the ascus ruptures. Dispersed ascospores germinate to form haploid hyphae, which form haploid mycelia which may reproduce asexually via conidia or other spores. If a haploid mycelium comes in contact with hyphae of a different mating type, sexual reproduction may be triggered.

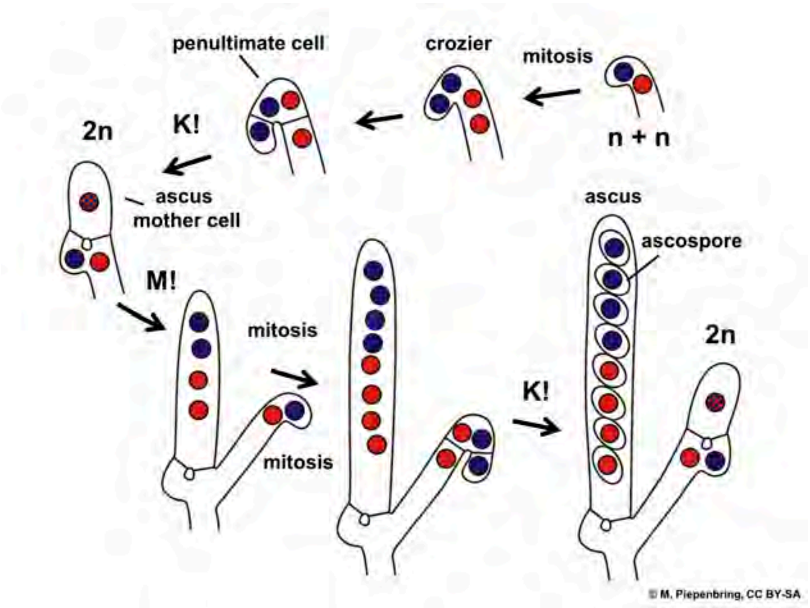

Fig. 11 Sex in Ascomycota. Some of the dikaryon hyphae in the fruiting body form bent cells called croziers. In the next to the last cell of these hyphae karyogamy occurs forming a diploid ascus mother cell which undergoes meiosis followed by a single mitotic division to produce 8 nuclei that develop walls and become ascospores.

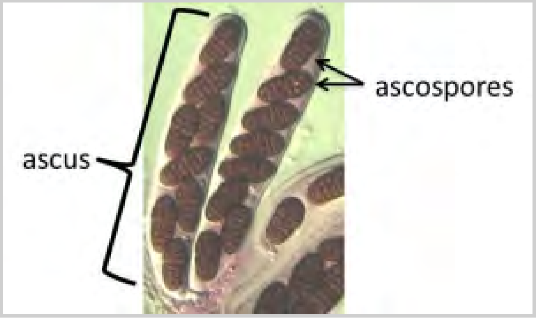

Fig. 12 The ascus—a characteristic feature of the Ascomycota

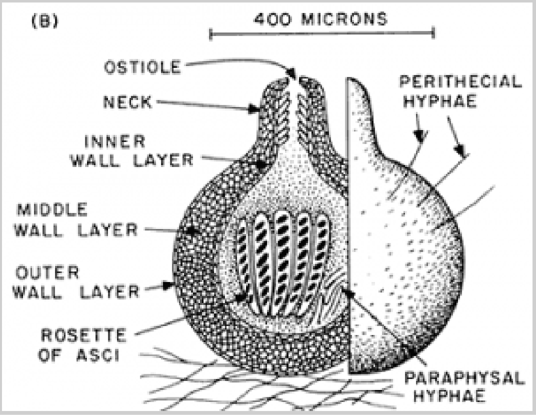

Fig. 13 Note size, many ascocarps (ascomycete fruiting bodies) are quite small

Basidiomycetes—club fungi

The club fungi are septate like the cup fungi (Ascomycota). Of all the fungal groups the club fungi have the most extensive dikaryon state. As is the case for almost all fungi, the

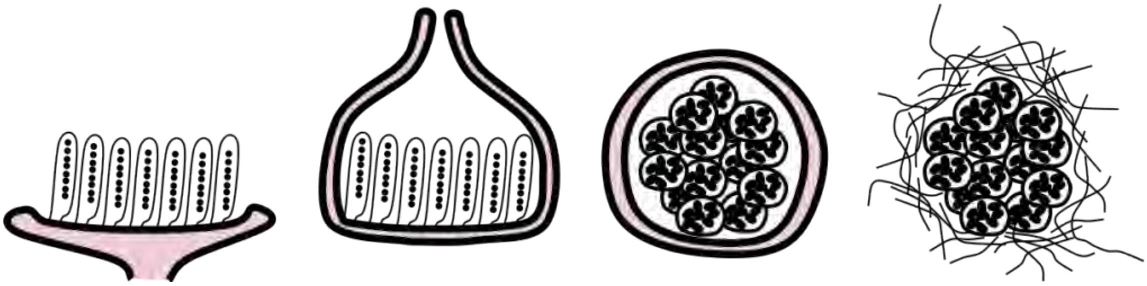

Fig. 14 Different ascocarp shapes, all but the left-most one are usually less than 1 mm.

Fig. 15 While most of the mushrooms that we eat are not Ascomycetes, two of the most famous and most desirable ones are Ascomycetes: the morel and truffle. This image above is a morel. Morel collecting is a common springtime activity throughout North America, Europe and China with foragers often getting over $50 a pound for fresh specimens. The high price is associated with low supply: morels have proved to be difficult to cultivate, and the exact conditions, e.g. associations with particular tree species or general forest conditions, that make an area likely to yield morels are not known with certainty although some western species appear to be particularly prevalent after fire.

dikaryon state is initiated when two compatible haploid, monokaryon hyphae find each other as a result of chemical attraction. Plasmogamy occurs, forming a dikaryon cell. This cell divides and grows extensively, forming a feeding mycelium that is dikaryon. Many of the basidiomycota produce 'clamp connections' (Fig. 17) that may help to maintain the dikaryon state as the hyphae elongate. The nuclei undergo mitosis, and cross walls formed.

Fig. 16 Truffles are even more prized than morels, fetching over $100 per ounce. They are somewhat unusual 'mushrooms' because the fruiting bodies (ascocarps) form below-ground, although they are far from unique in this respect. Although there are similar species found in North America, the most desirable species are European. Like morels, they have resisted cultivation and supplies are short because they can only be obtained by harvesting in the wild. Moreover, because they are below ground, finding them is a challenge and foragers must rely on dogs or pigs to locate truffles by scent.

As the terminal cell elongates an arch is formed between the terminal cell and its parental cell. When the two nuclei divide the arch allows one of the two nuclei to move to the parental cell as septa form. This ensures that both the daughter cell and mother cell has one of each type of nucleus.

Recall that that there is only a single dikaryon cell in the bread molds (Zygomycota) and the only dikaryon cells of the the cup fungi (Ascomycota) are found in the fruiting bod ies. Thus, if one encounters a dikaryotic hyphae outside of a fruiting body then it must be long to a club fungus (Basidiomycota). The dikaryotic hyphae of club fungi grow and feed extensively until appropriate conditions are encountered to trigger 'fruiting'. At this point the growth pattern of at least some of the hyphae changes from one where their substrate is explored for nutrition to one where hyphae intertwine with each other, forming the dense mass of hyphae that will become fruiting body. Often the fruiting body

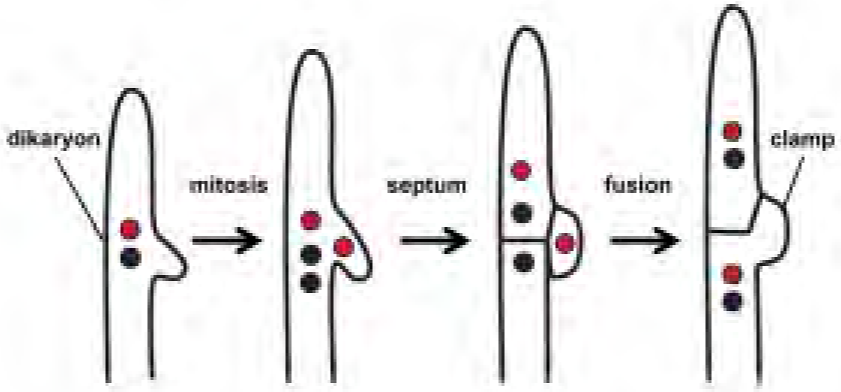

Fig. 17 Basidiomycota form characteristic clamp connections at their tips when the hypha is extending and creating a new cell.

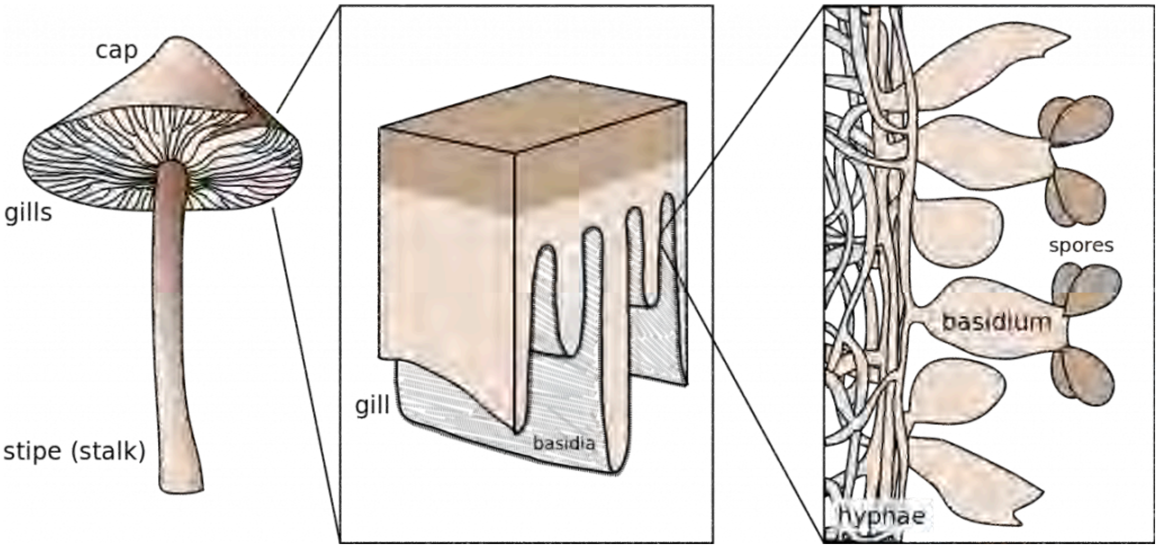

Fig. 18 Structure of a typical gill mushroom in the club fungi (Basidiomycota) group. Basidia are formed on the sides of the gills and produce basidiospore.

emerges from the substrate that the fungus is feeding on, e.g., a mushroom emerging from the soil or from the trunk of a tree. Somewhere on or in the dense mass of hyphae special cells are produced, termed basidia, that are 'club-shaped' (Fig. 18). Inside these cells karyogamy occurs, transforming them into diploid cells. The diploid nucleus undergoes meiosis to produce four haploid nuclei, but no cytokinesis occurs, making the basidium 'quadranucleate'. Four extensions grow out of the basidium and the four nuclei migrate into these. This is followed by cell wall formation to produce a basidium with no nucleus but with four loosely attached haploid cells, called basidiospores, extending off from them. The spores are ballistically released and are dispersed by the wind. When they germinate they form new haploid hyphae.

Unlike the cup fungi, whose fruiting bodies are generally small and not typically noticed, the fruiting bodies of many club fungi are often relatively large, 10-30 cm and have characteristic shapes that we describe as **mushrooms** (with a stalk and a cap) (Fig. 19-20) or **bracket fungi** (roughly hoof shaped and attached without a stalk to the trunks of woody plants). Two very common patterns of basidia distribution are (1) extending from thin fins of tissue termed 'gills', typical of the commercially available mushroom, or (2) basidia extending from tubes (cylinders) of tissue which, when viewed at the surface, appear as numerous pores.

Fig. 19 The fly agaric mushroom, with prominent gills. Basidia extend into the space between gills and basidiospores are forcibly released in a remarkable process that involves the rearrangement of a condensed water droplet and consequent generation of forces (see https://physicsworld.com/a/mushroom-spores-launched-by-catapult/). Most, but not all basidiomycetes utilize this process.

Fig. 20 This mushroom has pores instead of gills but the basic mechanism of basidiospore release is the same as in gill mushroom. Note that the entire mushroom is composed of densely intertwined dikaryon hyphae, forming the stalk and the different portions of the cap. Pores are more common in bracket fungi than in 'mushrooms' but can be found in both, as can gills. One of the most desirable edible mushrooms is the King Boletus, which is a mushroom with pores.

Fig. 21 This is a bird's nest fungus. They are small, 5-15 mm across, and the 'eggs' (peridioles) are where basidiospores are produced. The small cup-like structure ('splash cup') is a form similar to ones found in mosses and liverworts where they aid in dispersal of gemmae), and in the dispersal of sperm (spermatozoids) in some mosses. The energy of the raindrop is focused by the cup shape and the peridioles can be ejected over a meter from the nest. (look here to see a page of info including the link to a slow motion video). After dispersal the peridiole breaks down and spores are released into the air. Some puffballs are also dispersed by raindrops but in a much simpler mechanism: the raindrop pushes in on the puffball surface, compressing the air inside and forcing spores and air out opening in the puffball surface.

Fig. 22 Corn smut, a delicacy in Mexico, sold along with tomatillos and regular corn

Two large groups of Basidiomycetes, the smuts (Fig. 22-23) (Class Ustomycetes) and the rusts (Fig. 24-25) (class Teliomycetes) have slightly different and sometimes involved patterns of sex and reproduction associated with their obligate parasitic lifestyle. Many of these organisms are very important economically because they can drastically reduce yields of important crops. Neither form 'fruiting bodies', made solely of fungal material, but rather cause abnormal growth (galls) on the plant that they are growing in. These galls are composed of infected plant cells, uninfected plants cells growing abnormally because of the parasite, and some fungal hyphae interconnecting infected cells. While the typical basidiomycete (described above) has a single type of spore, the haploid basidiospores formed in the fruiting body, both rusts and smuts commonly produce teliospores, consisting of one to several dikaryotic cells. When teliospores germinate karyogamy occurs, followed by meiosis, producing a basidium with haploid nuclei that produce haploid basidiospores.

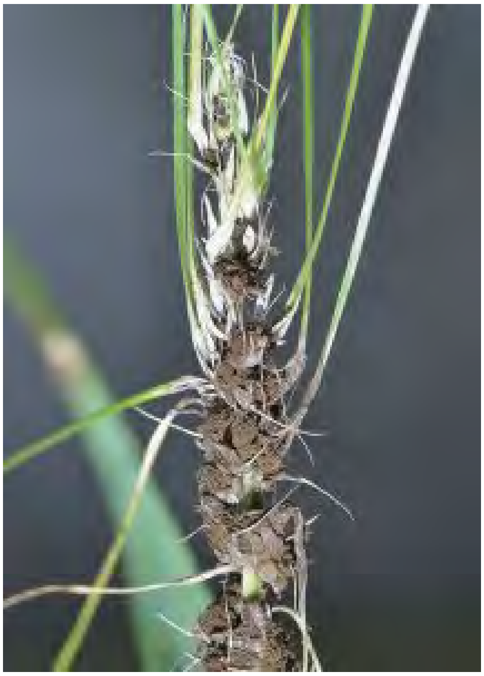

Fig. 23 Loose smut of barley. Smuts usually manifest themselves in developing fruits

Fig. 24 Wheat rust, showing lesions which are producing one of the five types of spores found in wheat rust

While most smuts only produce these two types of spores, rusts may have two or three more types of spores and a complicated life cycle that sometimes involves two hosts. An example of a rust with two hosts is discussed below (Fig. 26) and also in Chapter 30.

Fig. 25 Rust on rose; rusts get their name from the bright orange structures that are often produced.

Basidiospores infect host #1 (barberry) and form structure called pycnia on the upper surface of the leaf. Pycnia produce two structures that bring about syngamy. One of these produces haploid spores called pyncospores (or spermatia) that might be considered gametes. Pycnospores are released as single cells into a sweet 'nectar' that attracts insects who can transport them to other compatible (i.e., different mating type) pycni a where they can fuse (plasmogamy) with the second structure involved in syngamy that is produced by pycnia: 'flexuous hyphae' that extend out of the pycnia. Fusion of the pyncospore with the haploid cells of these hyphae brings about syngamy and forms the initial cell of a dikaryon hyphae. This grows to the bottom of the leaf, forms a cup shaped structure that releases dikaryon spores (aeciospores) that infect host #2 (wheat), causing it to form another type of dikaryon spore, uridinospores, that can infect more wheat plants. Late in the season the final type of spore, the teliospore, forms on wheat. Karyogamy and meiosis occur in teliospores and from them emerge promycelia (basically basidia) that produce basidiospores.

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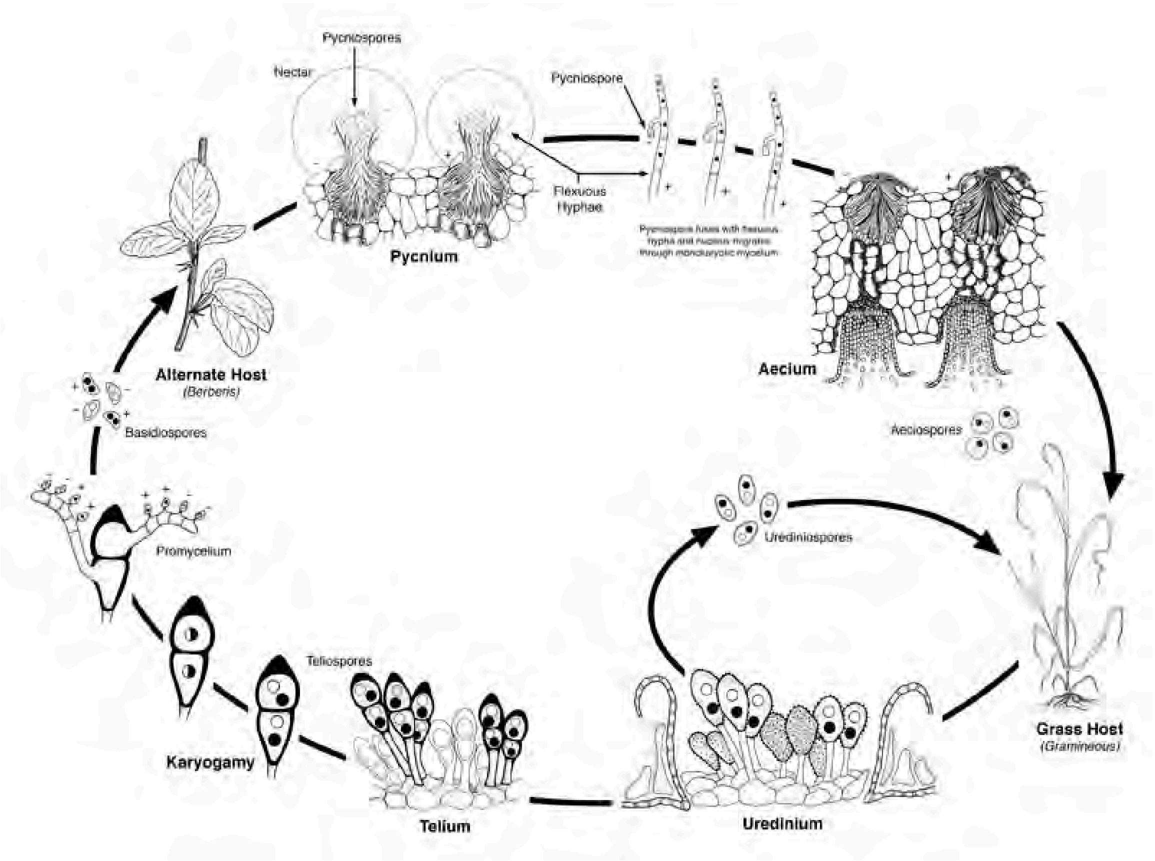

Fig. 26 The life cycle of a rust that alternates hosts.

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CHAPTER 13: SEX AND REPRODUCTION IN NON-SEED PLANTS

Almost all plants are capable of reproduction without sex. Most commonly this happens as a consequence of the plant being severed into pieces and these pieces being able to regenerate the parts that were lost. Additionally, some species have developed pieces that are particularly prone to be broken off, e.g., the gemmae (singular of gemma) of some mosses and liverworts. It is relatively common for flowering plants to produce asexual propagules in the places where seeds normally develop, producing seed-like structures without the normal process of sex. Although reproduction without sex is common in plants and for some species it represents their sole means of reproduction, most plants rely on sexual reproduction, and two innovations, the seed and the flower, have been particularly significant to the evolution of plants.

With respect to sex, the plant kingdom illustrates wonderful patterns of unity and diversification. On the one hand, all plant life shows a fundamentally similar pattern of sex, on the other hand, plants illustrate remarkable diversification of this common theme.

TOPICS

- Alternation of generations
- Mosses, liverworts and hornworts
- Ferns
- Horsetails
- Clubmosses

All plants exhibit alternation of generation s, they produce two types of multicellular organisms: one diploid and derived from the development of a zygote, and one haploid and derived from the development of a haploid cell called a spore. 'Development' involves the proliferation of cells, the differentiation of cells and the formation specific structures with specific roles, i.e.. morphogenesis.

All plants exhibit alternation of generations and alternate between haploid and diploid organisms. To complete the sexual cycle the haploid organism must produce gametes that unite to form the zygote. That is, among all the haploid cells that are produced as a result of cell divisions of a haploid spore, some of the cells are endowed with special capabilities that allow them to encounter and interact with another gamete to form a zygote. Similarly, of all the diploid cells derived from the zygote, some, called a 'spore mother cells', are endowed with the ability to undergo meiosis to produce haploid cells, spores, that grow into haploid individuals. Note that meiosis does NOT produce gametes, rather it produces spores that are dispersed and develop into haploid plants. The diploid plant that produces spore mother cells and spores is called a '**sporophyte**'. The gamete-producing organism, which is haploid, is called a **gametophyte**. Thus, there is an 'alternation of generations' with a haploid form alternating with a diploid form (Figure 1). Often one of the two forms is challenging to appreciate, largely because they are often challenging to see — they are often small, short-lived, and may not live a separate existence from the previous generation. That is, the haploid and diploid forms may not spatially distinct from each other; they may be temporarily, or permanently, a part of their parent!

Like those of familiar animals, the gametes of all plants are of two types, a larger, immobile egg and a smaller sperm that must in some way be mobile in order to encounter the egg. The gametophytes of plants may be bisexual (hermaphrodites), producing both egg and sperm, or unisexual, i.e., there are separate male and female gametophytes. In some plant groups, including all of those discussed in this chapter, the sperm is mobile because they possess flagella. Sperm swim away from the male gametophyte that produced it and are chemically attracted to the structure producing eggs. Because plants are terrestrial organisms, the water required for a flagellated sperm to swim to the egg but water is not always present. We will see in the next chapter that some plants have circumvented this problem by having male gametophytes become mobile, not the sperm they produce.

As in animals, the female gamete, the egg, does not move. It is retained in the organism that produces it. In the case of plants this is a haploid gametophyte (not a diploid individual as in mammals). And in some of the plants discussed in this chapter the zygote formed by the fertilization of an egg grows out of the archegonium (the structure in which an egg is produced) and produces a sporophyte attached to the gametophyte. Alternatively, the entire (female) gametophyte of some plant groups is embedded in the diploid plant (the

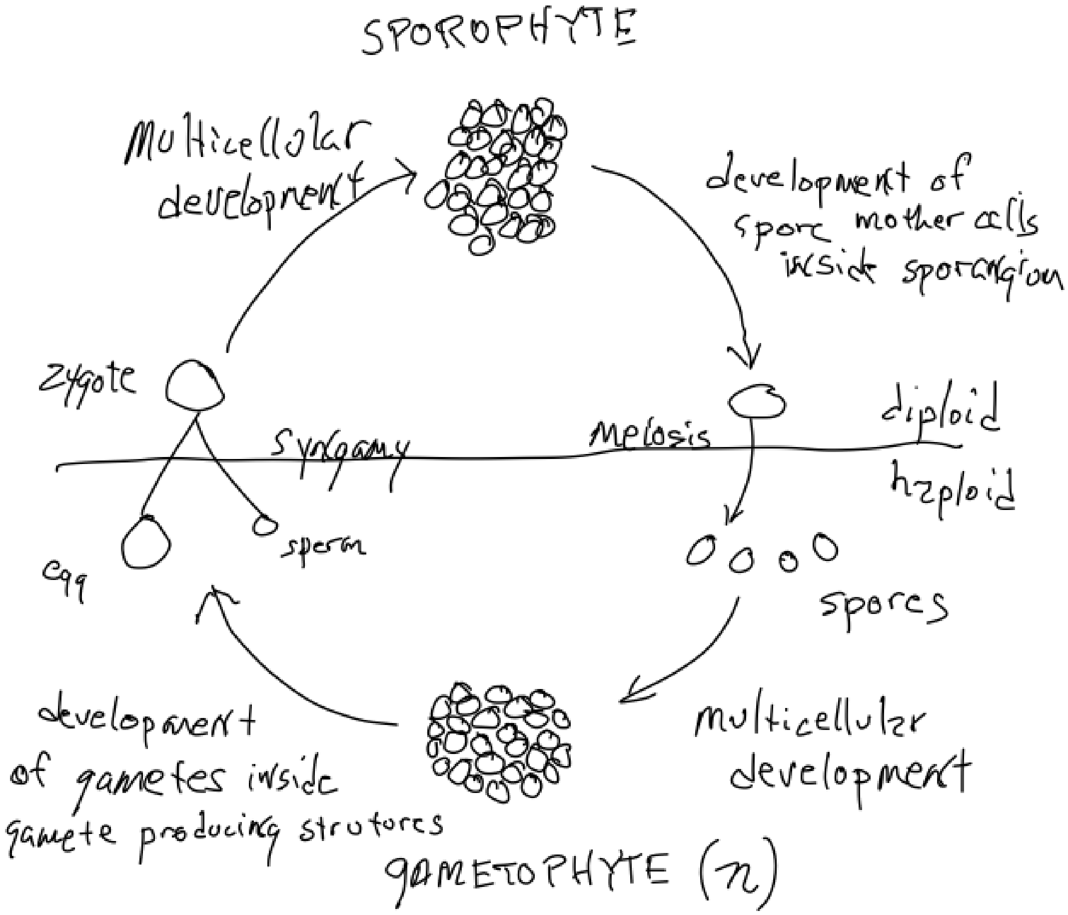

Fig. 1 Alternation of generations: the sexual cycle exhibited by all plants as well as protists.

sporophyte) that produced the spore that developed into the female gametophyte. That is, in some plant groups, the spores produced by sporophytes are not dispersed; instead the spore germinates where it is produced and grows to produce a gametophyte plant on or inside a sporophyte plant. Mobile male gametophytes and sedentary female gametophytes are features of a very few of the non-seed plants discussed in this chapter but are ubiquitous in seed plants, discussed in the next two chapters. In this chapter we consider the more readily observable and understandable alternation of generations that is found in plants without seeds.

Mosses Liverworts and Hornworts

Fig. 2 A moss gametophyte, showing a typical 'stem with leaves' construction.

In mosses, liverworts and hornworts (the three groups of plants lacking vascular tissue) it is the gametophyte plant that lives the longest and is the most visible. It produces a form capable of gathering materials for growth, primarily through photosynthesis (Fig. 2). The most common form, found in all mosses and many liverworts, is an elongate axis bearing flaps of tissue that increase the photosynthetic area. At some point, often once a year, the gametophyte produces gamete producing structures that are called archegonia (singular = archegonium) if they produce eggs and antheridia (singular = antheridium) if they produce sperm. These structures are typically produced in the midst of modified 'leaves' at ends of stems/branches in mosses or, in some liverworts, they occur on the underside of umbrella/mushroom-shaped structures that extend upwards from the main body of liverworts.. The antheridia (Fig. 3) are roughly spherical containers in which cells differentiate into flagellated sperm and are released when the antheridia break open. The archegonia are flask shaped structures with a single egg near the base and an elongate neck that develops a canal through which sperm can swim in order to fertilize the egg. The resulting zygote develops inside the archegonium, producing a sporophyte that eventually extends typically one to six cm beyond the archegonium and exists as an appendage of the gametophyte, never liv ing an existence independent from it. Although the sporophyte sometimes is green and capable of photosynthesis for part of its life, its structure, a simple stalk with no 'leaves' to increase surface area, is not particularly suited for photosynthesis. Rather the structure is suited for the dispersal of spores; the stalk usually elevates the capsule, which is the site where spore mother cells develop, undergo meiosis, and produce spores.

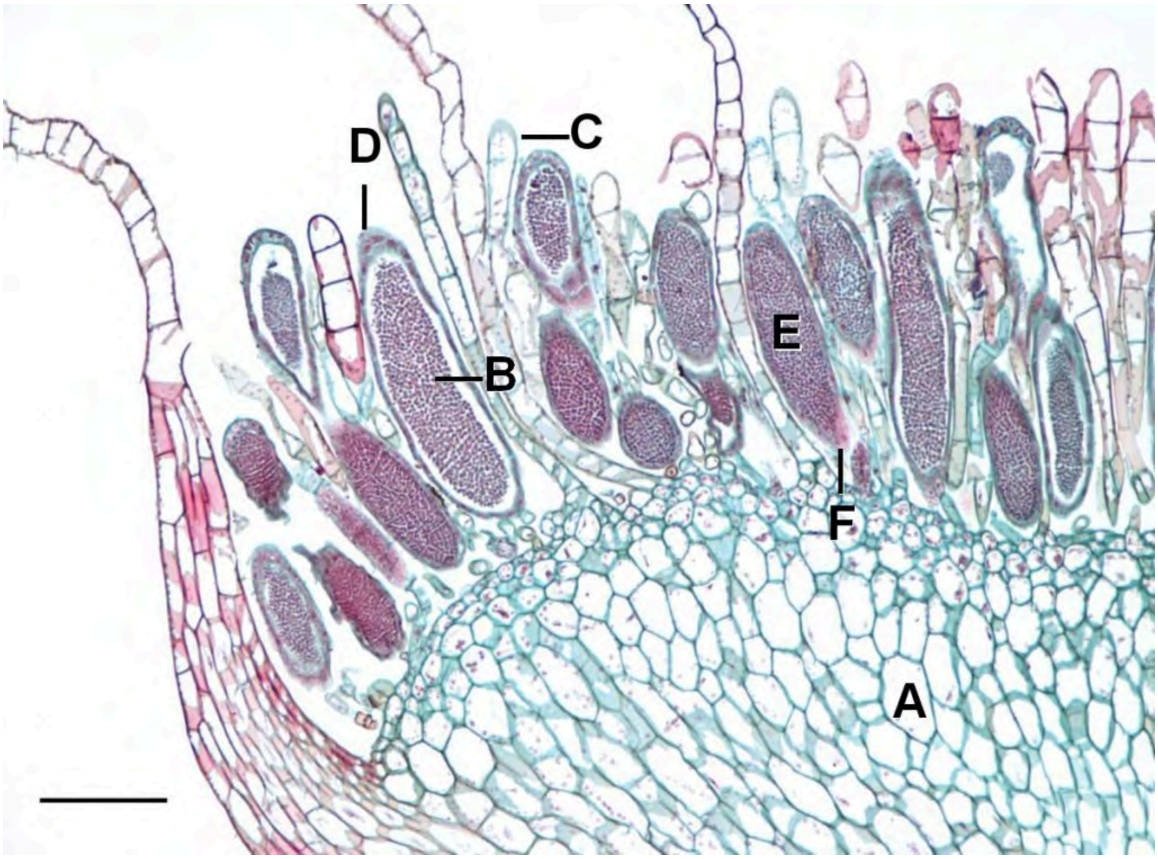

Fig. 3 Antheridia (B, E) on the tip of moss gametophyte stem

If 'spatial separation' is used rigorously to define an organism then these sporophytes would not be considered separate organisms, they are simply a part of the gametophyte (Fig. 5). But, in light of the sexual cycle and pattern of alternation of generations, it is helpful to consider them to be separate organisms. This is supported by fact that they have a different number of chromosomes than the gametophyte that they grow out of.

In all other plants besides mosses, liverworts and hornworts it is the spore producing plant that lives the longest and is the most visible; it is the form that we see and recognize as a plant. The sporophyte still begins its development growing out of the archegonium where the egg was produced and was fertilized, but the sporophyte's growth is such that it becomes completely independent of the gametophyte that it emerges from and eventually has a completely autonomous existence. Thus, when we see ferns, horsetails, club-mosses, and seed plants, what we are observing is a diploid plant that produces spores. In all these groups the gametophyte is small and elusive but the basic life cycle is the same as in all

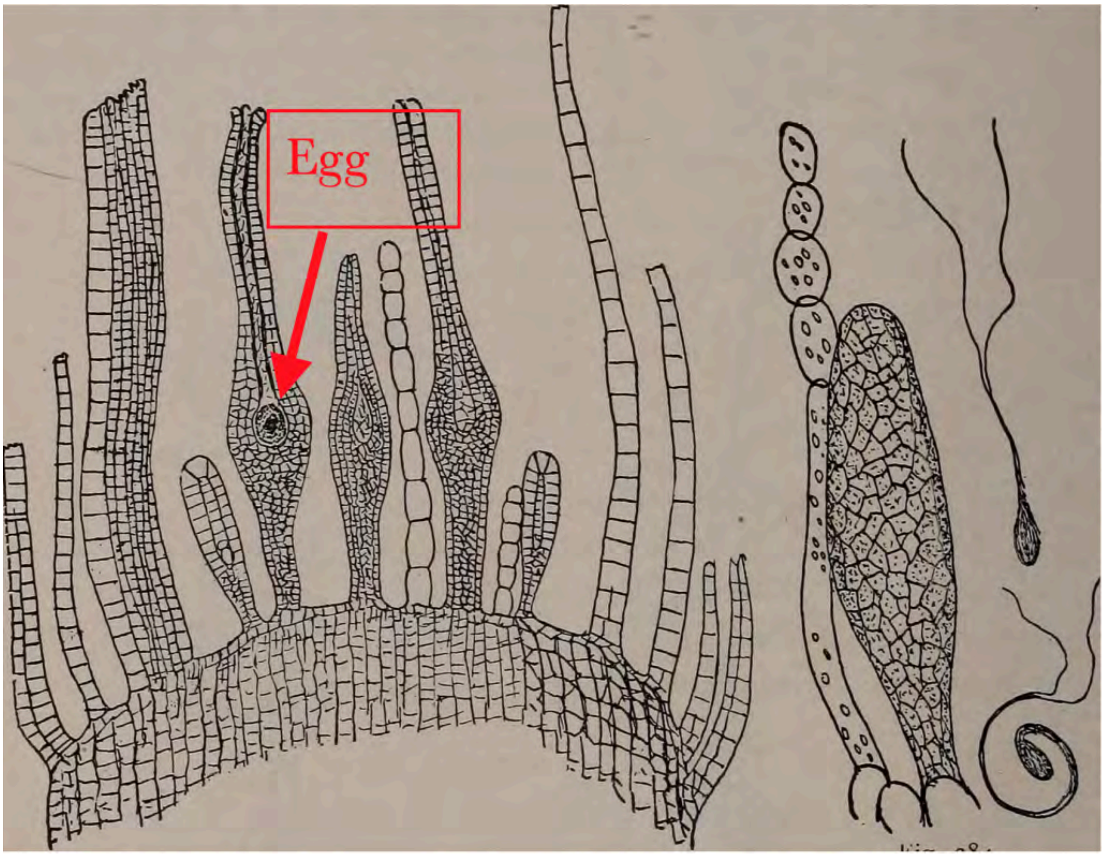

Fig. 4 The type of a moss 'stem' showing typical moss archegonia, one with an egg. On the right is an antheridium and a released sperm.

plants: an alternation of generations between a gametophyte and a sporophyte. Seeds and seed plants are discussed in the next chapter, below are considered aspects of the sexual cycle, in particular features of the less commonly seen gametophytes, that are produced by seedless vascular plants.

Ferns

Most ferns have a small, photosynthetic gametophyte that usually is less than 1 cm across and one cell thick, i.e., a sheet. It lacks a stem axis and is often 'heart-shaped' (Fig. 6-8 and 11). It is generally attached to a substrate via rhizoids (filaments of non-photosynthetic cells).

Fig. 5 Moss sporophytes emerging from archegonia at the top of gametophytes

As was the case in the mosses, the fern gametophytes produce structures where the egg and the sperm are produced as a result of cells dividing in a particular pattern to produce archegonia (Fig. 7-9) and antheridia. It is important to note that gametes are not produced by meiosis because all the cells of the gametophyte are haploid already.

Fern gametophytes are generally have flask shaped female structures (archegonia) located in the notch between the lobes and globular male structures (antheridia) located on the on the lobes. While most fern gametophytes are hermaphroditic, some are unisexual and for some their sexual expression depends on environmental conditions. All the cells of the gametophyte are haploid but it produces a cell, the egg, with special developmental abilities. The antheridia release sperm that have flagella which allow them to swim to the archegonia, where the eggs are located, and swim down a narrow canal to fuse with the egg cell at its base. The zygote develops into a sporophyte, producing stems and roots. The stems produce leaves which shade the gametophyte and it soon dies (Fig. 9)

The sporophyte continues to grow to produce the fern that we recognize. It has the same structure as most plants: a root-shoot axis with leaves produced by the shoot. Most of

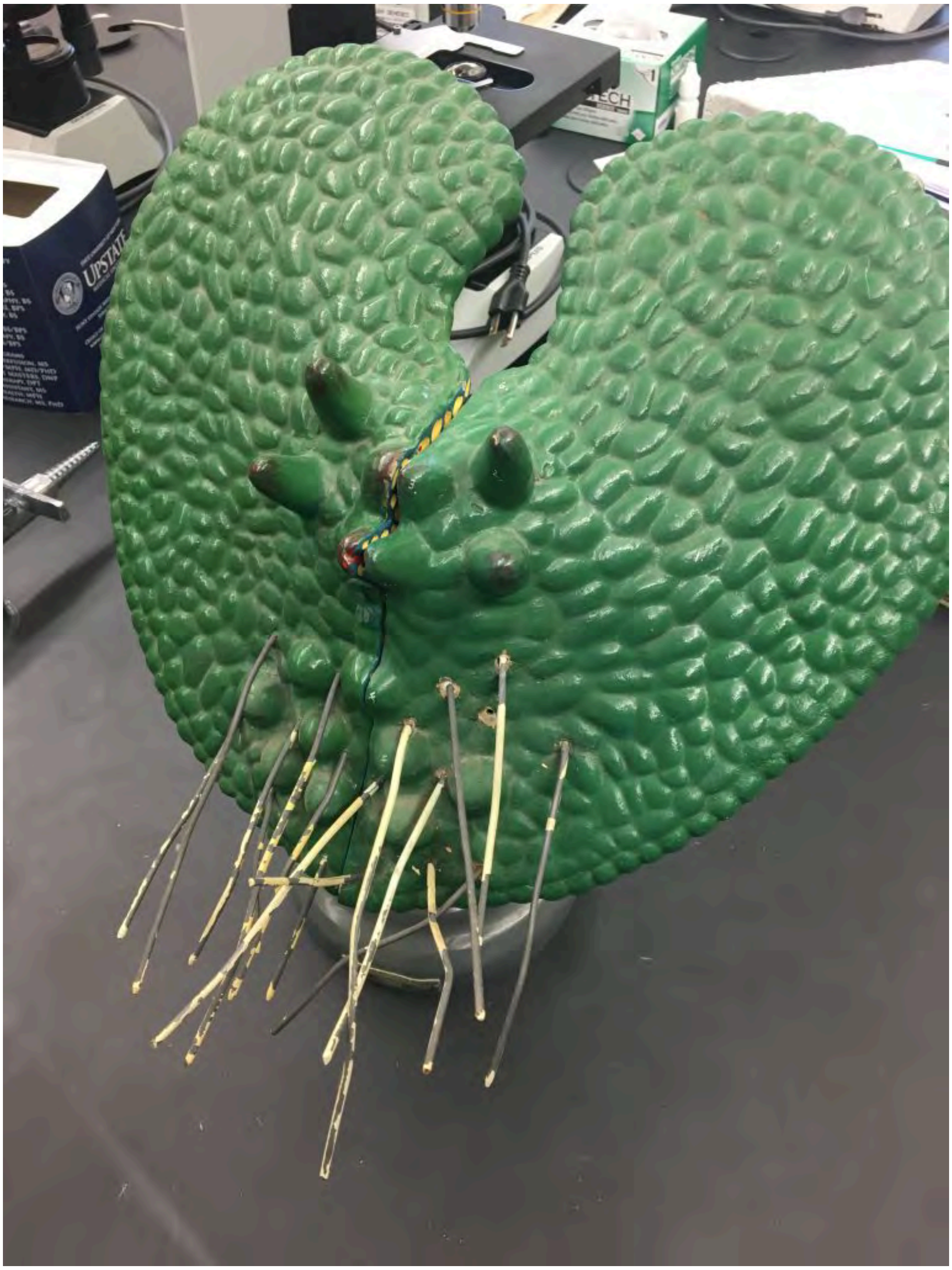

Fig. 6 Model of a fern gametophyte showing the underside with rhizomes, archegonia and antheridia

the ferns in this area have stems (rhizomes) that are below ground and relatively short. What we see are the leaves emerging above ground from this rhizome. At some point this diploid organism produces structures termed sporangia, inside of which are spore mother cells that undergo meiosis to produce a group of four (a tetrad) of haploid spores that are

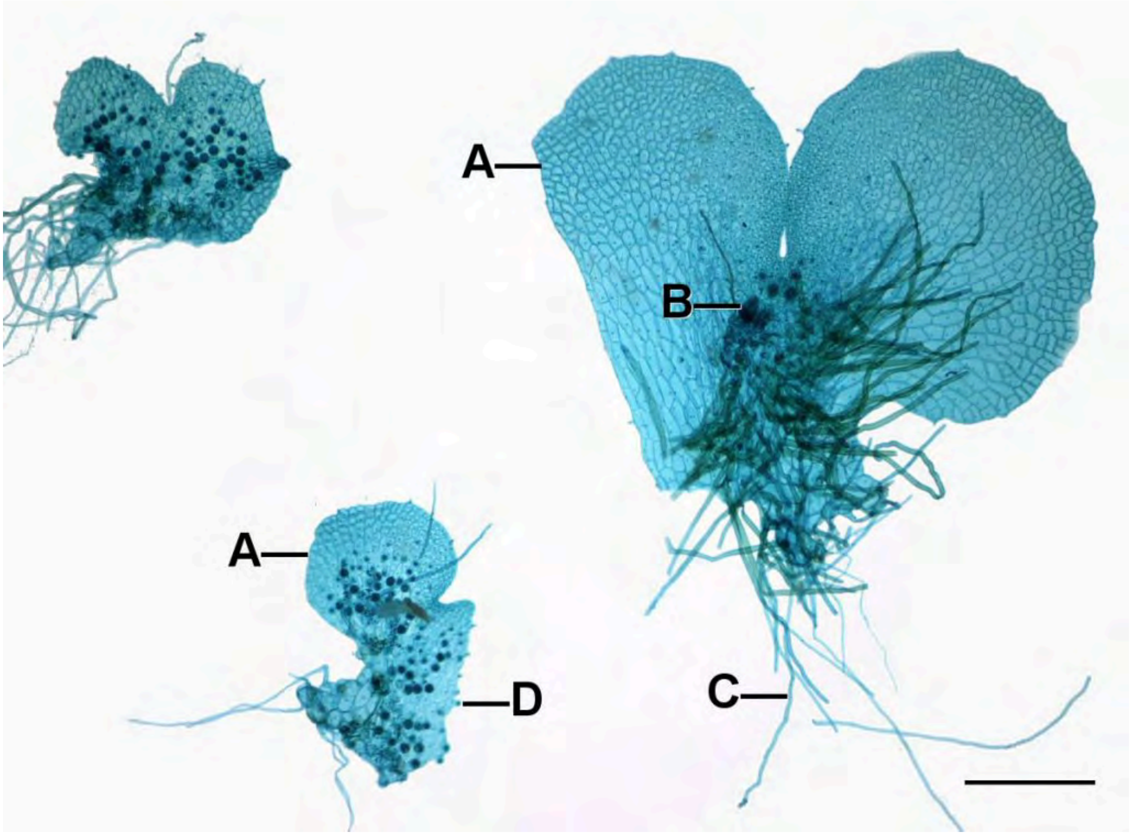

Fig. 7. Typical fern gametophyte, enlarged 5X. A= gametophyte, B= archegonium, C = rhizoid, D = antheridium, exposed as small bump when the gametophyte lobe is folded over.

released to the environment. When these germinate, they grow into haploid gametophytes and the process is repeated. Generally, the sporangia are produced in clusters called 'fruit dots' that are located on the underside of leaves (see **wood fern**). Other ferns have entire portions of their leaves that are obviously different and where spores are produced. A few ferns in this area are dimorphic (see **sensitive fern**), producing two types of leaves, some that are green and photosynthetic and which never produce spores and other leaves that are non-photosynthetic and produce abundant spores, while being nourished by the photosynthetic part of plant.

While this is the general pattern for ferns, there is some variation, one example of which is the water fern *Marsilea*, an aquatic fern that has several interesting features (see the information sheet on *Marsilea*). As is the case in a number of ferns, spores are produced on a specialized leaf that is very different looking from normal photosynthetic leaves. Whereas

Fig. 8. Model of a fern gametophyte showing the underside and a cross section. The antheridia are the small lumps and the archegonia the larger extensions. A cross section of each is shown. The egg cell colored blue. The minute sperm (red material inside the sectioned antheridium) are released when the the border cells of the antheridium are separated,

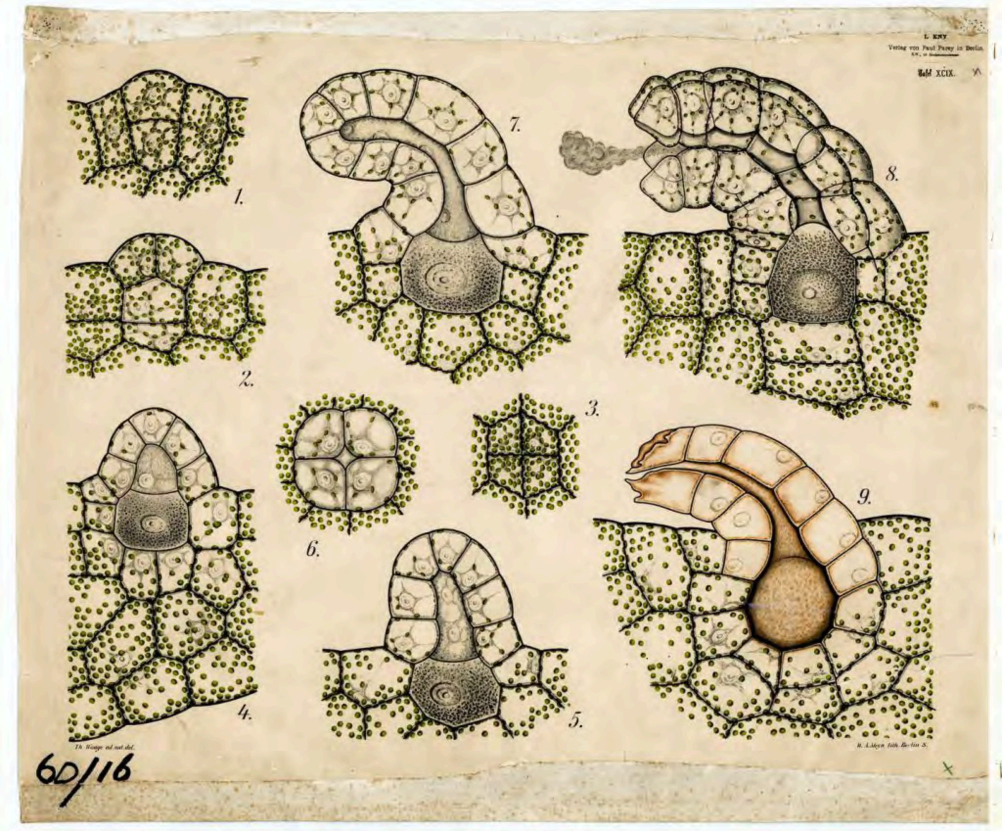

Fig. 9 Archegonial development in a fern occurs when cells divide to produce an extension that eventually has a 'canal' running from its tip to the base where a special cell, the egg, is produced.

the normal leaves are green and shaped like clover leaves, the spore bearing leaves are packaged into a seed-like structure, hard on the outside and capable of being dried out and revitalized (germinated) when re-wetted. At this time the 'fruiting' (i.e., spore bearing) leaf emerges into the water, looking very little like a leaf: it is without chlorophyll, very small and gelatinous. It produces spores in clusters. There are two types of spores, male spores called microspores and female spores called megaspores, each in separate sporangia. The technical name for plants that produce two types of spores is **heterosporous**. In contrast, most ferns are **homosporous**, producing only one type of spore that generally produces hermaphroditic (bisexual) gametophytes (described above) ; a few homosporous forms produce unisexual gametophytes, both male and female, but both coming from identical looking spore s.

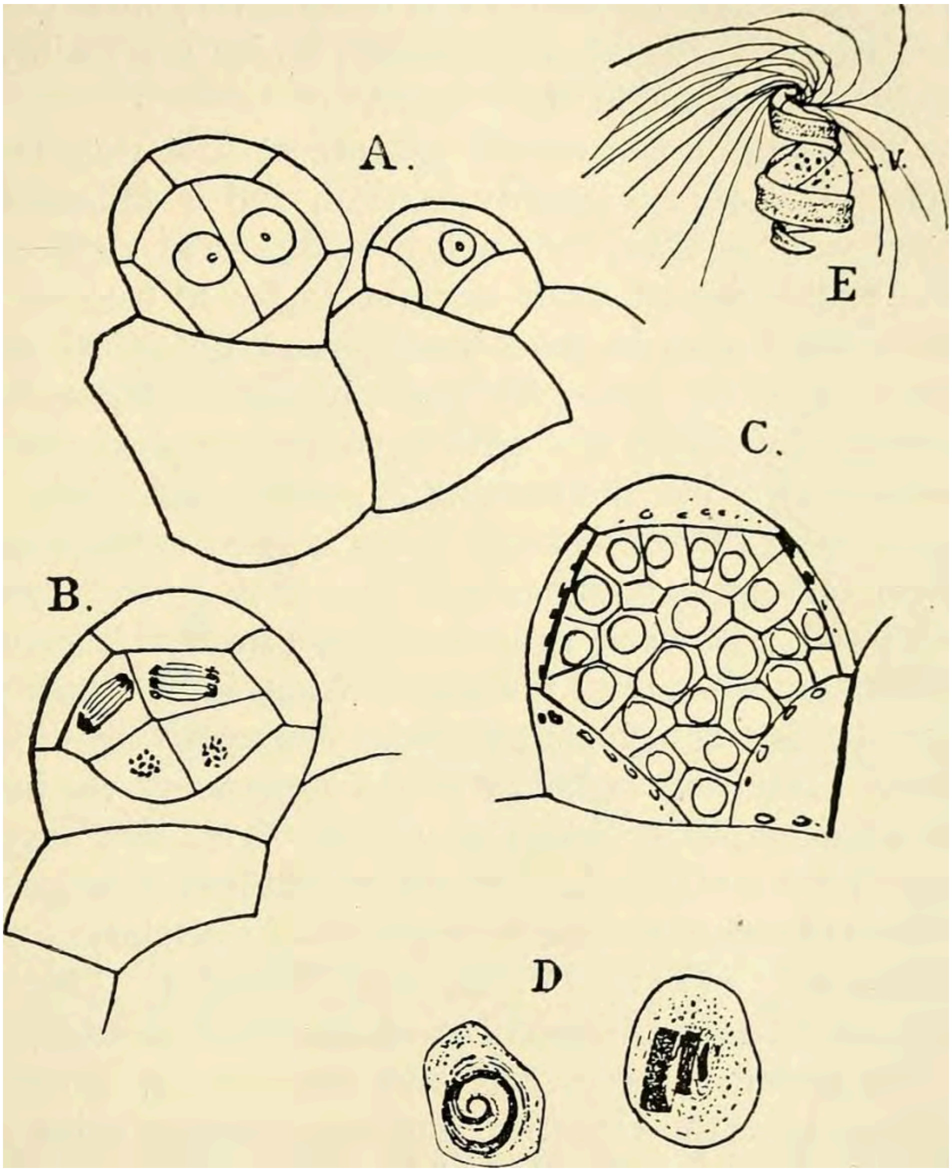

Fig. 10 Development of of fern antheridia occurs when cells proliferate (A-C) to form a globular mound with a 'jacket' of cells surrounding a group of cells that develop into sperm and are released when the jacket splits open. Mature sperm are shown in (E).

The two types of spores of *Marsilea* are readily distinguished by size. The megaspores are around 1 mm in length and germinate to produce egg-producing, female gametophytes. The microspores are only ~ 70 um in length and produce sperm-producing male gametophytes. Without any increase in size and without emerging from the microspore, the male spores germinate to produce a 'plant' with ~35 cells, 32 of them are spermatazoids,

Fig. 11 First leaf of a fern sporophyte at top, shown emerging from the archegonium of translucent gametophyte

multiflagellated corkscrew shaped sperm cells, roughly 10 um in size, that are released from the male gametophyte when the microspore wall is broken. The spermatazoids are chemically attracted to the female gametophyte. The female gametophyte is substantially larger than the male gametophyte but it still is small and, like the male gametophyte, exhibits **endosporic** development, meaning that its development occurs within the spore case of the megaspore, with only the very short neck extending from it. It produces a single archegonium with a single egg that the sperm swims to and fertilizes, forming a zygote. While the new sporophyte plant seemingly sprouts from the female spore, it actually is coming from a female gametophyte that is growing inside the spore case.

Further Reading

"Marsilea: Habitat, External Features and Reproduction" on Biology Discussion.com

- http://www.biologydiscussion.com/pteridophytes/marsilea-habitat-external-features-and-reproduction/53235

Another interesting fern is the Appalachian bristle fern, which is only known from the gametophyte form. Apparently, it has been reproducing asexually for millions of years! There are several other species of ferns known only as gametophytes.

Horsetails

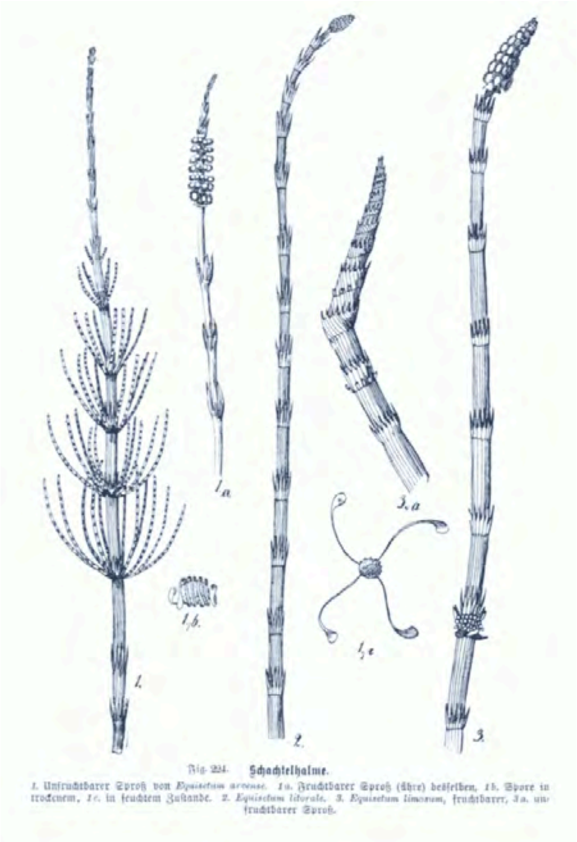

Fig. 12 Horsetail sporophytes; branches on 1, spore-bearing cones at the tip of 2 and 3. Spore with elators at 1a.

The basic pattern found in ferns, with a dominant sporophyte generation and a diminutive gametophyte generation, is found in the horsetails, a group of vascular plants that originated in the Paleozoic and produced a number of tree forms that were significant in producing extensive deposits that became coal and oil. There only remains one genus of horsetails and there are less than 20 species worldwide. All are herbaceous with perennial rhizomes that send up vertical branches that have a very distinctive pattern of growth with photosynthetic stems, very small scale-like leaves, and whorled branches or no branches. Spores are produced in a terminal cone-shaped structure, which is a cluster of specialized, spore bearing leaves. Spores are dispersed by the wind but their movement and release from the sporangium may be aided by structures called elators, strap-like appendages on the spore that move in response to the absorption and loss of water. Germination of the spore produces a small (~ 1-3 cm) photosynthetic gametophyte that looks like a pin cushion. Very short 'stems' are present with appendages that increase photosynthetic area. Antheridia and archegonia are usually both produced from the same gametophyte, although it may be unisexual for a period of time. Sperm are multi – flagellated and need to swim to reach the egg. Fertilization results in a zygote that develops into a diploid sporophyte that soon overgrows the gametophyte that it emerges from, producing roots and both horizontal stems (rhizomes) and vertical stems.

Clubmosses, Spikemosses and Quillworts

The se three groups are thought to be closely related and are grouped together as 'Lycopods' or 'Lycophytes', a group that also includes a number of fossil forms, including tree-like forms that were very important at the end of the Paleozoic era. The group has 1200 species and is considerably more diverse than the horsetails but much less diverse than the ferns (12,000 species). The sporophytes of extant clubmosses, spike mosses and quillworts are all herbaceous perennials. They generally spread extensively with above-ground and below-ground stems (tropical members are usually epiphytes). Although ancient members of the group exhibited woody growth, none of the species alive today do.

Clubmosses (Fig. 13) are unique in having gametophytes that are subterranean and non-photosynthetic, surviving as parasites by feeding off of fungi. These gametophytes live much longer than most gametophytes of vascular plants, some over 15 years. Spikemosses and quillworts are heterosporous and, like the aquatic fern *Marsilea*, the gametophytes develop endosporically; living off the material that was provisioned in the spore by the sporophyte plant. The male gametophyte is very short-lived and has little stored material (the microspore is small), but the female gametophyte is considerably bigger and lives for months on material present in the spore. Early growth of the sporophyte, out of the female gametophyte that is present in a megaspore, looks like a germinating seed (Fig. 14) and we will see in the next chapter that these are analogies — it is not thought that seed plants developed from the lycopods. Another feature of some spikemosses is that the 'female' spores, the ones that develop into female gametophytes, sometimes develop ON the sporophyte plant, a nother feature that is repeated in seed plants.

Fig. 13 Some clubmosses look like mosses but they are bigger, often up to 25 cm tall. Additionally, the plant you see is diploid not haploid as it is in mosses. Many clubmosses, including the one shown here, have stems that terminate in a ‘cone’ that consists of a cluster of specialized leaves with sporangia at their base.

Fig. 14 Root and shoot of spikemoss sporophyte emerging from megaspore where a female gametophyte has developed endosporically and produced an egg that was fertilized, producing a zygote that developed into the sporophyte

Further Reading and Viewing

- "Information about preparations for the Science Rendezvous (*Bring a Fern Baby Home for Mother's Day*) event" by Markham. Fern life cycle (nice images).
    - https://www.yorku.ca/planters/Fern_Babies/
- "Bryophyte Ecology" by Janice M. Glime. Bryophyte ecology, great site, more than just ecology.
    - https://digitalcommons.mtu.edu/bryophyte-ecology/
- "Australian Bryophytes – Bryophytes" by Heino Lepp. Bryophytes, hornworts, liverworts.
    - https://www.anbg.gov.au/bryophyte/index.html
- "Australian Bryophytes – What is a liverwort?" by Heino Lepp. What is a liverwort
    - https://www.anbg.gov.au/bryophyte/what-is-liverwort.html
- "Living together and living apart: the sexual lives of bryophytes" by David Haig. Bryophyte sex.
    - https://royalsocietypublishing.org/doi/10.1098/rstb.2015.0535

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CHAPTER 14: THE DEVELOPMENT OF SEEDS

Fig. 1 Familiar seeds of pea, corn and bean have been selected for thousands of years for large size.

Fig. 2 Many seeds are much smaller than the pea, corn, or bean seed. This figure compares a pea seed to a typical mustard seed.

Superficially, the production of seeds (Fig. 1-2) resembles the production of offspring in familiar animals: inside a diploid parent there develops a member of the 'next generation', which is nurtured inside its parent during the critical early stages of development and then is deposited outside its parent to finish its life. But appreciate that all plants exhibit an alternation of generations, so if a diploid (sporophyte) plant produces a new diploid (sporophyte) plant in a seed, one must account for the haploid gametophyte generation that had to come in between the two sporophyte generations. And one must also appreciate that seeds are NOT a substitute for spores, in fact, spores are critical to the production of seeds. The appearance of seeds (both in the sense of evolution and in the sense of development) is a complex story, one that involves the pattern of 'alternation of generations' shown in all plants. In light of this pattern, seeds represent a 'babushka' (Russian doll) with multiple generations found inside each other. An appreciation of this 'generation within a generation' is essential in understanding 'how seeds came to be' both evolutionarily and developmentally.

While it was long assumed that a structure as complex as seeds evolved once, many now feel that seeds evolved multiple times. Seeds therefore may represent an example of convergent evolution, where multiple lines have converged on a common feature. Whether or not this is actually the case, we can cite several features that allowed seeds to evolve and some of these features are exhibited in groups that do not produce seeds. Central to the appearance of seeds, in both a developmental and evolutionary sense, is the appearance of ovules, dynamic entities whose composition changes, ultimately ending up as a seed. In this chapter, we consider the transformations in the life cycle of plants that allowed for the development of seeds. In the next chapter, we consider the specific structures and patterns seen in conifers and flowering plants. Although we are focused on the seed, we will also consider a companion entity that is essential for the development of seeds: the pollen grain, which we will see is a miniaturized mobile, male gametophyte.

TOPICS

- Seed Structure
- Reduction
- Retention
- Arrested Development
- Provisioning
- Packaging

Seed Structure

A seed consists of three components: an embryonic sporophyte plant, a tissue that provides nutrition to that embryo, and a 'seed coat', the container tissue in which the embryo and nutritive tissue develop. The embryonic plant is diploid and it develops from a zygote formed by the union of egg and sperm. The seed coat is also diploid and it also is derived from a sporophyte plant, but it is an earlier sporophyte generation than the embryo. In both a temporal and also in a physical sense, a seed is a generation 'babushka, a Russian doll', with 'nested' generations. There are two sporophyte generations, the older one (seed coat) on the outside, and the new one (embryo) on the inside, with a gametophyte generation, or remnants of one, sandwiched between them. Seeds are the consequence of the megaspores not being dispersed but instead being retained in the sporophyte that

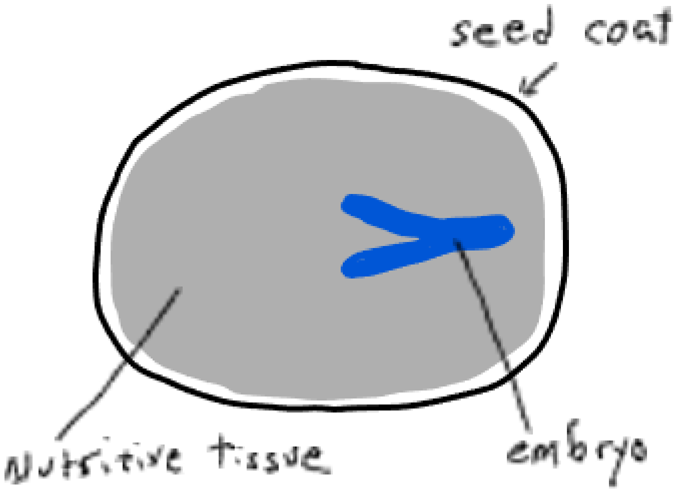

Fig. 3 Seed structure of a dicot, showing two cotyledons and a root/shoot axis

produces them. The spores germinate and egg-producing female gametophytes are consequently present on/in the sporophyte. Later, embryos, resulting from the fertilization of eggs produced by the gametophytes, are also present on/in the sporophyte. The structure where the retained spore is located and where the seed ultimately develops is called an **ovule**. Ultimately ovules develop into seeds containing a new sporophyte 'packaged' in the seed coat, a tissue derived from the original sporophyte. Prior to this, an ovule contains a female gametophyte; prior to this, ovules contain a spore that produces a female gametophyte; earlier still, they contain a megaspore mother cell that produces that spore. Finding gametophytes, both male and female, and understanding their development is key to the understanding of both the evolution and development of seeds.

Seed plants and their ancestors are heterosporous, producing two types of spores that develop into two types of gametophytes, one male and one female. Both the evolution of seeds and the development of any individual seed involve modifications of both the male and the female gametophyte, modifications in the structures that produce them, and modifications of the timing and location of important developmental processes.

We can describe the transformations that allowed for the evolution of seeds and also allow for the development of seeds with the acronym RRAPP: Reduction, Retention, Arrested development, Provisioning, Packaging.

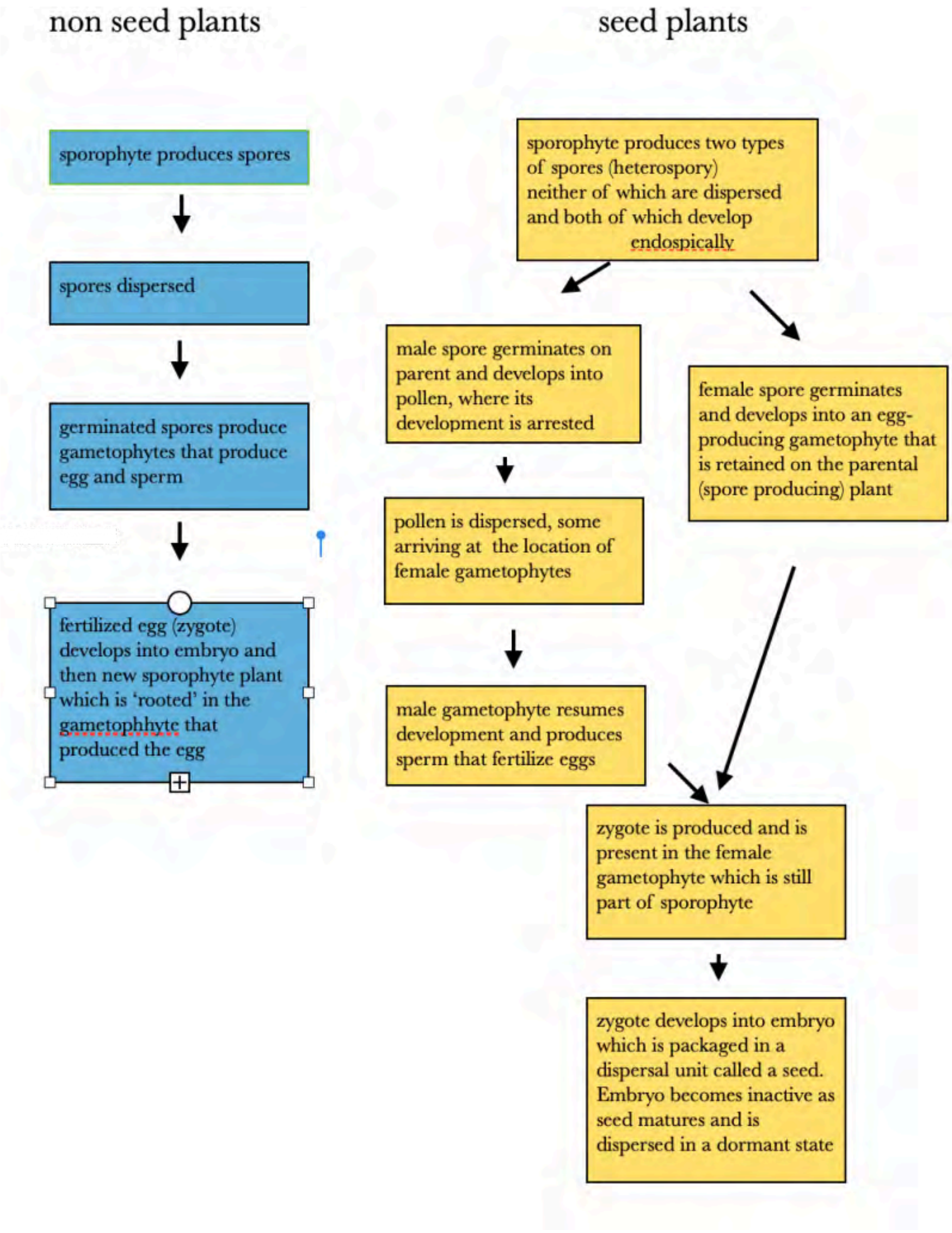

Fig. 4 A comparison of life cycles in seed plants and non-seed plants.

Reduction

Both the male and female gametophyte of seed plants are greatly reduced in size when compared to the gametophytes of other plants. The gametophytes of most plant groups are less apparent than the sporophytes, but in the seed plants they are so reduced that the pattern of alternation of generations is hard to see, and the misconception that plants reproduce like familiar animals, i.e. that there is no alternation of generations, that the only haploid cells are egg and sperm, is often assumed. The male gametophyte of seed plants is pollen, an organism of 3-6 cells that initiates its development from a spore on one sporophyte plant and completes its development on another sporophyte plant, in a location near that of the female gametophyte. For some groups, pollen releases a mobile, flagellated, sperm, but for the familiar groups, flowering plants and conifers, the male gametophyte is comparable to fungi in the sense that the gametophyte grows to (as opposed to swims to) the egg cell of the female gametophyte, fuses with it, and donates a sperm nucleus that joins with the nucleus of the egg cell to form a diploid zygote. Although the size of the male gametophyte is much reduced, it may live up to a year in conifers, starting its life on one sporophyte and ending it on another sporophyte.

The female gametophyte of seed plants is also severely reduced: it is only seven cells in flowering plants but may exceed one thousand cells in conifers. In all seed plants, the female gametophyte exists solely inside tissues of the sporophyte that produced it, having no independent existence whatsoever. Besides the reduction in **size** of the female gametophyte, there is also a reduction in the **number** of female gametophytes that are produced by any specific megasporangium. Remember that female gametophytes grow from megaspores that are produced after a meiotic ‘cell division’ (it actually is a process involving two cell divisions) of a megaspore mother cell. In all seed plants, only a single megaspore mother cell is produced inside the megasporangium. And although, typically, a megaspore mother cell produces four spores after meiosis, in seed plants three of the haploid nuclei degenerate after meiosis, leaving a single megaspore inside the megasporangium. Its structure is not at all spore-like, having no special spore wall at all; it has no need for protection because it is always buried inside of sporophyte tissue. Similarly, the megasporangium, the container in which megaspores develop, is very different from the sporangia of non-seed pants because it is not a container exposed to the environment but instead is a container embedded in sporophyte tissue. The development of the female gametophyte of seed plants occurs in an ovule, inside the megasporangium that develops in the ovule.

In seed plants, the megasporangium is called a nucellus, and in some groups, the nucellus remains as a feature of the fully developed seed.

Retention

There are multiple retention steps involved in the production of seeds and only the final steps are specific to just seed plants. First, there must be retention of the egg in the organism that produces it. In organisms that have gametes differentiated into a 'sperm' (a mobile, usually flagellated, cell that is released from the organism that produces it) and 'egg' (defined as a gamete that is larger and immobile), retention of the egg is often (e.g., *Oedogonium*, water molds), but not always (e.g., *Fucus)*, the case. Retention of the egg requires that fertilization occurs in/on the egg-producing organism. This is the case for mammals. For organisms that show alternation of generations, this means that the egg is fertilized in the gametophyte. The next retention found is a characteristic of all plants and is why the group is sometimes referred to as 'embryophytes'. It is the retention of the zygote, and the embryo that grows from it, in the female gametophyte plant. The retention of the egg, zygote, and embryo in the gametophyte allows the early development of the diploid generation to occur in a more controlled environment, with resources provided by the gametophyte. Note that this retention results in a sporophyte growing from a gametophyte, again something that is found in all plants.

The next retention step is the retention of the gametophyte on a spore-producing plant. Gametophytes develop from spores produced in a spore case (sporangium) present in/on a sporophyte plant. In seed-producing plants (and a very few non-seed producing plants, e.g., some spikemosses) gametophytes are retained on the sporophyte plant that produces them because the spore is retained in, not dispersed from, the sporangium of the spore-producing plant. For the female gametophytes of seed plants this retention is permanent, the female gametophyte is only found living on/in a sporophyte plant, in a megasporangium, the structure where the megaspores (the large spores that develop into female gametophytes) were produced. The male gametophyte also exhibits retention, but only temporarily; microspores (small spores that develop into male gametophytes) are retained in the microsporangium of the parent (sporophyte) plant and the initial development of the male gametophyte occurs there to produce a pollen grain. It is then dispersed and completes its development on another sporophyte plant, in the structure where the female gametophyte is found (the female cone of conifers, the flower of angiosperms).

Arrested development

An essential aspect of reproduction is dispersal. Especially for plants, with their indeterminate lifestyle, reproduction is of little significance unless there is a potential of dispersing to a new location. Dispersal is a significant aspect of sex as well. Although the processes of syngamy and meiosis can generate variability even when self-fertilization occurs, it is far more effective in producing variation, the raw material of evolution, if genetically distinct organisms participate. For sedentary plants, this requires movement of one individual to another, i.e., dispersal. For non-seed plants, dispersal is affected by two dispersal agents, the spore and the sperm. Spores have a tremendous dispersal ability because they are small and can be (generally) dispersed by the wind over large distances. This is only possible because the living thing inside the spore, the single cell, is extremely 'life-less'; that is, if one were to observe it, one would see very little biological activity. Metabolism is minimal, very few chemical reactions are occurring; it is a very stable structure and is in a state of 'suspended animation', the normal functions of life have been suspended temporarily. These life functions resume if the spore reaches a habitat that can trigger spore germination, which returns the spore to the animated state. In contrast, the other mobile agent of non-seed plants, sperm, are highly animated, they have a very substantial metabolic rate, not just because of their mobility (metabolism is required in order for the flagella to move) but their overall structure, in terms of organization of the membranes and cytosol, is much more typical of living things than that of dormant spores. Sperm are consuming stored energy supplies ('food') in order to sustain their life functions. Since sperm have a very limited ability to acquire food, their lifespan is set by the amount of the stored reserves that they are provisioned with when dispersed. The consequence is that sperm do not live very long and do not move very far.

Seed plants also have two dispersal agents: the seed and pollen. Both of them are 'in suspended animation' in the same way that spores are. This allows both of them to travel substantial distances. It is significant that both the seed and the pollen are not single cells, they are partially developed organisms that have begun their development on a 'parent' plant, yet have arrested their development and entered a 'resting stage' where they can survive adverse conditions and live without any additional resources. While the production of dormant cells (e.g., spores) are found in diverse groups of organisms, arresting development of a multicellular organism and having it enter a dormant stage is much less common, but it is essential to the development of seeds. Male gametophytes start their development inside the sporophyte plant when microspores are produced and develop into pollen. They are then dispersed in a dormant state, only to be revived if they reach the site of a female gametophyte, located on/in a sporophyte plant. Here, their development resumes, and they are able to produce a cell that can fertilize the egg.

Similarly, the new sporophyte generation found in a seed exhibits arrested development. After fertilization, the zygote that is produced generally quickly divides and develops into an embryo with a root/shoot axis, root and shoot apical meristems, and one or two leaves that are 'seed leaves' = cotyledons. Then the development ceases, no cell division or differentiation occurs in spite of the fact that nutrients are available and environmental conditions are favorable, at least temporarily. The metabolic rate drops to very low levels and the tolerance of the embryo to extremes in temperature, etc., substantially increases. In this state, the seed is dispersed, and it only resumes growth and development if conditions favorable to germination are met.

Provisioning

Seeds contain nutrients, both nutrients that can 'supply energy', i.e. materials that can be used in cellular respiration, and nutrients that are building materials for the construction of more plant cells. These energy and material supplies are very significant to a young autotroph because 'it takes money to make money' : in order to feed itself a plant needs structure but the structure isn't possible without energy and material supplies. Provisioning allows an organism to produce a structure that can obtain matter and energy on its own. Provisioning is accomplished in spores, but to a lesser extent; they do possess some materials, but the quantities are limited because the spore is generally only a single cell and generally small in size to promote dispersal.

Seeds are provisioned with materials that are stored in several different tissues:

1. Materials can be stored in the female gametophyte which sometimes is a component of the seed: in conifer seeds, the female gametophyte is a structure of roughly 1000 cells, all of which can store materials,
2. Material can be stored in the embryo itself, specifically in the cotyledon(s), the 'seed leaf / leaves' produced by the embryonic plant while growing inside the seed. In many angiosperms, the cotyledon(s) enlarge during development and store a substantial amount of materials. Many of our crop species possess large cotyledons that take up most of the seed volume and possess most of the stored material.

3. Material can be stored in the endosperm tissue, a unique tissue found in the seeds of angiosperms that are formed as a result of a second fertilization event, besides the one that created the zygote. The next chapter will discuss how this tissue is formed and develops. Although all angiosperms have endosperm tissue at some point in their development, some angiosperms lose their endosperm as the cotyledons expand and the seed is left with enlarged cotyledon(s) but little endosperm.

Fig. 5 Note the vascular traces ('threads') that connect to each seed. These contain vascular tissue that allows the seed to be provisioned with material from the parent plant. Each pea is a ripened ovule.

Wherever/however they are stored, the nutrients come from the parent sporophyte plant via phloem tissue. Careful examination of developing seeds will reveal that each is attached to the parent plant via a vascular thread.

Packaging

Seeds are eventually dispersed as a package inside of which is an embryo and stored food. The outside of the package (the seed coat) develops from sporophyte tissues of the parent plant that are called integuments, one or several layers of sporophyte tissue that form the outer layers of the ovule. Part of the transformation of an ovule into a seed is the transformation of the integuments (or part of the integuments) into a seed coat. The seed coat develops through a process of cell division and differentiation to form what is usually a rigid outside coating of the seed. These cells usually have thick secondary cell walls.

Thus, a seed is an embryo and stored food enclosed in a seed coat. The development of a seed, also known as the ripening of an ovule, involves three distinct developmental processes:

1. The development of a zygote into an embryo. The zygote is the new sporophyte generation. It divides to produce new cells and these grow and develop to produce an embryo with both a root and shoot apical meristem and one to several leaves,

called cotyledons, or seed leaves.

2. The transformation of the sporophyte tissues of the ovule into a seed coat. This typically involves the production of new cells, allowing for the ovule to increase in size, and the differentiation of these cells to produce a protective container.
3. The development of nutritive tissue to supply materials to the seed after it has been dispersed. As mentioned above, the nutritive tissue develops from different sources in different seeds but it always involves a proliferation of cells and an expansion of these cells as the material is supplied to them from the parental sporophyte.

Plants with seeds have been successful for multiple reasons including: (1) the early development of the sporophyte occurs in a very protected location inside of the previous sporophyte generation, (2) two items are dispersed: pollen, whose dispersal is focused on getting gametes together, and seeds, whose dispersal is focused on getting the next generation of sporophytes to new locations, (3) seeds are dispersed in a package that generally contains substantial quantities of nutrients, increasing the likelihood that the next sporophyte generation will be able to become established.

Further Reading and Viewing

- “The Seed Biology Place” by Gerhard Leubner
    - http://www.seedbiology.de/index.html
- Ancient date palm seeds.
    - http://www.thehistoryblog.com/archives/57817
- “The Surprising Lives of Cycads” by Jennifer Frazer. The surprising lives of cycads.
    - https://blogs.scientificamerican.com/artful-amoeba/the-surprising-lives-of-cycads/

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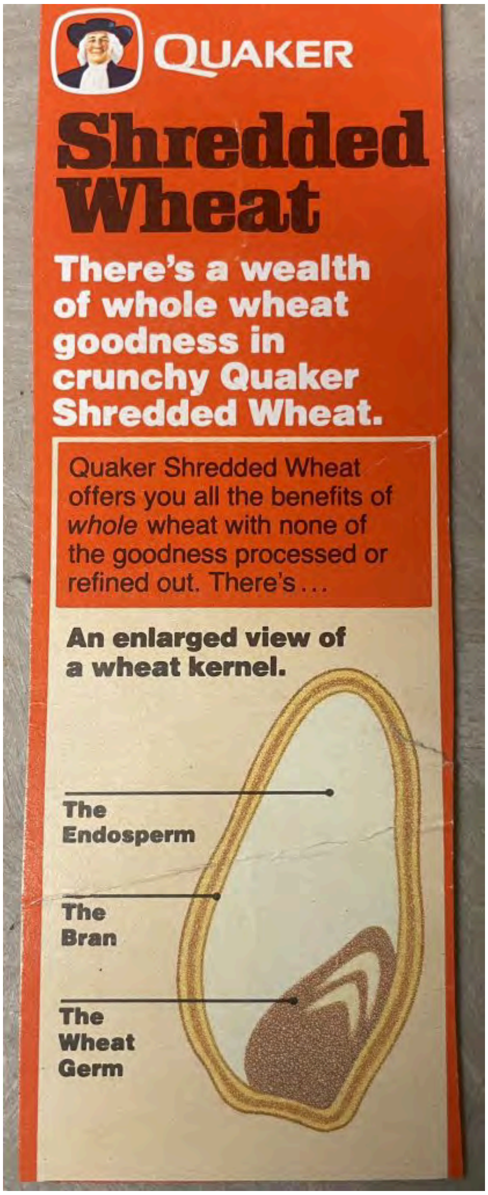
- shredded wheat



QUAKER

Shredded Wheat

There's a wealth of whole wheat goodness in crunchy Quaker Shredded Wheat.

Quaker Shredded Wheat offers you all the benefits of *whole* wheat with none of the goodness processed or refined out. There's…

An enlarged view of a wheat kernel.

Fig. 6 Depiction of a wheat seed (actually fruit). The germ is the embryo. The endosperm is stored food and the bran is the fused seed coat and fruit wall. White bread is made from wheat that has had the bran and germ removed.

CHAPTER 15: SEX AND REPRODUCTION IN SEED PLANTS

Seeds are a remarkable innovation that have been highly important to the evolution of plant life. The vast majority of plants that we observe and utilize possess seeds and seed plants dominate most terrestrial habitats. The last chapter described in general terms what seeds are and what modifications in the general plant life cycle of alternation of generations had to occur in order for seeds to appear. This chapter fills in some of the details for the five groups of seed plants:

- flowering plants, with 250,000 species, by far the most diverse and ubiquitous plant group
- conifers, although with only 1000 species, they are very commonly encountered and ecologically and economically important
- cycads, a small group of around 300 species with limited distribution and importance
- gnetophytes, a small group of only three genera and around 100 species
- Ginkgo, a single species that survives only where cultivated

In addition to these five extant groups, there are several groups of seed plants well represented in fossils but no longer present. These extinct species are sometimes lumped as 'seed ferns,' but both the lumping and the designation as a group are not thought to be accurate: they are not closely aligned with ferns and they probably represent an artificial (polyphyletic) grouping. Most workers believe that seeds evolved more than once and therefore that there should be no phylogenetic entity corresponding to either seed plants or to gymnosperms (i.e., seed plants lacking flowers) although these categories do persist. We will consider the details of the life cycle, in particular the form of the female gametophyte and the mechanisms associated with pollination and fertilization, for the five groups of extant seed plants.

TOPICS

- Conifer seed development
- Seed development in other gymnosperms
- Seed development in angiosperms
  - Flowers
  - Floral modifications
  - Fruits

Conifers

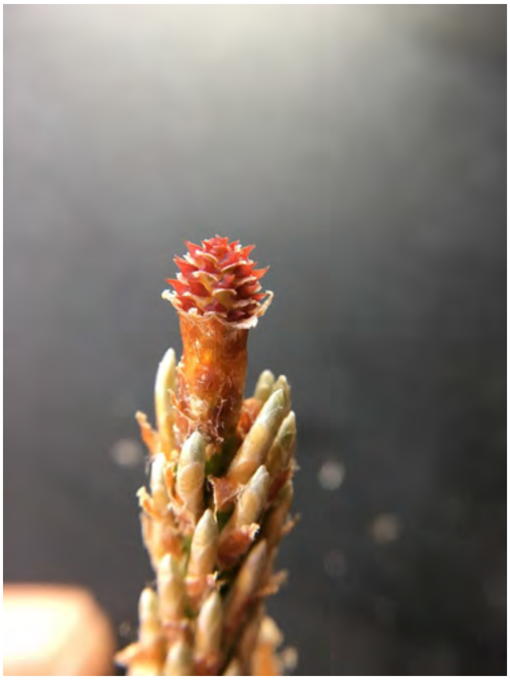


Fig. 1 Young female pine cone at the stage where it would be pollinated. Female cones appear in the spring at the tip of newly elongated branches. Below the cone are clusters of leaves just starting to expand.

Pines are the most commonly seen conifers and the group that will be described below but the basic pattern holds for all of the group. The plants that are recognized as pines are diploid, sporophyte plants. All conifers, including pines, are heterosporous and produce two kinds of spores, both on the same tree. The sites of spore production are the cones. The cones that most people recognize as 'pine cones' are female pine cones. These are not only the site of megaspore production but also the site of: megaspore germination that forms a gametophyte, egg production by that gametophyte, egg fertilization, and ultimately seed development. All these events take place in a location described as an ovule. These processes generally take multiple years and the structures one usually recognizes as pine cones have been living and developing over a time of two years or more, with many of the significant events occurring when the cone is much smaller and not as easily observed (Fig 1). A female cone consists of an axis (stem) bearing scales subtended by bracts, with the scales thought to be derivatives of modified branches. Upon the upper surface of the scale are the ovules, the structures that develop into seeds.

Male spores are produced in less familiar, but certainly easily observed, male pine cones, which grow more quickly than female cones but are present on the tree for a much shorter time. Typically, they are produced in the fall and are visible as a cluster of structures at the base of bud. These expand in the spring/early summer (Fig. 2) and dry up and wither a month later. In contrast to the female cones, male cones are simple in structure: a branch with tightly packed spore bearing leaves (sporophylls) , each with a pair of relatively large sporangia on their lower surface.

Fig. 2 Male pine cones are produced in clusters and are located below the current year's growth (expanding needles are seen above the male cones). Male cones wither and dry up soon after release pollen early in the summer but may remain on the plant until fall.

The gametophyte generation develops from microspores and megaspores that are produced and retained in the male and female cones. Gametophytes are highly reduced and, especially for the female gametophyte, largely invisible because of its small size and location. Male gametophytes are produced in the microsporangia of the male cones. These initially contain cells that undergo meiosis to produce microspores. At first, the spores are in clusters of four, reflecting their origin in the two divisions of meiosis (one cell to two cells to four cells). The spores eventually separate and undergo a very limited period of development, producing a haploid organism with four nuclei, usually in three cells (i.e., one cell has two nuclei), and possessing two wing-like air sacks (Fig. 3). Particularly significant to the development of the pollen grain (aka male gametophyte), is the fact that its development is arrested. This, and the fact that the microsporangium breaks open, allows the pollen to be dispersed by the wind.

Fig. 3 Pine pollen, typically about 60-100 um.

Fig. 4 A pine ovule at the time of pollination contains a megaspore mother cell.

Pollination is the name of the transfer of the male gametophyte (pollen) from where it is produced to the location of the female gametophyte, in conifers, a movement from a male pine cone to a location inside the female cone. At the time of pollen release, female cones are very small and are 'open' with spaces above each individual cone scale that are open to the outside (Fig. 4). Each female cone scale bears on its upper surface two ovules, each with a megasporangium imbedded in sporophyte tissue called integuments. Early in ovule development there is an opening, the micropylar canal, between the integuments that connects to a space between the cone scales. Pollen grains (male gametophytes) in the air can slide between the female cone scales and be deposited in the space next to the micropylar canal. The ovule secretes a liquid 'pollination drop' into this space and pollen grains end up in the liquid and rehydrate. In a mechanism not completely understood, the liquid with the pollen grains is withdrawn through the micropylar canal to a space on the inside of the integuments adjacent to the megasporangium.

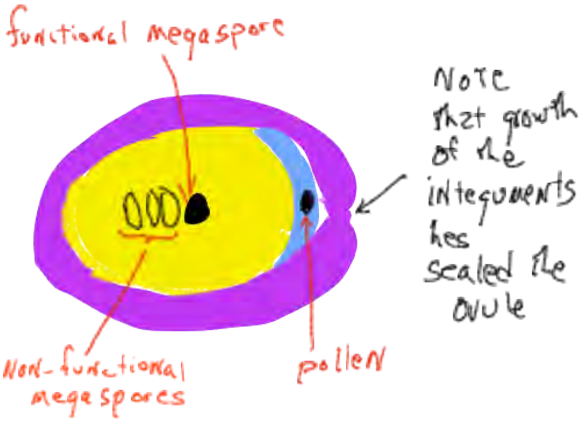


Fig. 5 Depiction of a pine ovule after pollination, typically in the summer after the female cones appear.

Soon thereafter the integuments grow to block the micropylar canal and the cone scales grow to seal the female cone off from the outside. At this time the megasporangium has a single megaspore mother cell destined to undergo meiosis. After meiosis, only one of the four daughter cells remains as a megaspore. The megaspore is not dispersed but develops within the megasporangium into a female gametophyte of several thousand cells that generally produces two or three archegonia, each of which produces a single egg. All of this occurs inside the female cone that is attached and is part of the sporophyte plant. The female gametophytes of conifers are highly reduced 'organisms' found within the ovulate cones, imbedded inside sporophyte tissue of the plant.

At the time of pollination there usually is no female gametophyte, only a megaspore. Inside the cone, the male gametophyte s continue their development, albeit very slowly in pines, requiring 12 months between pollination and fertilization.

Fig. 6 Depiction of a pine ovule just before fertilization, typically a year after pollination. The pollen has germinated and started growth towards the female gametophyte.

As the megaspore produces a spore that slowly develops into a female gametophyte, it goes through a 'free nuclear' stage where mitotic divisions are not accompanied by cell wall formation (the organism is coenocytic). Eventually cell walls form and the female gametophyte forms structures described as archegonia, each with a single egg.

As the female gametophyte develops, the pollen germinates and a single cell elongates from the grain, growing through the megasporangium (the nucellus) towards the female gametophyte (Fig. 6).. A little over a year after pollination this tube cell fuses with the egg cell and two sperm nuclei are released, one of which fuses with the egg nucleus, forming a zygote while the other nucleus disintegrates. During the time between pollination and fertilization, the female cones grow only a small amount and they remain closed to the outside. Note that no swimming sperm is produced, the male gametophyte grows to the egg by means of an elongate cell.

Following fertilization, the zygote develops into an embryo, imbedded in, and nourished by, the female gametophyte. Tissues surrounding the female gametophyte develop into a seed coat, often producing a wing structure that allows the seed to be dispersed by the wind. As the seed develops, the cone surrounding it also develops, often growing substantially. Following fertilization, seeds may mature in as short a time as one year but for most species it is two years or longer. In most pines, the cones eventually re-open, allowing the seeds to fall out and be dispersed by the wind. Sometimes the cones remained closed and only open following the intense heat of a fire. The female cones of junipers and yews develop fruit-like features that attract animals who facilitate seed dispersal by consuming the 'fruits' and defecating the seed in a new location.

Other gymnosperms

The three other groups of seed plants without flowers, Gnetophytes, Cycads and Ginkgo exhibit the same basic pattern of seed production: male spores develop into pollen grains which are dispersed from the sporophyte to finish their development in the structure that produces female spores and hence the female gametophytes. Pollination in at least some cycads and in some gnetophytes involves insects; in ginkgo and most gnetophytes pollination is by the wind. Gymnosperm literally means 'naked seed' and one feature that unifies the non-flowering seed plants is that, at the time of pollination, the ovules are accessible, not buried in tissues that the male gametophyte must grow through; instead, the ovules are available, at least for a brief period of time, because the cone scales have not fused with each other and the micropylar canal is open. However, the male gametophyte generally DOES have to grow through the megasporangium (the nucellus) to reach the egg. In cycads, the male gametophyte actually develops a type of feeding structure (called an haustorium), a branched filamentous structure permeating the nucellus and apparently obtaining nourishment from it. Eventually a flagellated, mobile sperm is released and swims through the fluid of an 'archegonial chamber', an area of fluid between the nucellus and the female gametophyte. Flagellated sperm are also found in ginkgo.

Flowering plants

The basic process of seed development in flowering plants is the same as in conifers. The major differences include the following:

- Male (pollen producing) and female (seed producing) organs are usually found together in the same structure, the flower, not separated on two distinct branches as they are in conifers.
- The ovules are produced inside a structure called an ovary, that is not open to the outside, thereby requir ing the male gametophyte grow through a substantial distance of sporophyte tissue in order to contact the female gametophyte
- The transfer of pollen (pollination) often involves biological agents (insects, birds, rarely mammals) and a variety of floral features enhance pollination.
- The female gametophyte , which is called an embryo sac (Fig. 7).

because it eventually contains the embryo, is even more reduced than in other seed plants, drastically so, usually consisting of only seven cells, six haploid cells, one of which is the egg, and one larger central cell with two haploid nuclei.

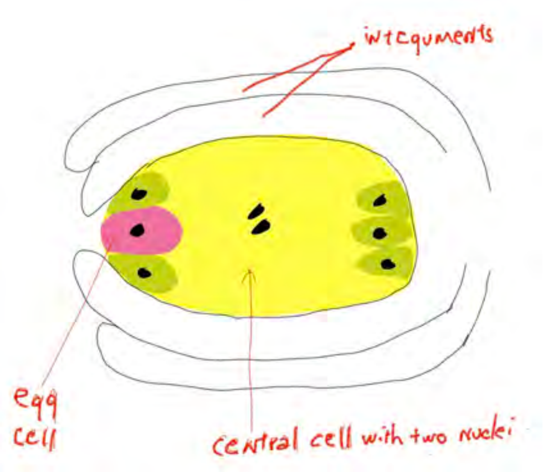


Fig. 7 An angiosperm ovule containing a mature female gametophyte (aka embryo sac). The gametophyte contains only seven cells, one an egg that gets fertilized to form a zygote and a large central cell that gets fertilized to form the triploid endosperm tissue. The surrounding integuments develop into the seed coat.

- Both of the sperm nuclei produced by the male gametophyte participate in a fertilization (syngamy) event. One fuses with the egg to form a zygote and the second fuses with the central cell. This sperm nucleus combines with the central cell's two nuclei to form a triploid 'endosperm' nucleus. The central cell then proliferates, forming a tissue, endosperm, that has a limited development and is only found during seed development and often, but not always, in the mature seed. The initial stages of endosperm development involve a 'free-nuclear' stage where nuclei divide with no cell wall formation, creating a multinucleate, all triploid, (coenocytic) cell. This material is called 'liquid endosperm' and is familiar as coconut milk, which is actually cytosol.
- In contrast with other seed plants, e.g., the conifers, in angiosperms the female gametophyte, which is very limited both in size and lifespan, is not the nutritive tissue for the developing embryo. In angiosperms the nutritive tissue for the developing embryo is the endosperm, the tissue resulting from a second fertilization event.

The flower

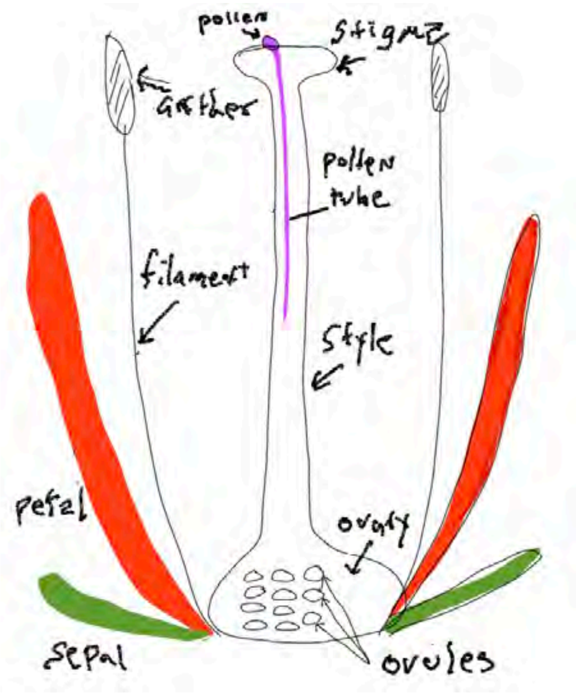


Fig. 8 An angiosperm flower usually consists of four whorls: sepals, petals, anthers (composed of a filament and an anther) and carpels (composed of a stigma, style and ovary). The ovary contains one to many ovules.

The flower is a highly modified stem, typically with four whorls that are bunched close together at the end of the branch. The components of each of the four whorls is thought to represent modified leaves, with the inner two whorls being highly modified spore bearing leaves (sporophylls) (Fig. 8-9). The elements of outermost whorl (**sepals**) are the most leaf-like, although often quite small. The elements of the next whorl (**petals**) are often leaf-like in form but usually are large and colorful structures that lack chlorophyll. The next whorl consists of **stamens** that often made up of of a stalk (a filament) terminating in a structure called an **anther** in which pollen is produced. Initially, the anthers possess microsporangia containing microspore mother cells. These produce microspores by meiosis and these spores germinate and develop into male gametophytes, aka pollen grains, composed of only two or three cells. When pollen is mature the anther generally opens up to make the pollen accessible to pollinators or the wind. **Carpels** are the innermost whorl and often are fused together so the central structure of the flower is a single ('compound') pistil. Carpel(s) generally consist of an enlarged base (the ovary), with a stalked structure (the style) emerging from its top that terminates with a surface (the stigma) that receives pollen. Inside the ovary are produced one too many ovules that eventually become seeds. Prior to this, the ovules are sites of megaspore production, female gametophyte (= **embryo sac**) development, fertilization and finally the process of seed development. Following pollination, the two-or-three celled male gametophyte (pollen) germinates on the stigma and grows through the style and then gains access to an ovule by growing through the micropylar canal, an opening between the integuments that surround each ovule. Pollen tube growth involves the expansion of a single cell, called the pollen tube, that delivers two male gametes to the embryo sac with the egg cell. The tube cell fuses to the embryo sac and delivers two sperm to bring about double fertilization, allowing for the subsequent development of the zygote and endosperm.

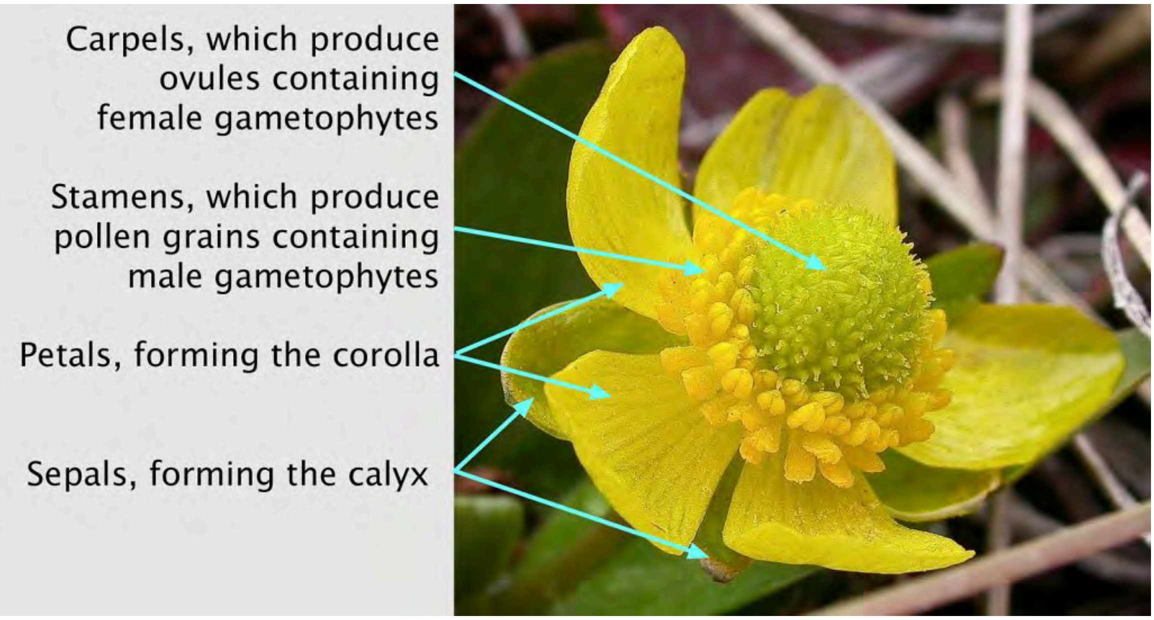


Fig. 9 Labelled image of *Ranunculus glaberrimus*

Floral modifications

The variations in the basic plan of flowers are one of the amazing stories of botany and of all biology. In general, the changes can be attributed to the forces of natural selection acting on the interaction between pollinators and plants. Some of the common transformations from the pattern described above include:

- fusion of the parts of a whorl, e.g., all the petals fused together to form a cup or funnel
- fusion of the members of two whorls (e.g., fusion of stamens on to the petals)
- reduction in the number of members of a whorl, in particular a reduction from many pistils to a single pistil as found in the flowers of Asteraceae flowers
- change from radial symmetry (all parts of a whorl being the same size and oriented in a similar fashion, Fig. 9-10) to bilateral symmetry with flowers having two sides that are mirror images of each other (Fig. 11), or sometimes to have no symmetry at all.

- placement of the ovary below the point of attachment of the other whorls
- elimination of multiple parts, sometimes forming unisexual flowers (Fig. 12).

Fig. 10 Like the buttercup flower above, Hepatica flowers have numerous stamens (inside of the petals) and carpels (the central part of the flower). Inside the stamen's cells are produced that undergo meiosis to produce haploid cells that undergo a limited development to produce pollen grains, minute male gametophytes. These complete their development if they arrive at a stigma (the tip of the carpel) and a triggered to germinate and grow to produce a pollen tube.

Fig. 11 This flower is not radially symmetrical but is bilaterally symmetrical. It has four stamens, two of which are longer than the other. The petals are fused and have numerous hairs on the inside. The pistil is composed of four fused carpels.

The fruit

After fertilization, the ovule transforms into a seed in a process that involves the coordinated development of three distinct tissues:

1. the zygote grows into an embryo;
2. the endosperm proliferates, first in a 'free-nuclear' pattern (nuclear divisions are not accompanied by cell wall formation) and subsequently by producing new cells, and finally, in some groups, the endosperm disappears as the embryo enlarges its cotyledon(s);
3. the tissues surrounding the embryo and endosperm develop into a seed coat.

Fig. 12 These are the male flowers of birch. Birch have separated male and female flowers and the male flowers are clustered together on a specialized branch called a catkin. Each individual flower lacks petals and pistils but has four stamens.

Note again that the genetic makeup of these three components differs—the embryo is a 'new generation' and is diploid, the endosperm is triploid and the surrounding tissues are diploid but are of a generation before that of the embryo.

While the ovule transforms into a seed, the ovary, and sometimes other tissues surrounding the ovary, develop into a structure called the fruit. The transformation of the ovary into a fruit generally involves the production of new cells, the growth of these cells and the development of features specific to plant being observed. The fruit generally has features that enhance the dispersal of seeds and often has features that protect the seed. Although it is generally easy to distinguish the seed from the fruit, occasionally there is no obvious demarkation between them or there may be a demarkation that is deceiving. For example, almonds are derived from a fruit that is like a cherry (in fact cherries and almonds are very closely related). We eat the fleshy part of cherries, which is part of the fruit. The 'pit' is not actually a seed but rather it is the seed surrounded by the innermost layer of the fruit. When you 'shell' an almond you are cracking open fruit tissue to reveal a single seed inside. In this case the protective role of the seed coat has been taken over by a portion of the fruit (Fig. 13). Similarly, a sunflower 'seed' is actually a one-seeded fruit and shelling the 'seed' is actually splitting open the fruit (Fig. 14).

Fig. 13 An almond 'nut' (on the left) is actually the innermost layer of the almond fruit enclosing a single seed (on the right). Unlike most seeds, the seed coat of an almond is not particularly rigid but the innermost part of the fruit is.

Fig. 14 A sunflower seed on the left and the entire sunflower fruit on the right.

Further Reading and Viewing

- "The Botanist in the Kitchen" by Katherine A. Preston. Great site with a

variety of excellent essays.
  - https://botanistinthekitchen.blog
- Plant of the week forest service posts.
  - https://www.fs.usda.gov/wildflowers/plant-of-the-week/index.php
- "Alsomitra macrocarpa – High Fliers" by Scott Zona. Winged seeds (also search for Alsomitra macrocarpa).
  - http://atanitokyo.blogspot.com/2008/07/high-fliers.html
- "The ancestral flower of angiosperms and its early diversification" by Hervé Sauquet. The ancestral flower of angiosperms.
  - https://www.nature.com/articles/ncomms16047
- "Asphodelus aestivus" by Tamara Bonnemaison. Nice site that is not posting new photos but has nice archive. Botany flower of the day.
  - https://botanyphoto.botanicalgarden.ubc.ca/2015/07/asphodelus-aestivus/
- "Apple Growth and Crop-load Management" by Steve McArtney. Apple fruit growth.
  - http://umassfruitnotes.com/v76n1/a3.pdf

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- Sunflower seed © Kaldari is licensed under a Public Domain license

CHAPTER 16: REPRODUCTION: DEVELOPMENT AND PHYSIOLOGY

Reproductive/sexual behavior and the life of the organism

The act of reproduction is central to the concept of an organism and it requires transformations in the behavior and physiology of the organism, transformations from simple maintenance to something more. Even for the simplest of unicellular organisms, reproduction requires a shift in the 'normal' activities. The 'cell cycle' (Fig. 1) describes the pattern of activities that the cells go through in order to reproduce (i.e., undergo mitosis).

As the cell goes through this cycle its activities change. Changes in gene expression result in changes from 'growth and synthesis' activities (G1, S, G2 stages) to mitosis activities. The transformations are even more substantial if a unicellular organism's reproduction involves sex. At some point in the sexual cycle meiosis has to be induced, requiring cells to drastically reorganize themselves in a manner that will halve the number of chromosomes in a very specific way. Additionally, cells with unique abilities, the ability to fuse with one another, need to be produced.

For multicellular organisms the required changes to bring about reproduction or to bring about the sexual process usually involve profound changes: new structures may appear and the and the behavior of the multicellular organism often shift s, sometimes in drastic ways, ways that may even end the life of that particular organism. This chapter considers some of the common patterns seen as organisms shift their physiology and structure in order to reproduce.

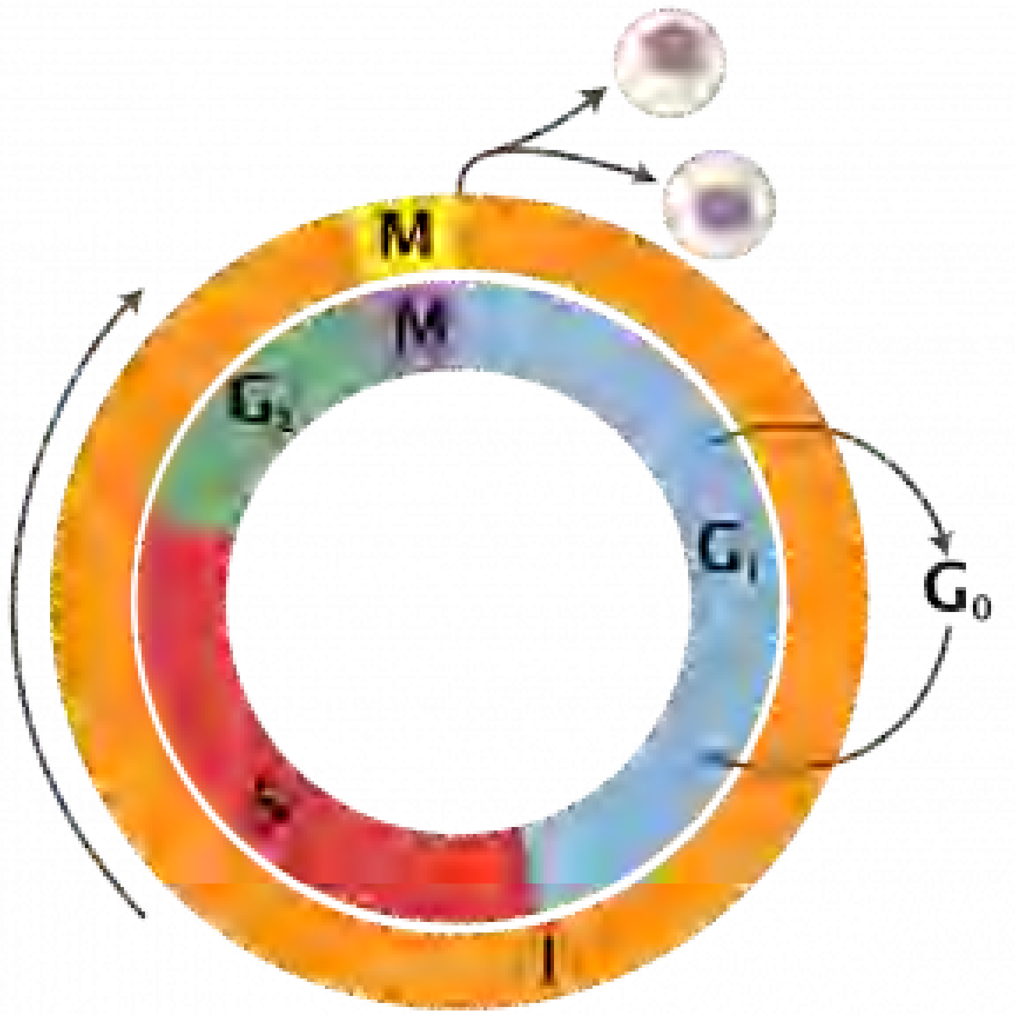

Fig. 1 The cell cycle: the outer ring divides cellular activities into two phases, interphase and mitosis. The inner ring separates interphase into 'gap' or growth stages (G1 and G2) and a synthesis (S) stage. During interphase a cell must acquire materials and synthesize molecules to be partitioned between the two daughter cells.

TOPICS

- Reproduct ive structures: production patterns in time and space
- Developmental control of sex and reproduction — general cues
- Patterns of reproduction in flowering plants
- Photoperiodism

Reproductive structures: production patterns in time and space

For most organisms, the normal activities involve the acquisition of matter and energy and the act of reproduction shifts resources from structures that acquire matter and energy to those that are involved in reproduction. For a plasmodial slime mold the shift in structure and behavior is dramatic and involves the whole organism: the coenocytic film that has been spreading across the substrate, finding food, suddenly shifts to a completely different structure, one that is immobile and unable to feed but one that is able to produce propagules.

Fig. 2 Cinnamon fern has two types of leaves, the brown ones produce spores but do no photosynthesis and the green ones photosynthesize but produce no spores. Both types of leaves are produced periodically, in the spring, but young ferns will only produce vegetative leaves until the plants reach a certain stage. Similar patterns are seen in sensitive fern.

For other organisms, the processes of both sex and reproduction involve specific structures that are specialized for those purposes. These may be either continuously or periodically produced. For example, normal fungal growth produces hyphae that are able to explore the medium it is growing in and obtain materials needed for growth. To reproduce asexually, e.g., with conidia, a fungal filament grows in a different direction (usually upwards) and produces a series of small, easily detached cells that can be dispersed. Thus, the fungus has shifted some of its activities from its normal growth mode to reproduct ive mode. Another example would be dimorphic fronds in ferns (Fig. 2, see also sensitive fern) and horsetails; the plant makes one kind of leaf for reproduction and another type of leaf for photosynthesis–consequently its ability to photosynthesize is reduced as its ability to reproduce increases.

For some plants, sexual reproduction involves a dramatic reorganization comparable to the slime mold. Remember that a flower is a transformed branch and that branches are 'new modules', significant not only for their growth but also because of its potential to produce even more modules. The transition of that branch to a flower changes all this — it converts an indeterminate structure, capable of growing and producing more modules, into a determinate structure that produces a flower or flowers and then a fruit and then dies, eliminating that module, and removing its potential to produce any other modules. If all the shoots of a plant transition to flowering at the same time, then the plant as a whole becomes determinate and will die after fruiting. This is what happens in wheat (Fig. 3).

Fig. 3 Maturing (and dying) wheat plants

We can identify two ‘extremes’ in the pattern of allocation of resources to reproduction, one involves partitioning the organism in space and the other involves partitioning it in time. Some organisms, like cinnamon ferns, most algae and many fungi, simultaneously produce parts for reproduction and parts that conduct ‘normal’ activities. While the degree of partitioning may vary with time, the organism grows and reproduces more or less continuously. At the other extreme are organisms that spend part of their life growing and and then transform into a different type of organism in order to reproduce. Examples include butterflies, mayflies, carrot (Queen Anne’s lace) , burdock, beet and mullein, all of which produce a very short stem with multiple leaves and no branches in the first year of life. In the second year the stem elongates, branches form and flowers and fruits are produced. Most of the material stored from the first year of growth is directed to the developing seeds. In addition, the leaves are dismantled to provide additional resources. Consequently, the ability of the plant to photosynthesize disappears and the plant dies in the process of flowering and fruiting. In the first year the plant focuses on growth (acquisition of materials) , in the second, on reproducing.

Control of reproduction and sex

In most organisms the ability to reproduce is controlled by cues from the environment that are sensed and bring about changes in structure and allocation of resources. Although it is often assumed that reproduction (and hence population growth) is dictated by resources, there certainly are situations where resources are available but organisms do not utilize these resources to reproduce. Instead of being tied to resources, many organism s’ reproduction is tied to specific cues in the environment–they respond to these cues by reproducing. Stated another way, although adequate resources are necessary for reproduction, they are often not sufficient to bring about reproduction. Among other things this makes predicting population growth more difficult. This topic will be considered more when discussing the behavior of populations. Here we will discuss the particular cues that organisms utilize to trigger the reproductive process, sexual or asexual, and then consider the (primarily sexual) reproductive patterns found in flowering plants and some specific cues that control many plants’ reproductive patterns.

Cues to initiate reproduction and/or sex

Growth/development

For many unicellular organisms reproducing by mitosis, reproduction simply involves the achievement of a particular stage in cellular development. This is generally somehow tied to growth, i.e., the accumulation of enough materials that the cell can be partitioned in two. Growth is connected to time ('cells have to reach a certain age to reproduce') but only as mediated by material acquisition. Bacteria that divide every 20 minutes are not timing the intervals, there are processes taking place, some of them fundamentally tied to the acquisition of materials, that take 20 minutes to occur. If you change the temperature or change the availability of materials, bacteria will take a longer time to divide. Also, as noted above, organisms have the ability to change their rate of material acquisition, i.e., they control how fast they grow, and because of this, they can control their rate of reproduction.

Time

Although all eukaryotes appear to be able to keep time, very few have reproduction or sex cued specifically by time (i.e., have a stopwatch that is initiated and then reproduces at the end of a specific time). However, it is common, especially for plants that have been selected for cultivation, that an integration of time and temperature determines flowering. Plants need to grow to a certain stage in order to reproduce and this requires time and favorable temperatures. Many seed packets for home gardeners state something like 'flowers in 60 days'— this is assuming a 'normal' temperature regime; if temperatures are cold, it might take 70 days. This idea of integrating time and temperature is discussed more in Chapter 26.

Nutrients

As discussed above, nutrition (i.e., the acquisition of resources required for growth) clearly can be a factor influencing growth and development, but sometimes nutrition plays a more specific role. *Chlamydomonas* sex is triggered by low nitrogen levels; fungal reproduction often requires a specific media formulation different from the medium that brings about growth; slime molds can be induced to sporulate (a phase of sexual reproduction) by specific nutrient regimes. The ability of some perennial plants to respond to flowering cues has been associated with carbon/nitrogen ratios in the plant that can be affected by both photosynthetic activity and nutrient availability.

Adverse/favorable conditions

Surprisingly, both good and bad conditions may trigger sex or reproduction, depending on the species. A number of organisms change their activities when conditions become unfavorable (e.g., high or low temperatures, drought, high or low pH, toxic levels of certain chemicals) and often the change involves reproduction and/or sex. For example, slime mold plasmodia (the multinucleate giant cells) are induced to form sporangia when the conditions are poor. A number of tree species are known to flower particularly well when they are about to die. These behaviors might be considered adaptive since it produces structures (seeds, spores) that are resistant to harsh conditions at a time when conditions are deteriorating. Such structures may also be beneficial because they also provide for dispersal and movement to new, and possibly more favorable, conditions. At the same time, a cessation or reduction in the production of propagules during adverse conditions can be justified because the resources are needed to keep the organism alive and not used on the 'frills' of reproduction and sex.

Cues that are useful in predicting upcoming conditions

Many species live in environments that vary seasonally and that have certain portions of the year that are much more favorable to activities related to reproduction/sex than other periods. The most obvious activity related to reproduction/sex is material acquisition but other factors might include: availability of dispersal agents (e.g., wind or perhaps specific pollinators or fruit eaters), lack of predators for offspring, etc. The most common cue that predicts upcoming conditions is photoperiod (the amount of light and darkness within a day). Photoperiodic control of flowering will be considered after describing the patterns of reproductive effort found in flowering plants.

Patterns of reproduction and sex in flowering plants

Angiosperms can be divided into two groups based on their flowering behavior: monocarpic plants, that flower a single time and die, and polycarpic plants, that flower multi-

Fig. 4 Senescing soybeans. Soybeans are a monocarpic, annual plant that converts all its meristems into flowers that produce fruit and cause the entire plant to senesce, as evidenced by the yellowing leaves.

ple times. Monocarpic plants will die after flowering because all of their meristems have been converted from indeterminate vegetative shoots into determinate flowering shoots. After flowering, the flowers develop into fruits and the plant dies both because there are no more vegetative shoots to produce more leaves and because the leaves that were already present have been 'scavenged' as a source of materials for the developing seeds and consequently have been destroyed. This was discussed above and is found in a number of crop species including corn, wheat, soybean (Fig. 3 and 4).

Many monocarpic plants are annuals, living for only a year. Whatever it takes to get the plant to flower occurs within a year of the germination of the seed. If a specific cue is involved, then within a year the plant develops a sensitivity to the cue and can respond. Note that some of the annual plants in northern (and southern) latitudes, especially those grown in gardens, may be annuals only because of the elimination of favorable conditions in the fall—they simply are killed by frost and cold and would live longer if the conditions were more favorable. Most of these plants are not native to this area; most of the annuals that are native to this area kill themselves off in the flowering process. In temperate North American habitats, most monocarpic annuals germinate in the spring and flower during the summer, but some, called winter annuals, germinate in the fall, overwinter and flower in the spring. Most of the wheat grown in the northern U.S. would be considered a winter annual, although in central and southern parts of the country the wheat grown is a regular annual and planted in the spring.

Monocarpic plants may also be biennials, sometimes defined as plants that live for two years but more accurately described as plants that live for two growing seasons. These plants are generally found in habitats that are seasonal, i.e., have part of the year favorable for growth and part unfavorable for growth, usually because of low temperatures, but occasionally because of lack of moisture. Biennials behave the way they do because during the first growing season they are not responsive to the cues that induce flowering, while in the second season they are. An example would be beet s, a species that needs a cold winter in order to be able to respond to the cues (photoperiod, see below) that trigger flowerin g. It does not flower the first growing season even though it receives the photoperiodic cue to flower but does flower the second year after being exposed to cold. Biennials are monocarpic and generally exhibit a substantial dimorphism between the first and second year, often having a very short stem and no branches the first year and elongating and branching stem the second year. As mentioned earlier, one might think of the form the first year being associated with acquiring resources and the form the second year being associated with reproduction.

Although uncommon, a few monocarpic plants are perennial, living for multiple years and then flowering once (Fig. 5). Examples include century plant (*Agave),* bamboo, and some gentian species. The case of bamboo is particularly significant to panda bears because they feed almost exclusively on the vegetative (i.e., non-flowering) bamboo plants which can grow for up to 70 or more years while forming an extensive clone. When the plant flowers, acres of bamboo, the product of 70+ years of growth, produces seeds (which pandas do not eat) and in the process the bamboo dies, leaving the panda with no source of food.

Fig. 5 Agave, a perennial, monocarpic plant. Three plants are visible: on the left is a dying plant that has just flowered and developed fruit; in the middle is a dead plant that has toppled over; on the right is a plant yet to flower.

Polycarpic plants are perennial. They potentially live forever because only some modules are turned into flowering shoots on any particular year. Since all of the plant is exposed to the same set of cues, the different behaviors of different meristems, some producing flowers and some not, is the result of differing sensitivity to cues. A common pattern is that only stems that are one-year-old respond to the flowering cue (see coltsfoot). Thus, a plant will have two groups of shoots, shoots of the current year that do not respond, and shoots of the previous year that do respond, and therefore produce flowers and fruits and die. Hence, in the spring of the year, these plants are composed solely of the shoots that will become flowers. But before they flower, they produce branch shoots that will not become flowers until the next year. A version of this pattern is seen in many varieties of raspberry/blackberry. Although the plant is perennial, this is the result of underground stems. The vertical stems, called canes, are biennial, the first year growing vegetatively, the second year producing flowers and fruits and dying. A raspberry patch is perennial but the stems you see only live for two years, each cane behaving like a biennial.

Flowering plant cues for reproduction

While a few plants, especially plants selected for cultivation, require no specific environmental cue to induce flowering, they simply flower after the plant has grown sufficiently, the majority of plants require specific environmental cues to trigger flowering. However, for many plants, the cue alone is not sufficient to trigger flowering; the plant itself must be able to respond to the cue, i.e., the plant initially is not responsive and does not respond to particular cues. With time, the plant develops a sensitivity to the cue and can respond when the cue occurs. Thus, when we consider what makes a plant flower, we must consider the possibility that two processes are involved: one triggering responsiveness and a second triggering the flowering itself. A good example of this is the flowering of beet: in order to flower it must first be exposed to cool temperatures for a period of time; this develops its ability to respond to a specific cue that induces flowering, which is photoperiod, a particular combination of light and dark in a 24-hour period. Beet will not respond to photoperiod unless it has first been exposed to cool temperatures. Hence, it grows the first year without flowering, and only during the second summer, after a period of cool temperatures during the winter, will it be induced to flower.

Photoperiodism

A wide variety of organisms, including plants, animals, fungi and protists, respond to the photoperiod, relative amount of light and dark in a 24-hour period. For many organisms, including many plants, it is one of key determinants influencing reproduction (Fig. 6). Specifically for flowering plants, photoperiod often determines when a plant flowers, and photoperiod has probably been most extensively studied in this context. But it is important to appreciate that in addition to reproduction, photoperiod may affect a wide variety of organism features: physiology, structure, and behavior. Additionally, photoperiod's mechanism of action is at the molecular level, i.e., by influencing which genes are being expressed.

Photoperiod is a significant cue for organisms living north or south of the equator because the photoperiod predicts upcoming conditions. The approaching winter can be sensed by the shortening photoperiods; an upcoming spring can be sensed by lengthening photoperiods.

Plants have turned out to be excellent organisms to study photoperiodism because, for some of them, a single day of a particular photoperiod can result in a measurable response. In contrast, for some organisms, and indeed for most plants, a response is only apparent after prolonged exposure to particular photoperiods.

Early studies established the fact that it is the night period that is critical. An interruption of the dark period can change a response while an interruption of the light period does not alter behavior. The ability to respond to photoperiod requires two abilities: the ability to sense light vs. dark, i.e., a photosensor, and the ability to keep time. In all organisms studied, the timing mechanism appears to be associated with an internal 24-hour rhythmicity, something described as the circadian clock because the rhythms in behavior have a periodicity of around (circa = around) 24 hours. A circadian rhythm is probably found in all eukaryotic organisms, certainly it seems to be a feature of most eukaryotic organisms where it has been looked for.

Fig. 6 Chrysanthemum flowers in the fall in response to short days.

The actual photoperiodic response is the result of a particular pattern of light and dark that is imposed on an organism's internal 24-hour rhythm. As a result, the behavior observed after giving an organism 12 hours of light and 12 hours of dark depends upon what portion of its 24-hour cycle that the 12 hours of dark is applied. The timing mechanism is not a stopwatch that times the dark period, what is critical is how periods of light/dark interact with internal rhythms that have a 24-hour periodicity. Stated differently, there is a periodicity in plants response to darkness.

The most commonly encountered photoperiodic responses involve reproduction but more generally photoperiod can be an organizing factor determining the patterns of growth and development that an organism exhibits. Some of these are listed below:

In flowering plants:

- flower production
- temperature tolerance
- production of vegetative buds
- activation of buds
- activation of lateral buds
- formation of tubers (Fig. 7)
- seed gemination

In non-flowering seed plants:

- production of cones
- formation and activation of buds

In dinoflagellates:

- cyst formation

Fig. 7 Potatoes form when the tips of short underground stems enlarge and store carbohydrates. This transformation is a photoperiodic response, triggered by shorter days.

In both red and brown algae:

- pattern of growth and formation of reproductive structures

In animals:

- development of ovary and testes in birds and other animals and consequent changes in behavior

For flowering plants, the photoperiodic flowering response is generally put into one of three categories:

- long-day plants, which flower only if daylengths (periods of light) are **longer** than some **critical value.**

- short-day plants, which flower only if daylengths (periods of light) are **shorter** than some **critical value.**
- day neutral plants whose flowering is not obviously tied to photoperiod.

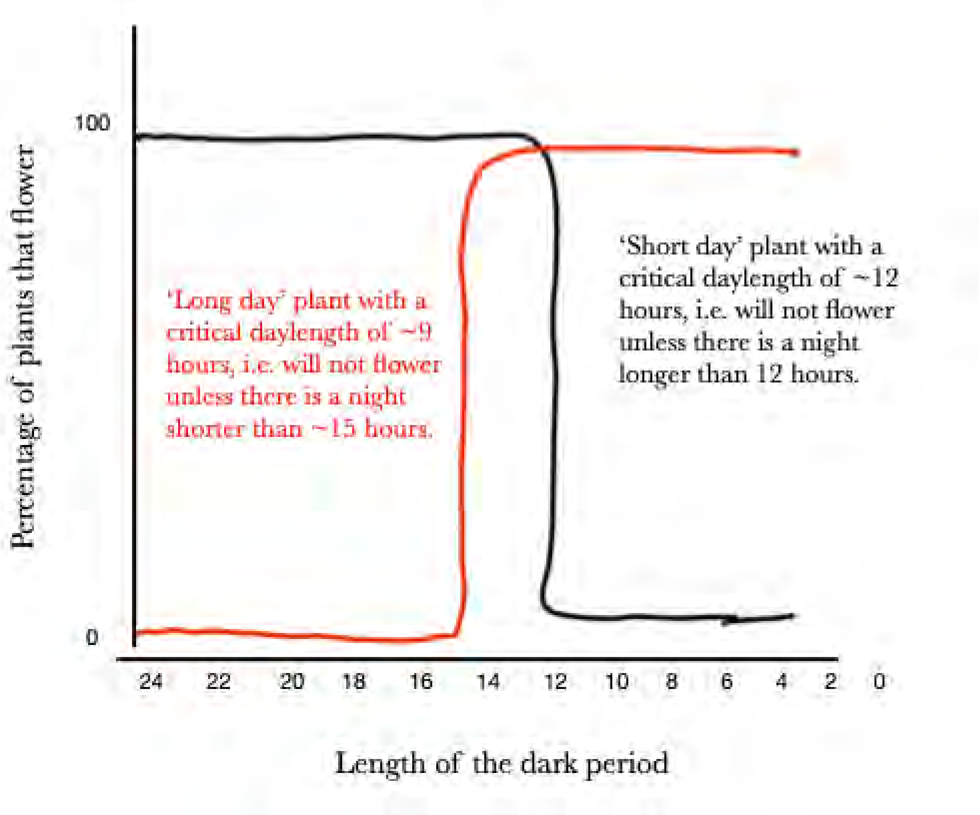

Fig. 8 Response to photoperiod in long day (red) and short day (black) plants.

Short-day plants (black line) need night periods longer than some critical value in order to flower (Fig 8). Long-day plants (red line) need night lengths shorter than some critical value in order to flower. The actual critical daylength (i.e., the vertical part of the line) may shift to the right or left depending upon the particular species (or variety within a species). Note that neither of the two plants illustrated here would be flowering with night lengths between 15 and 12 hours. Similarly, if the red line were shifted enough to the right, or the black line enough to the left, one would have situations where both long-day and short-day plants would flower at the same photoperiod.

Although the names refer to periods of light in a 24-hour period, it is actually the night period that is critical. Hence long-day plants might better be called short-night plants and short-day plants might better be called long-night plants (but they aren't!!). Another confusing factor to appreciate is that although we might consider that any day with more than 12 hours of light is a 'long-day' (and 'short-night'), what is critical is the actual length compared to the critical value. Hence, one can have both long-day and short-day plants flowering under the same photoperiod: a photoperiod of 10 hours light and 14 hours dark would trigger flowering in a long-day plant with a critical value of 9 hours of light and also a short-day plant with a critical value of 11 hours of light.

While plant responses fall into these three general types, the actual responses are often complicated by two factors. One is that a plant response to a particular treatment may not necessarily 'all or nothing' (described as a 'qualitative response'), meaning that the plant will not flower unless it receives the appropriate stimulus. For many plants the response to an appropriate stimulus is 'quantitative' meaning that the plant flowers more quickly or with more flowers if receiving a particular stimulus (the transition lines on the graph above may not be vertical but instead have a slope). A second complicating factor is that photoperiodic sensitivity may involve multiple sequential signals, including ones that do not involve photoperiod. For example, some plants will only respond to long-days after short-days or respond to long-days only after a period of time under cool temperature conditions.

In plants there appears to be two pigments, phytochrome and cryptochrome, that can interact with circadian rhythmic phenomena and produce photoperiodic responses. While both of these pigments interface with several different physiological processes, the flowering response appears to be the result of changes in gene expression resulting from signal transduction systems that influence protein/DNA interactions. Specifically, the appropriate photoperiodic stimulus appears to result in production of specific mRNA molecules that are important in transforming vegetative shoot apical meristems into floral meristems.

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- Potatoes © BASFPlantScience is licensed under a CC BY (Attribution) license

Further Reading and Viewing

- "The Molecular Basis of Diversity in the Photoperiodic Flowering Responses of Arabidopsis and Rice" by Ryosuke Hayama and George Coupland. A good summary of the molecular basis for photoperiodic phenomena.
    - https://www.ncbi.nlm.nih.gov/pmc/articles/PMC514104/

CHAPTER 17: SEX, EVOLUTION, AND THE BIOLOGICAL SPECIES CONCEPT

Sex, Evolution, and Species

Fig. 1 A population of cottongrass in the Pyrenees mountains.

Although for many organisms sex is crucial to the ability to reproduce, sex is an important concept to biology for more reasons than this. Sex is critical to two other highly significant biological topics: the process of evolution and the concept of species, two things that are in fact interconnected. Evolution describes changes through time. What is it that changes? It is not an individual organism, whose changes are described as 'development'. What evolves are groups of organisms, i.e., populations (Fig. 1). Populations are usually described as a group of organisms of the same species. The criterion that puts individuals together into a group called a species is the ability to interbreed, i.e., species are groups of organisms united by the fact that they can potentially interbreed, and the only way to interbreed is through sex. Sex is the process that connects individuals together in to something called a species, a group of interbreeding organisms. Species, i.e. interbreeding groups, are thought to be the biological entity that evolves. Additionally, sex is significant to the process of Darwinian evolution because:

- sex can be an important process that generates variation within a population and variation is significant to the evolution ary process, providing the 'raw material' upon which the process of natural selection can act.

- sex provides a mechanism to spread particular features within a population, allowing favorable characteristics to spread.

It should be pointed out that sex is certainly **not** required for the process of evolution. There are a number of groups (e.g., bacteria) that evolve readily and have no sexual process (although bacteria DO have processes that allow characteristics to spread within a population, it is not sex).

Moreover, groups that do not have sex cannot be categorized as having species (although oftentimes they are!) because sex is what delineates an 'interbreeding group', which is the criterion usually used to define species. Thus, although sex and species are significant to evolution, they are not essential to evolution. As noted earlier, several of the groups considered here (e.g., dinoflagellates) do not have sex, but the groups' diversity clearly point to the fact that evolution has been, and presumably still is, operating.

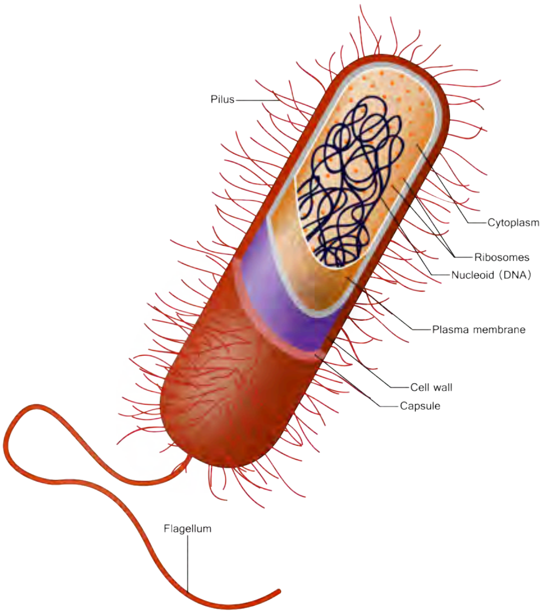

Fig. 2 Bacteria and archaea have no sex, yet they have other methods to exchange genetic material and they certainly do evolve.

Even within groups that are considered to be sexual, e.g., flowering plants, there are groups that do not participate in sex. Dandelions produce seeds but do so in a manner that does not involve sex. Such groups might be considered evolutionary 'dead-ends,' yet, as noted above, sex is not essential to the process of evolution.

The process of sex is significant to the grouping and naming practices discussed in Chapter 2. To deal with diversity, biologists group organisms that are phylogenetically connected (reflected in the fact that organisms within the group 'look alike'). There are different levels of relatedness that correspond to different 'levels' in a biological classification: phylum, class, order, family, genus, species, variety. Except for the species level (and perhaps not even there!), all of these levels are not defined, e.g., there is no rule about what constitutes a family, about how similar organisms have to be to put them together in family grouping. As a consequence, there certainly can be some workers who will take a group, e.g., the pea family, and say that it should be considered as three families, making three groups, each of which is more uniform than is the group when considered as a single family. The species level is unique in having a criterion that defines who should be in any particular group.

However, in spite of the fact that there IS a concrete definition of species, i.e., an interbreeding group, this does not mean that it is easily applied or that when it is applied the appellation is based on the definition. It is not that easy to discern who is breeding with whom and this is especially the case with plants and fungi. Studies to determine mating behavior are time consuming and the overwhelming majority of species (even in the animal groups) have not been checked to see if what is being called a species actually is an interbreeding group. And many, many groups that are known to be asexual (all prokaryotes, most dinoflagellates, many fungi, some flowering plants) are grouped into entities called 'species.' Thus, at every taxonomic level workers still rely on subjectivity to delineate the extent of taxonomic groups; and one finds both 'lumpers' (people who tend to lump groups together and have fewer groups with more variation in each) and 'splitters' (people who tend to split groups up and have more groups with less variation in each).

Consider again the example of asexual dandelions (Fig. 3). The entity *Taraxacum officinale* is asexual, and is generally considered to be a species represented by its Latin binomial. But should it really be considered a species? Some workers consider the *T. officinale* to be an assemblage of several hundred 'microspecies', each of which is a clonal population.

Fig. 3 A 'flower' (actually a cluster of many flowers) of dandelion, an asexual 'species'.

For sexual populations, who breeds with whom is controlled by a number of parameters specific to the species being considered. Collectively, these factors describe a 'breeding system' and it turns out that flowering plants offer a rich diversity of breeding systems. A 'closed' breeding system is one where outcrossing (breeding with another individual) unlikely. An 'open' breeding system is one that encourages outcrossing. One might think that flowering plants, the vast majority of which produce bisexual flowers with male and female parts in close proximity, would have closed breeding systems. But there are a number of processes that can make their breeding system more open.

- Being dioecious, having unisexual flowers on plants that bear either male or female flowers but not both (Fig. 4). About 5% of flowering plants are dioecious including aspen, cannabis and holly.

Fig. 4 Holly plants and flowers: on the top a male plant and close up of a flower, lacking female parts. On the bottom a female plant with flowers lacking functional male parts

- Being monoecious, having unisexual flowers, but both male flowers and female flowers are on the same plant, for example corn, cattail and most species of squash.
- Having bisexual flowers with parts that mature at different times, e.g., having flowers where first the pollen matures and is disseminated and then the stigmas are produced and are able to receive pollen.
- Having incompatibility systems that prevent pollen from being able germinate and/or grow on stigmas of the same plant and therefore unable to fertilize its own flowers.

- An inability to form seeds unless the sexual process is accomplished.

It is significant that each of these features is not 'all or nothing'—there are plants that are generally unisexual but may have a few flowers of the second sex; there are plants that mostly have unisexual flowers but have a few bisexual ones; there are plants which have separate maturation times for the male and female parts of the flower but have multiple flowers so that on any one plant there can simultaneously be both functional male and female parts; there are plants that have flowers where self pollen can grow on but just not as fast as non-self pollen; there are plants that will produce seeds without sex but only if sex didn't happen (e.g., pollination didn't occur); there are plants that almost always produce seeds asexually but occasionally will go through the sexual process; there are plants that produce megaspore mother cells that undergo meiosis to make haploid megaspores which then fuse with each other to form a diploid cell that behaves like a zygote!

Breeding systems are important because they influence plant evolution, patterns of variability and the reality of things that we identify as 'species.'

Further Reading and Viewing

- "Plant Mating Systems Often Vary Widely Among Populations" by Michael R. Whitehead. Plant mating systems.
    - https://www.frontiersin.org/articles/10.3389/fevo.2018.00038/full
- "Ernst Mayr and the modern concept of species" by Kevin de Queiroz. The biological species concept.
    - https://www.pnas.org/doi/10.1073/pnas.0502030102
- Images of monoecious plants (separate male and female flowers on the same plant for squash and oak).
    - Squash: https://awkwardbotany.com/tag/squash-flowers/
    - Oak: https://www.treeguideuk.co.uk/oak-tree-flowers/
- "Plant mating systems in a changing world" by Christopher G. Eckert. Interesting examination of human population's effect on plant breeding systems.
    - http://www.cbs.umn.edu/sites/default/files/public/downloads/Eck-

hertETAL.pdf

Media Attributions

CHAPTER 18: MATTER, ENERGY AND ORGANISMS

One of the activities that define organisms is that at some point in their life, or throughout it, they grow. Growth requires the acquisition of matter and both the acquisition of matter and the incorporation of this material into a living form (i.e., into biomolecules) involves energy. Both matter and energy are needed but it is important to keep in mind that they are two distinct entities that are NOT interconvertible. The energy transformations that organisms carry out involve manipulations of matter but they DO NOT involve converting matter into energy. Energy is obtained by rearranging matter, mostly by converting carbohydrates and oxygen into carbon dioxide and water. What complicates understanding is that matter is needed in two ways (Fig. 1): (1) materially, providing the materials that become part of the organism, mostly carbohydrates or carbohydrate derivatives, (2) energetically, because energy can be made available as matter is rearranged, e.g., converting carbohydrates and oxygen into carbon dioxide and water. Although matter is being rearranged, it is not being transformed into energy.

Matter, Energy and the Laws of Thermodynamics

Matter and energy are key players in the process of life at all levels: cell, organism, and ecosystem. Both matter and energy are familiar ideas, yet misconceptions are common, especially about energy and the interplay between matter and energy in biological systems. Matter is straightforward: it has mass, occupies space and can be categorized into elements (e.g., carbon, hydrogen, oxygen) that often are usually present in specific mixtures termed molecules (e.g., carbon dioxide, glucose) that have a characteristic composition of elements and are arranged in specific ways. Living things are made of matter and have a characteristic material composition, being made of biomolecules such as proteins, carbohydrates, and nucleic acids. Life may be partly defined by the ability of living things (organisms) to acquire matter and incorporate it into themselves, i.e., to grow. Life can also be defined on the basis of its ability to manipulate matter in characteristic ways that involve energy transfers.

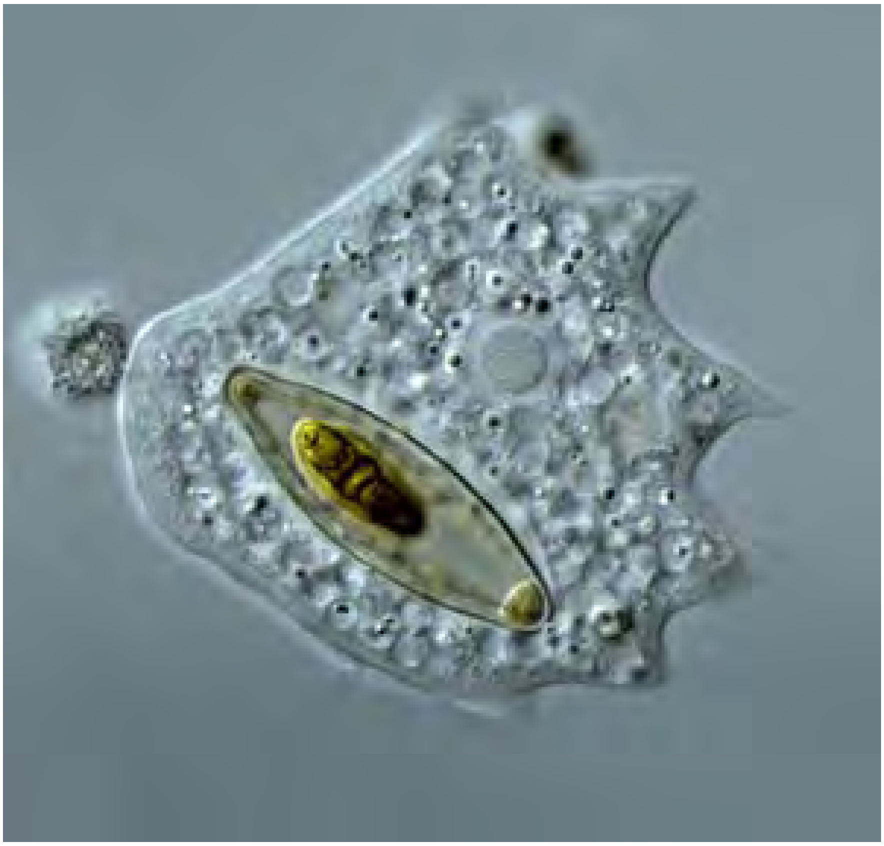

Fig. 1 This is an amoeba that has just engulfed a diatom. Materials present in the diatom will be used to allow the amoebas to grow and eventually reproduce. The ingested material ('food') is used both as a material source and also as an energy source. In contrast, the diatom obtains the material to grow from 'raw materials,' e.g., carbon dioxide, present in its environment. To convert these raw materials into biomolecules needed for growth, the diatom requires the energy of sunlight. Diatoms make their own 'food' and then eat themselves for energy while saving some of the food as a material for growth.

While matter is an easy concept, energy is much more elusive; consider the following:

1. Energy has the ability to affect matter by rearranging it or moving it from one place to another.
2. Energy is dynamic and the energy associated with a given bit of matter, e.g., a molecule, depends on circumstances; it is a function of the situation matter finds itself in, the speed it is moving, the location that it is in, in particular its position relative to other matter or relative to electric, magnetic and gravitational fields (which are

controlled by matter).

3. Energy is a property of systems, i.e., an assemblage of matter in a particular place and with specific relationships with each other.
4. Energy describes the ability of a given assemblage of matter (a 'system') to change the organization of another bit of matter (another 'system' or perhaps 'the surroundings').
5. Energy could cause atoms or molecules to move in relationship to each other, e.g. a chemical reaction, or cause an object to change position in a gravitational field (rise or fall), or cause a charged molecule or object to change position in an electrical field.
6. Just as energy can cause movement of matter, the movement of matter (i.e., matter changing position) changes the energy content and allows energy to be 'transferred' from one system to another or one molecule to another.
7. Energy can also be transferred to material via electromagnetic radiation, waves of electricity and magnetism that are given off by any bit of matter with a temperature above absolute zero (i.e., every bit of matter!!!).
8. Electromagnetic radiation is a 'form' of energy that is important to all forms of life but especially so for photosynthetic organisms. Electromagnetic radiation has a dual nature and can be described as (1) a rhythm of electric and magnetic fields, a series of waves with a certain frequency and wavelength, moving at a constant speed, the speed of light, or (2) packets of energy called photons. The energy in a packet (a photon) is related to the wavelength of the waves of electricity and magnetism. Note that these photons/waves of electricity and magnetism are able to interact with matter and transform it, thereby transferring energy to the matter.
9. Two other concepts related to energy are heat, which can affect matter by changing its kinetic energy, changing the average speed that molecules are moving, and work, which can change the position of objects in a gravitational field, or perhaps concentrate chemicals in a particular spot (chemical work). While both heat and work are connected to energy and are sometimes considered 'forms' of energy, they might better be described as interactions between systems or between a system and its surroundings.

A common feature of both matter and energy is that both are conserved, something described in what is known as the first law of thermodynamics. Although modern physics has demonstrated that matter can be converted into energy and it is their collective entity (matter + energy) that is conserved, in biological systems matter and energy are NEVER converted from one to the other and consequently we can consider each to be conserved — there is always the same amount of matter and the same amount of energy. Neither one is created, destroyed or 'used up.' The conservation of matter is easily understood, matter can be moved from one place to another, e.g. accumulated in an organism, lost (or gained) by diffusion from (or to) an organism. Elements can be rearranged, e.g. carbon transformed from carbohydrate to carbon dioxide in the process of cellular respiration, but the amount of matter is constant —the same number of carbons, hydrogens and oxygens. Similarly (and **much** less appreciated) , energy is conserved. It can be 'moved' from place to place, or transformed from one form to another (as molecules are rearranged or moved relative to each other and relative to gravitation al, electrical and magnetic fields), but the amount of energy is constant, unchanging. Living systems, non-living systems and combinations of living and non-living systems rearrange matter, and by rearranging matter they redistribute energy. But the first law of thermodynamics states that in all these rearrangements there is a constraint: after any rearrangement, the amount of matter and the amount of energy must be the same as it was in the beginning.

Living things constantly reorganize matter: molecules combine, molecules separate into pieces, molecules move from one place to another. In all of these transformations, matter must be conserved. In addition, the energy must be conserved; consequently, organisms may release energy during some transformations (because the final arrangement of material in the organism has less energy than the initial arrangement); or, if the final arrangement has more energy than the initial one, the organisms must somehow have acquired energy to bring about the transformation.

Since matter and energy play in zero-sum games then one might think that their transformations are rather tedious and potentially circular, with losses in one spot being exactly matched by gains somewhere else, and the potential of ending up exactly where you started. This is not the case, there is a direction to the transformations and it is strictly a one-way flow: you can never return to the starting point. This constraint is dictated by the second law of thermodynamics which states that in spite of the fact that energy is conserved, the amount of energy that can be used to do work is always decreasing. To most, this statement is startling because they assume that all energy can be used to do work; but some energy is not 'useful' and the second law states that the amount of 'useless' energy is always increasing. The second law of thermodynamics is extremely powerful and this is reflected in the fact that it can be defined in a variety of ways. Fundamentally, its utility rests in the fact that it puts an arrow on rearrangements of matter. Given two possible arrangements, A to B, each with the same amount of matter and energy, the second law dictates that the direction of the rearrangement will **always be to** a situation that has less useful energy. The second law points out what rearrangements of matter will be 'spontaneous', i.e., occur 'on their own.' Rearrangements in the opposite direction (the non-spontaneous direction) will only occur if energy, useful energy, is supplied.

The second law adds a second constraint on transformations; not only must matter and energy be conserved but the amount of useful energy must decrease. Consider a system A with a certain amount of matter and energy at a particular time, and the same system, now called A', a time later; the second law dictates that, barring interaction with the surroundings, the only change in A that is possible as it transitions to A' is one where there is a decrease in energy available to do work; thus once you leave situation A, you can't return to it (i.e., get from A' back to A). A lthough the energy in both is the same, the amount of energy available to do work is diminished as it transitions from A to A.' This reflects one of the common ways that the second law can be stated: there are no perpetual motion machines. A device can't get back to where it started without energy from the 'outside'.

Organisms, matter and energy

How is all of this significant to organisms?? Organisms are defined in part by their ability to grow and since growth requires the acquisition of matter, all organisms need to be able to acquire the specific materials that they construct themselves with. Moreover, growth requires useful energy because work is done in the construction of most new molecules for growth. What complicates understanding is that matter ('food') plays a dual role: (1) materially, providing the materials that become part of the larger organism, (2) energetically, providing energy that is made available as matter is rearranged. The transformations of matter and the transfers of energy performed by organisms are intertwined in ways that allow misconceptions to easily be acquired but it is important to remember that matter and energy are two different entities.

But growth isn't the only reason that organisms need matter and it isn't the only reason why organisms need energy.

Why organisms need energy

1. In addition to needing energy for growth, organisms need energy because they 'do work' in a physical/chemical sense. They create electrochemical potentials, they develop pressure, they generate forces that result in movement. Particularly significant is that they perform chemical work as they grow: many biomolecules consist of arrangements of matter that contain more useful energy than the materials these molecules are constructed from, and therefore energy is needed to synthesize them. The process of growth requires organisms to rearrange material, reposition it, in ways that cause the new material to possess more useful energy than what it was made from. This is only possible if organisms have a 'supply of energy' and the work that they do is possible because part of the energy in this supply is 'used' to allow for the rearrangements of materials. Note that energy is conserved, but the amount of useful energy, the amount that can be used to do work, is diminished.
2. But even in the hypothetical situation where an organism is not growing (making more biomolecules) and not doing work (e.g., moving itself or materials within it self), it would still need energy simply to maintain itself. Organisms exist in an organized state that spontaneously degrades to a less organized state. The maintenance of the organized state requires energy. An easily understood example of this involves the charge difference found across the cell membrane, with the inside being negative relative to the outside. This organized situation spontaneously 'breaks down' to a less organized one because electrical forces push negative ions out across the membrane and positive ions in. Maintenance of the organized state requires energy because the process of organizing (in this case moving ions across a membrane so they are more concentrated in one place than another) requires energy.

How organisms obtain energy

Organisms' energetic needs are largely satisfied by acquiring biomolecules (food), generally carbohydrates, and processing them in a group of reactions called cellular respiration. Cellular respiration (Chapter 19) is a controlled 'burning' process whereby carbohydrates react with oxygen (the carbohydrates are oxidized), producing carbon dioxide and water. If one compares the energy content of equivalent amounts of carbohydrate plus oxygen to that in carbon dioxide plus water, there is substantially less energy in carbon dioxide plus water. If you burn carbohydrates in a fire the difference in energy is released as heat and light, but in cellular respiration, less energy is released as heat, and none as light, because some energy is 'captured' in chemicals, in particular one called ATP. Because the products of the reaction (carbon dioxide and water) are invisible gases many believe that cellular respiration converts matter to energy. But this is impossible, the first law forbids it! The original carbon, oxygen and hydrogen are still present, just now in different places relative to each other. Similarly, the original energy remains but is now present in the ATP that is formed and the heat energy that is released.

Why organisms lose material because of their energetic needs

As an organism carries out cellular respiration it produces two materials (water and carbon dioxide) that are easily lost and sometimes 'purposely' eliminated (e.g., in humans, where breathing, i.e., ventilation, facilitates the loss of water and carbon dioxide). As a consequence of cellular respiration, organisms are continually los ing matter as carbon dioxide and water and consequently are also los ing weight. Thus, in order to maintain its weight, a respiring organism must acquire more 'food'.

Obtaining matter and energy

In order to satisfy their energetic needs, an organism requires a supply of carbohydrates (or other biomolecules) to utilize in cellular respiration. These carbohydrates may be obtained in two basic ways: (1) by consuming biomolecules that have been produced by other living things—carbohydrates or molecules like proteins that can be metabolized to produce carbohydrates or (2) by consuming 'self-constructed' carbohydrates that are produced in reactions (usually photosynthetic reactions) that synthesize carbohydrates from carbon dioxide and water. Such reactions utilize 'sources' of energy (e.g., sunlight) that allow a chemical reaction to occur where the products have more energy than the reactants. The synthesized carbohydrates are then used to power cellular respiration, i.e., they are converted back to carbon dioxide and water. The group of organisms that consumes carbohydrates that other organisms have produced are termed heterotrophs (hetero-other, troph-eat; literally 'eat others'), and the group of organisms that make their own carbohydrates to 'eat' are termed autotrophs (auto-self, troph-eat; literally 'self-eaters'). It is important to realize cellular respiration occurs in both groups, they differ only in how they acquire carbohydrates to be oxidized in cellular respiration.

It is critical to keep in mind that matter and energy are two different things but they are intertwined. Energy that is present in carbohydrates and oxygen can be 'released' when the material is rearranged in to carbon dioxide and water. The 'released energy' might end up as heat, or as work, or in a new arrangement of molecules (e.g. ATP is a rearranged version of ADP plus inorganic phosphate). However, the second law requires that the total amount of energy in the new arrangement (e.g., carbon dioxide, water and ATP) must possess less ability to do work than the earlier arrangement (in this example, carbohydrate plus oxygen plus ADP plus inorganic phosphate).

Appreciate that the 'food' that organisms obtain, either by finding it (heterotrophs) or making it (autotrophs) serves a dual function, providing (1) energy (through cellular respiration) and (2) material (through a variety of metabolic pathways where carbohydrates are reconfigured to produce other biomolecules (proteins, fats, nucleic acids). If food provides energy through the process of cellular respiration it is transformed into carbon dioxide and water and these cannot be used materially to make biomolecules. Alternatively, food can provide 'building materials' that are used to make more cell membranes, cell walls, cellular enzymes, but this food will NOT be 'providing energy'. Food **cannot** provide both energy and building materials at the same time! You cannot 'have' your cake (build with it) and 'eat' (use it for cellular respiration) it too.

The major topics to be covered in the next six chapters on the growth of organisms are outlined below. As described above, almost all energetic needs of almost all organisms are a consequence of **cellular respiration (Chapter 19)**—the oxidation of carbohydrates by oxygen, producing carbon dioxide and water. Satisfying the material needs of heterotrophic organisms is a relatively simple story; however it is more complicated for autotrophs, where it involves both **photosynthesis (Chapter 20)** and **mineral nutrition (Chapter 22)**, the acquisition of mineral elements like nitrogen and phosphorus. Although most prokaryotes satisfy their material and energetic needs in typical heterotroph or autotroph fashion, we will also consider some of the **metabolic diversity (Chapter 21)** found in some prokaryotes that reveal very different patterns of satisfying energy and material requirements. This diversity is an interesting contrast to the familiar, normal ways of life and also plays a significant role in the nutrition of plants by influencing the availability of certain plant nutrients. We will briefly consider how organisms **move materials throughout their bodies (Chapter 24)**, a process that usually (but not always!)

'requires energy'. We will also consider the **nature of soils** **(Chapter 23),** which serve as reservoirs for the nutrients and water that plants require. A final aspect of growth that we will consider is the **rhythms of growth (Chapter 25)** that organisms, especially plants, exhibit and how this growth might be modeled.

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CHAPTER 19: CELLULAR RESPIRATION

Fig. 1 Photograph altered by artist to recreate the Washburn A Mill explosion of 1878.

Although most bakers don't realize it, they work with explosive material. Flour is highly flammable and under appropriate conditions flour dust can explode. On several occasions flour mills have exploded, perhaps the most famous being near Minneapolis in 1878 when a recently built mill, one that at the time was the largest in the world, was totally destroyed and 18 workers killed (Fig. 1). More recently, in 2008, a sugar mill in Georgia exploded, killing 14 and injuring 40 more. These examples demonstrate that there is energy present in carbohydrates, chemicals with the general formula of CH_2O, i.e., a 'hydrated' carbon. Often the carbohydrates are polymers of six carbon sugars, molecules with a formula of $C_6H_{12}O_6$. Cane sugar, what exploded in the Georgia mill, is made up of two such 'hexose' (six-carbon) sugars, glucose and fructose, bound together. Starch, the main component of flour, is made up of long chains of glucose molecules bound together. Glucose, fructose and starch are all carbohydrates and like all molecules they 'contain' energy. If carbohydrates react with oxygen to form carbon dioxide and water, energy is released.

The energy of carbohydrates and its release when interacting with oxygen is central to the biology of most organisms. And understanding how the energy is obtained and utilized is significant not only because the energy released is essential for the functioning of organisms but also because it represents a unifying feature of all living things, every living organism carries out this process, or part of this process, or something similar to this process.

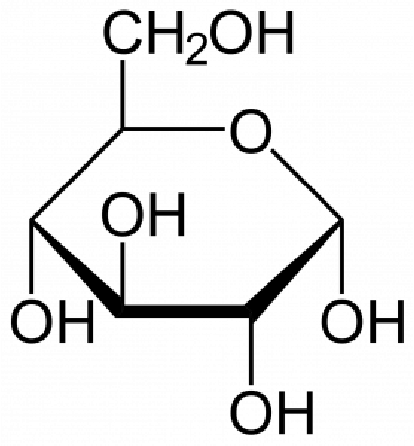

Fig. 2 Glucose—a six-carbon sugar with the formula of $C_6H_{12}O_6$

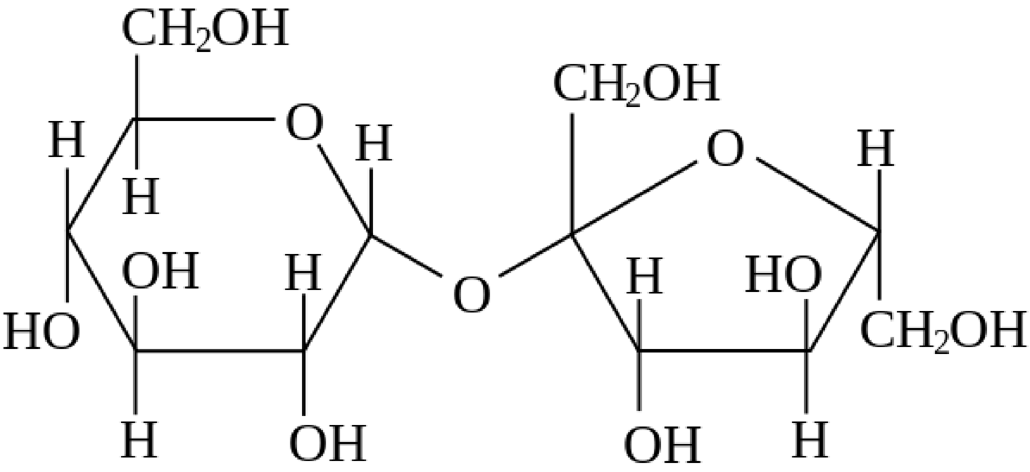

Fig. 3 Sucrose—a disaccharide made up of two six-carbon sugars, glucose on the left and fructose on the right with the formula of $C_6H_{12}O_6$

Organisms need energy for growth, maintenance, and for the performance of work such as the motion of the whole organism, e.g., swimming, or internal motion, e.g., pumping materials within the organism or moving materials within a cell, that are essential for the organism's livelihood. Many, but certainly not all, of these energy-requiring processes 'run' on energy 'supplied by' adenosine triphosphate, ATP, and most of an organism's supply of

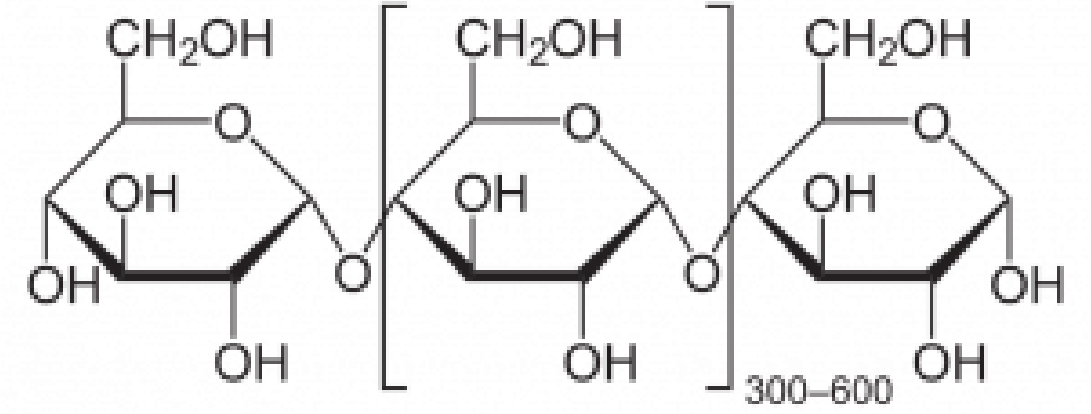

Fig. 4 Starch—a polysaccharide made up of hundreds of six-carbon sugars glucose units, each with a formula of $C_6H_{12}O_6$

ATP is provided by cellular respiration, a process that synthesizes ATP while carrying out a chemical reaction that utilizes carbohydrates. Exactly how ATP participates in metabolism varies and its action is often not direct and obvious in the way that the energy of falling water allows a mill to 'do work.' The action of ATP often involves 'coupling' different chemical reactions (examples below) with the consequence being that the participation of ATP makes unlikely events more likely to happen and/or events that occur slowly more likely to proceed rapidly. ATP's participation in cellular activities causes the molecule to lose one or two of its three phosphate groups, forming either adenosine diphosphate (ADP) or adenosine monophosphate (AMP). Obviously, the regeneration of ATP is significant to an organism's functioning and for most organisms, this regeneration is the result of a group of reactions described as cellular respiration.

TOPICS

- Overview of cellular respiration
- Four parts of cellular respiration
    - glycolysis: glucose to pyruvate
    - pyruvate decarboxylation
    - citric acid cycle (Kreb's cycle)
    - oxidative phosphorylation
- Mechanisms of ATP synthesis

- Summary

Overview of cellular respiration

Fig. 5 A burning campfire involves the same chemistry as cellular respiration: the oxidation of carbohydrate. In a campfire all the energy released by the reaction is evident as light and heat. In cellular respiration, energy ends up in ATP.

Cellular respiration describes a set of chemical reactions that together convert carbohydrates and oxygen into carbon dioxide and water. Collectively, these reactions allow a cell to obtain chemical energy in the form of ATP from the same basic process that allows causes a flour mill to explode and allows campers to obtain heat and light (other forms of energy) when wood (which is largely carbohydrate) is burned in a campfire (Fig. 5). The chemical process of burning is an oxidation, or more properly a reduction/oxidation, a type of chemical reaction where an electron is transferred from one molecule to another. The molecule that loses electrons is said to be 'oxidized'; the one that receives electrons is 'reduced'. The process is generally 'driven' by the fact that some molecules/atoms have a higher affinity for electrons than others. In a thermodynamic sense, this is similar to the fact that rocks move downhill in response to gravity; one might say that 'low spots' (in a gravitational field) have a higher affinity for rocks than 'high spots'. It takes energy to move rocks up in a gravitational field and (most of) the energy expended moving a rock up 'ends up' in the rock now in its new, higher position. If the rock then rolls down it 'gives up' energy and, after descending, the rock ends up with less energy than at the bottom than it had before. The first law of thermodynamics tells us that the energy is somewhere, where is it? One can state that the energy has been 'released' as rocks move downhill and also that this energy can be 'captured' in various ways, i.e., work can be done in the process (can you think of a way to capture the energy of a falling rock?). In a similar manner, electrons move 'downhill', from molecules that have less affinity for them to molecules that have a greater affinity for them, and as they move 'downhill' work can be done. Keeping track of electrons and the affinity of different compounds for electrons is sometimes challenging and we won't pursue it in detail here, except to say that the task is made easier when what is transferred is an electron plus a proton, i.e., a hydrogen atom and in these cases the oxidation/reduction is easy to trace by seeing what loses hydrogens and what gains hydrogens.

The summary equations for cellular respiration, in words and formula, are:

- carbohydrate plus oxygen forms carbon dioxide plus water
- specifically, glucose plus oxygen forms carbon dioxide plus water
- $C_6 H_{12} O_6 + 6 O_2$ —— > $6 CO_2 + 6 H_2 O$

In cellular respiration what is oxidized are the carbons in a carbohydrate molecule of the general formula $C_nH_{2n}O_n$ and what is reduced is O_2. The carbons of the carbohydrate have lost hydrogens while forming carbon dioxide (CO_2). The oxygen has gained hydrogens while forming water (H_2O). It is important to realize that the carbohydrate does NOT react with oxygen (although it does if a log is burned in a fire) ; the equation merely summarizes a group of reactions occurring simultaneously and have the net effect of converting carbohydrates and oxygen to carbon dioxide and water.

We can split these reactions into four basic parts:

1. Glycolysis

A process that converts a glucose (six carbon sugar with six carbons, 12 hydrogens and six oxygens) into two pyruvic acid molecules, each with three carbon molecules and with the formula $C_3H_4O_3$ (Fig. 6).   Note that the carbons of the carbohydrate have been oxidized (lost hydrogens) as pyruvic acid has been formed. What has been reduced is a metabolite called NAD^+ which has been reduced to NADH. Because the NAD^+ has a higher affinity for hydrogens than the carbon in a carbohydrate, this group of reactions is 'downhill'. Also occurring in glycolysis is the synthesis of some ATP from ADP and phosphate ion (iP). Thus, some energy present in the hexose is now present in the forms of NADH and ATP (and some has been released heat and some is present in the pyruvic acid molecules).

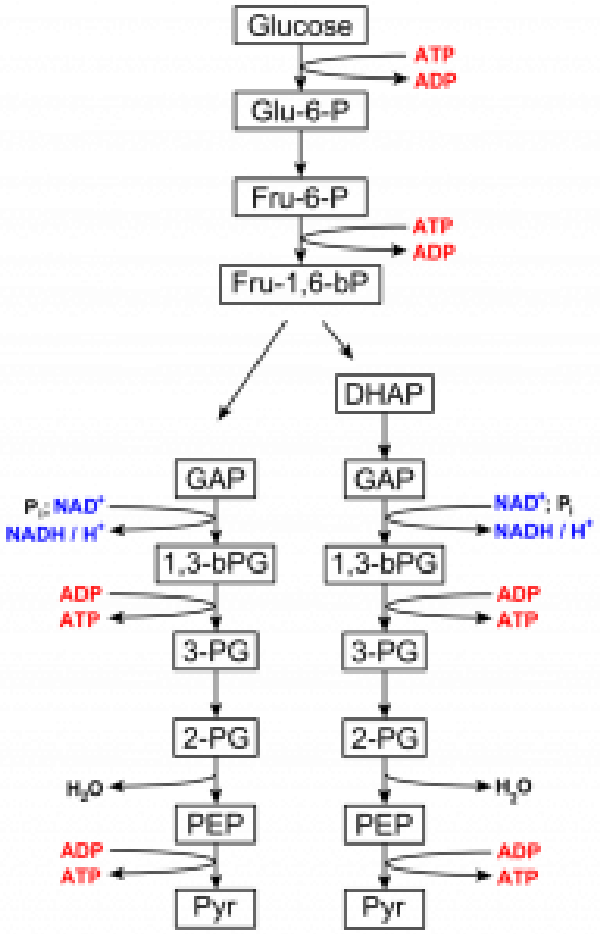

Fig. 6 The reactions of glycolysis, starting with glucose ($C_6H_{12}O_6$) and ending with the production of two molecules of pyruvic acid ($C_3H_4O_3$). Note that fructose 1, 6 bisphosphate is split into two three carbon molecules, GAP and DHAP, and the DHAP is converted into GAP.

2. Pyruvic acid decarboxylation

Each of the two pyruvic acid molecules is 'oxidatively decarboxylated', removing a carbon as a carbon dioxide and producing a two carbon ('acetyl') fragment attached to the metabolite coenzyme A. The lost carbon has been oxidized as NAD^+ is reduced to NADH. Because NAD^+ has a higher affinity for electrons than the carbon in the pyruvic acid this reaction is 'downhill'.

3. Krebs cycle

The remaining two carbons derived from each pyruvic acid are added to a four-carbon compound making a six carbon compound that is then oxidatively decarboxylated twice and then goes through a series of oxidative steps to regenerate the original four carbon compound that can receive another two-carbon unit. This is what is known as both the Kreb's cycle or the citric acid cycle.

The net effect of steps 1-3 is the total oxidation of the carbohydrate to carbon dioxide, accompanied by the reduction of a number of NAD^+ molecules to NADH and also the reduction of a similar molecule, FAD, to $FADH_2$. Some ATP has been synthesized in both glycolysis and the citric acid cycle, but the majority of the ATP generated in cellular respiration comes from step 4 below where the 'reducing power' of NADH and $FADH_2$ is utilized to 'power' an elaborate mechanism that 'utilizes' energy from the reduced molecules to accumulate protons and create a charge and concentration gradient across a membrane. This gradient is then used to synthesize ATP.

4. Oxidative phosphorylation (electron transport chain)

Like the citric acid cycle, oxidative phosphorylation occurs in a mitochondrion, an organelle with two membranes with two aqueous spaces: in between the two membranes and inside the inner membrane (Fig. 7). Oxidative phosphorylation transfers electrons, donated by NADH and $FADH_2$, through a series of membrane bound carrier molecules located in the inner membrane, ultimately delivering them to oxygen. Oxygen simultaneously picks up protons and form s a water molecule, H_2O. Oxygen is essential to the process because it is oxygen's affinity for electrons that drives the electron movement. To again use a gravitational analogy, oxygen is a 'low point' to which electrons move. If there isn't a low point there would be no movement. The movement of electrons through a membrane operates an 'electrogenic pump': it causes protons (H^+) to accumulate in the space between the two membranes, creating an electrochemical gradient, a charge and concentration difference, across the membrane. In an energetic sense, the pumping is 'uphill' and it is made possible by a coupling to the 'downhill' movement of electrons to molecules with higher affinity for them. The proton gradient thus created is a source of energy that can be utilized to synthesize ATP from ADP and iP. In oxidative phosphorylation there are two things moving ‘downhill’ in an energetic sense: (1) electrons move from NADH ‘downhill’ to oxygen because it has a higher affinity for them, (2) protons that have been ‘pumped’ uphill then move ‘downhill’ across a membrane, from a place where they are in high concentration to a place where they are in low concentration. If one ‘follows’ the energy it goes from glucose to the reducing power of NADH/$FADH_2$, to a proton electrochemical gradient, to ATP. Besides producing ATP, another very important consequence of the process of oxidative phosphorylation is the regeneration NAD^+ and FAD, compounds that are needed in glycolysis and the citric acid cycle. These processes cannot proceed unless NAD^+ and FAD are available (this point will be discussed further in Chapter 21 on metabolic diversity).

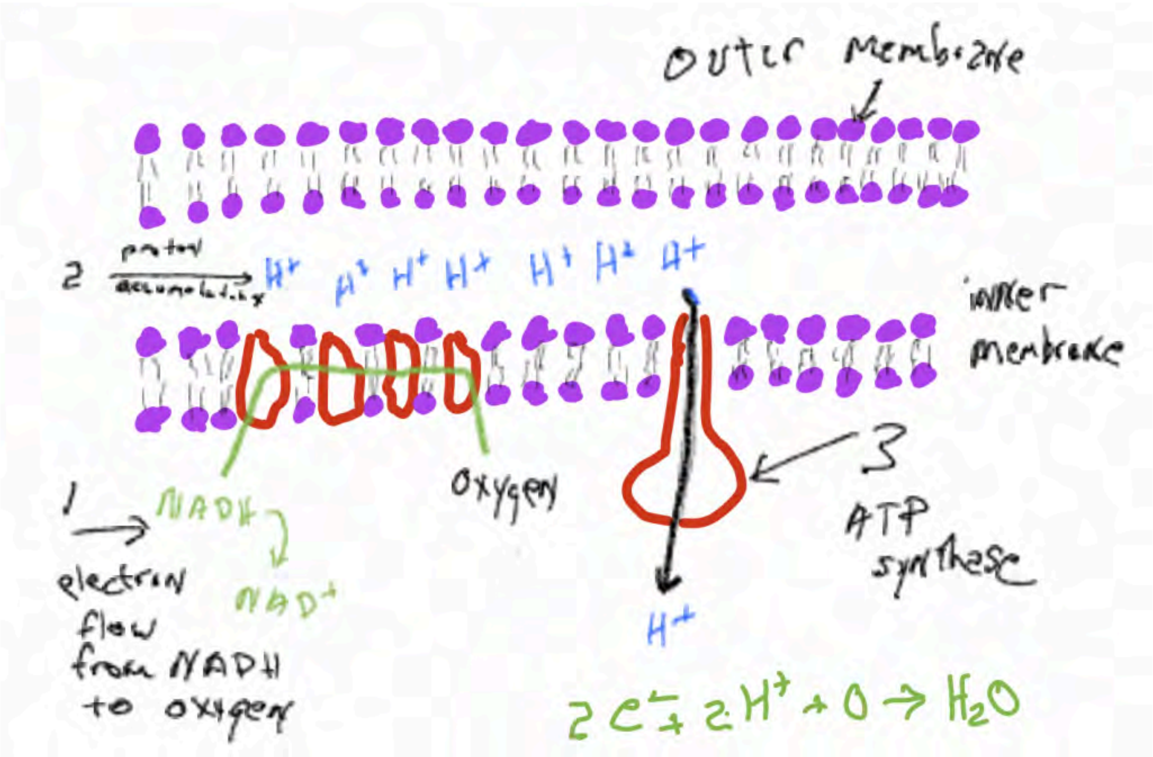

Fig. 7 Oxidative phosphorylation occurs in the mitochondria which have two membranes, an outer and an inner. (1) The inner membrane is spanned by numerous proteins (in red), some of which are proton pumps and some are proton channels; (2) electron flow from NADH to oxygen; (3) this flow of electrons pumps protons (H+) into the inner membrane space. Proton flow through the channel proteins powers the synthesis of ATP. The net effect is the synthesis of ATP and water while NADH is oxidized.

Mechanisms of ATP synthesis

During cellular respiration ATP is formed in two very different ways, both of which involve energy transfers and the concept of 'coupling', in these cases the coupling of ATP synthesis to other reactions that 'provide energy'. Examining these reactions is not only important to the energy relations of a cell, but they also provide examples of 'coupling'.

ATP is formed when a phosphate group (PO_3^-) is added to ADP, an 'uphill' reaction with ATP having more energy than ADP plus phosphate and under most circumstances, this reaction is very unlikely. Most of the ATP formed by eukaryotic living things occurs in organelles called mitochondria where the electron transport chain discussed above results in a high concentration of protons on the outside of a membrane (remember that membranes are generally impermeable to charged items like protons). Embedded in the membrane, with openings to both sides, is a large enzyme, a polymer of amino acids, that has a very specific and complicated three-dimensional structure, a structure that is a consequence of the sequence of amino acids in the polymer. This enzyme binds ADP and phosphate and also has a path, a channel, through which protons can flow through the protein (and also through the membrane) from high concentration to low. The movement of protons through the protein causes the enzyme with attached ADP and phosphate to be bent in a way that makes it much more likely that phosphate binds to ADP, thereby forming ATP. Note that the charge and concentration difference of protons across the membrane represents a 'source of energy' that can be used to do things, in this case, bend the molecule and synthesize ATP. The energy from the proton gradient makes an unlikely reaction, ATP synthesis, much more likely. Stated another way, ATP synthesis is coupled to protons moving from high concentration to low.

A second way to synthesize ATP from ADP and phosphate is seen in glycolysis. Instead of directly transferring a phosphate group to ADP it is first added to GAP (Figure 1). This reaction by itself is unlikely (uphill) but it can be made more likely if the GAP is simultaneously oxidized while NAD^+ is being reduced, a reaction that is favored (downhill) because NAD^+ has a higher affinity for electrons than GAP. The combined reaction results in the conversion of GAP to 1,3 bPG, with the GAP being simultaneously oxidized and phosphorylated. And while the attachment of a phosphate group directly to ADP is 'uphill' (unlikely), the transfer of a phosphate group from the 1,3 bPG to ADP is 'downhill' (likely), thus there is coupling between oxidation of GAP and ATP synthesis. A similar mechanism operates where ATP is formed in the citric acid cycle. Coupling is an important aspect of both ATP synthesis and hydrolysis and represents ways that energetically unfavorable (uphill) reactions can be made more likely by coupling them somehow (and there are multiple ways) to favorable (downhill) reactions.

Summary

Thus the net effect of cellular respiration is the complete oxidation of carbohydrates to form carbon dioxide and water. In the process, ATP is synthesized from ADP and phosphate. Although the process as described above 'starts' with glucose, a number of other molecules can provide six carbon sugars to be utilized in glycolysis, e.g., starch (a polymer of glucose), sucrose (a disaccharide containing glucose and fructose), galactose (a six carbon sugar), lactose (a disaccharide made of glucose plus galactose), mannitol (a six-carbon sugar alcohol). In plants, sucrose and starch are the most important sources of substrates for glycolysis. Besides hexose/hexose polymers, other materials can be 'burned' in cellular respiration, including fats and the carbohydrate portion of the amino acids of proteins. These 'food sources' enter the metabolic pathways of cellular respiration in several different places.

Although cellular respiration is generally thought of as being a degradative process (catabolism), it can also be synthetic (anabolism—the making of biomolecules). When this happens the material entering the cellular respiration exits the process before being completely oxidized, thereby providing metabolites that are used to construct biomolecules. For example, intermediates of cellular respiration can be used to synthesize fats and amino acids. When this happens less (or no) ATP energy is obtained because less of the process of cellular respiration is occurring.

Further Reading and Viewing

Ion the spring, skunk cabbage flowers generate heat by decoupling proton flow from ATP synthesis (as do some animals when they emerge from hibernation). Energy that might have been "used" to make ATP is released as heat. Learn more about this interesting plant in Plants are Cool, Too! Episode 3 on YouTube and in the article “Living together and living apart: the sexual lives of bryophytes” by David Haig published by the *Royal Society*.

- https://youtu.be/iX7n24ZeqAw
- https://doi.org/10.1098/rstb.2015.0535

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CHAPTER 20: PHOTOSYNTHESIS

Plants are literally formed 'out of thin air'. While a small portion of their (dry weight) mass comes from the soil, approximately 98% comes from the atmosphere. A typical serving of potatoes is 6 oz = 170 grams. Since potatoes are roughly 80% water a serving of potatoes is about 34 grams of dry weight. This weight is nearly pure starch which has a chemical formula ($C_6 H_{12} O_6$). Carbon atoms represent 40% of the weight of starch (or of any hexose or hexose polymer) so that 34 grams of potato has 13.6 grams of carbon = 1.13 mols of carbon. This has been derived from the air which is roughly 400 ppm carbon dioxide. In order to acquire the carbon needed for a serving of potatoes the plant has to extract carbon from approximately 67 thousand liters of air. This photosynthetic ability is even more remarkable because it involves a transfer of the energy of light (electromagnetic radiation) into chemical energy present in the carbohydrate that is produced. The synthesized hexoses have considerably more energy than the raw materials (carbon dioxide and water) used to produce them.

TOPICS

- Overview
- The light dependent reactions
- The carbon dioxide assimilation reactions
- Photosynthetic constraints: the photosynthesis/transpiration compromise
- C4 photosynthesis
- CAM photosynthesis

Overview

Photosynthesis produces carbohydrates. The name reveals what they were originally considered: hydrated carbons (i.e., water added to carbon), but research has revealed that a more accurate description of carbohydrates is reduced carbon dioxide. This is illustrated in the overall equation for photosynthesis:

$$CO_2 + H_2O \longrightarrow (CH_2\,O)_n + O_2$$

Hydrogen is added to the carbon dioxide, i.e., it is reduced, and hydrogen is being removed from oxygen, i.e., it is being oxidized. Note that, as in the case for cellular respiration, the overall equation is a summary of the net effect of multiple reactions taking place simultaneously. Specifically in photosynthesis, carbon dioxide does NOT react with water. Instead, both water and carbon dioxide are consumed in a group of reactions that ultimately produces oxygen and carbohydrates.

The overall reaction as written is exceptional because oxygen is a highly electronegative atom, one that attracts hydrogens strongly, much more strongly than the carbon atom that the hydrogens are transferred to. For this reason, the reaction is 'uphill' and unlikely to occur, while the reaction in the opposite direction is much more likely to occur, with carbohydrates being oxidized by oxygen to produce carbon dioxide and water (see the previous chapter). The last chapter illustrated that cellular respiration (carbohydrate oxidation) is 'driven' by the electronegativity of oxygen; this electronegativity 'pulls' electrons through the inner mitochondrial membrane, ultimately uniting them with oxygen. Thus a significant question concerning photosynthesis is what pulls electrons away from the oxygen of a water molecule—what has a stronger 'pull' for hydrogens than oxygen (i.e., what is a more powerful oxidant than oxygen)? Light interacting with the pigment chlorophyll plays a critical role in generating the strong oxidant. Also critical is the structure of the chloroplast which, like mitochondria, consists of a complex structure of membranes separating aqueous compartments. The membranes contain chlorophyll (Fig. 1) as well as other pigments and proteins, organized in very specific ways.

The light-dependent reactions of photosynthesis

Light's role in photosynthesis is in rearranging specific chlorophyll molecules, causing them to lose electrons (oxidizing them) and thereby making them oxidants that remove electrons from other molecules and ultimately from water. Light is a form of energy and consequently is able to change the circumstances of the material that it interacts with. In particular, light changes the electron configuration of chlorophyll, shifting an electron from its normal position to a situation where it is more likely to escape from the chloro-

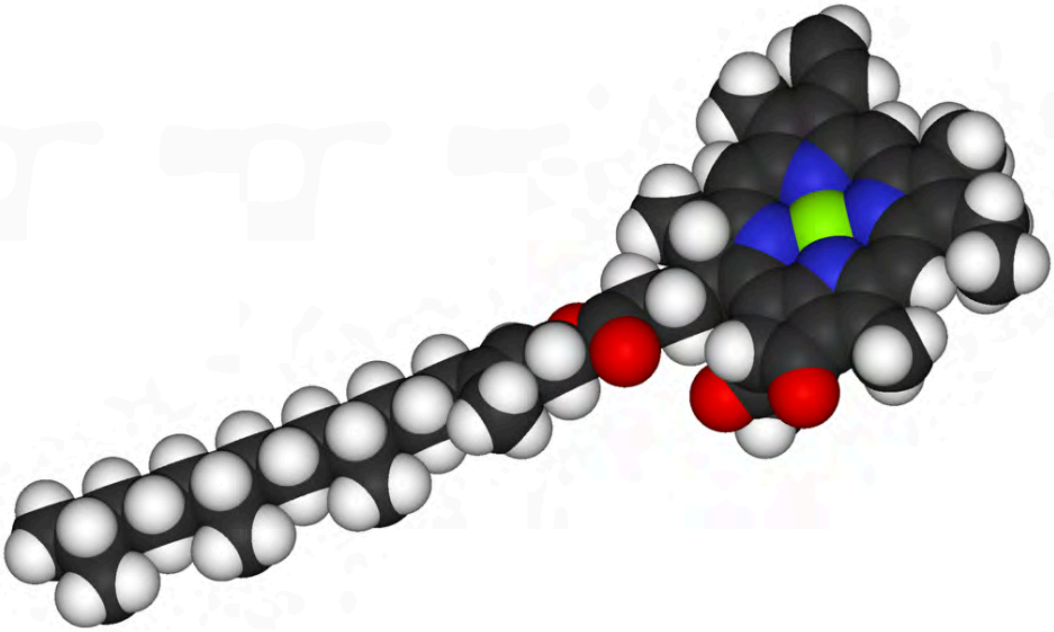

Fig. 1 A space filling model of chlorophyll: white = hydrogen, black = carbon, red = oxygen, blue= nitrogen, green = magnesium. The abundance of carbon and hydrogen and the scarcity of oxygen makes this molecule prefer to be in membranes

phyll molecule, i.e., after absorbing light, the chlorophyll is more likely to be oxidized. The oxidation of chlorophyll is made even more likely because there is a molecule nearby in the inner membrane of the chloroplast that is capable of accepting the electron. The electron lost from chlorophyll ultimately (after many steps) ends up associated with the carbon of a carbon dioxide molecule, forming carbohydrates. The oxidized chlorophyll molecule (i.e., the one missing an electron) is not a strong enough oxidant to extract electrons from water. But it can act on the 'oxygen evolving complex', an enzyme complex that contains four manganese atoms. A chlorophyll lacking an electron is capable of oxidizing one of the four manganese atoms. After this process is repeated three more times and all four of the manganese atoms are oxidized, the molecule is now a strong enough oxidant to act on two water molecules, removing four electrons, one each from the four hydrogens, and these replace the electrons that had been lost from each of the four manganese ions. This process produces four protons (H^+) and one molecule of O_2.

The electron lost from chlorophyll follows a path through a membrane similar to the flow of electrons through the inner mitochondrial membrane in the process of 'electron transport' (= oxidative phosphorylation) of cellular respiration, sometimes utilizing similar electron carriers.

And, similar to some of the steps in oxidative phosphorylation, some of the electron transfers have the effect of moving protons from one side of the membrane to the other. Moreover, the 'splitting' of water, performed by the manganese-containing protein, adds protons to that same side of the membrane. The accumulation of protons on one side of the membrane creates an electrochemical gradient across the membrane. And, because of the electrochemical gradient, ATP can be synthesized as it is in the electron transport chain of cellular respiration. But in this case the electrons are not flowing to oxygen. They move first to a different chlorophyll atom, but only after it, like the chlorophyll molecule described earlier, has been oxidized by the action of light. When this second chlorophyll receives an electron from the electron transport chain it is converted back to its normal state, and in this state the chlorophyll can once again absorb light, be excited, and lose an electron, thus continuing the process. Note that we have identified two distinct chlorophyll molecules, both of which absorb light and lose electrons. One chlorophyll molecule (called chlorophyll 680) obtains 'replacement' electrons from a manganese containing protein; the second chlorophyll (called chlorophyll 700) obtains replacement electrons from the electron transport chain. The flow of electrons described so far is:

water — >

manganese enzyme complex — >

chlorophyll 680 — >

electron transport chain — >

chlorophyll 700.

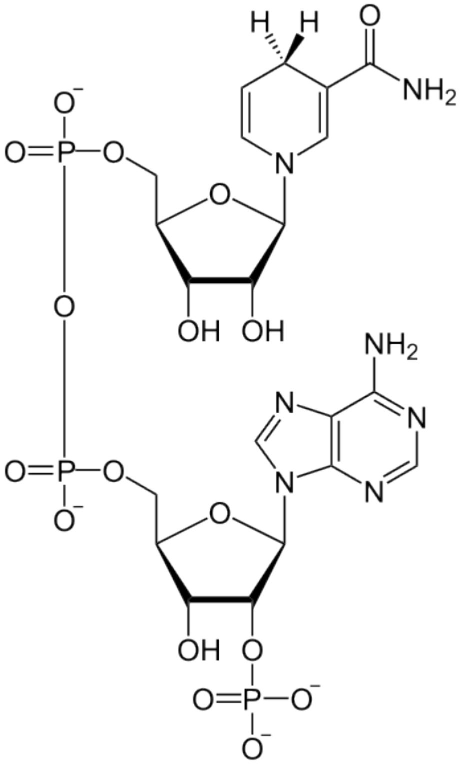

Fig. 2 The electron carrier NADP+/NADPH

But they haven't finished their journey yet! Ultimately these electrons will be reducing carbon dioxide, but before getting to the carbon of a carbon dioxide they are transferred to another important intermediate, $NADP^+$ (Fig. 2) , a compound very similar to the NAD^+ that operates in the mitochondria during cellular respiration. Like NAD^+, $NADP^+$ can accept two electrons and a proton to form NADPH and can lose the same elements to reform $NADP^+$, i.e., it is an electron carrier that (as $NADP^+$) can oxidize compounds and (as NADPH) can reduce compounds. $NADP^+$ receives electrons from carrier molecules that receive them from an 'excited' chlorophyll 700 molecule. NADPH is a relatively stable molecule and is water-soluble, unlike many of the electron carriers involved in photosynthesis that are soluble only in the lipids of the chloroplast membrane.

In total, what we have described so far is a light-driven flow of electrons from water to $NADP^+$, forming NADPH along with O_2 (Fig 3). The flow occurs in the inner chloroplast membrane and involves two steps where the energy of light is significant in making electron transfer (i.e., redox reactions) more likely. The flow of electrons through a membrane is capable of creating a proton gradient, as it does in the inner mitochondrial membrane. And, as is the case in mitochondria, this gradient in protons can be used to synthesize ATP. This group of reactions, powered by light and creating NADPH and ATP from $NADP^+$, ADP and inorganic phosphate, is called 'the light reactions' and is summarized as:

$$H_2O + NADP^+ + ADP + iP \longrightarrow NADPH + ATP + O_2$$

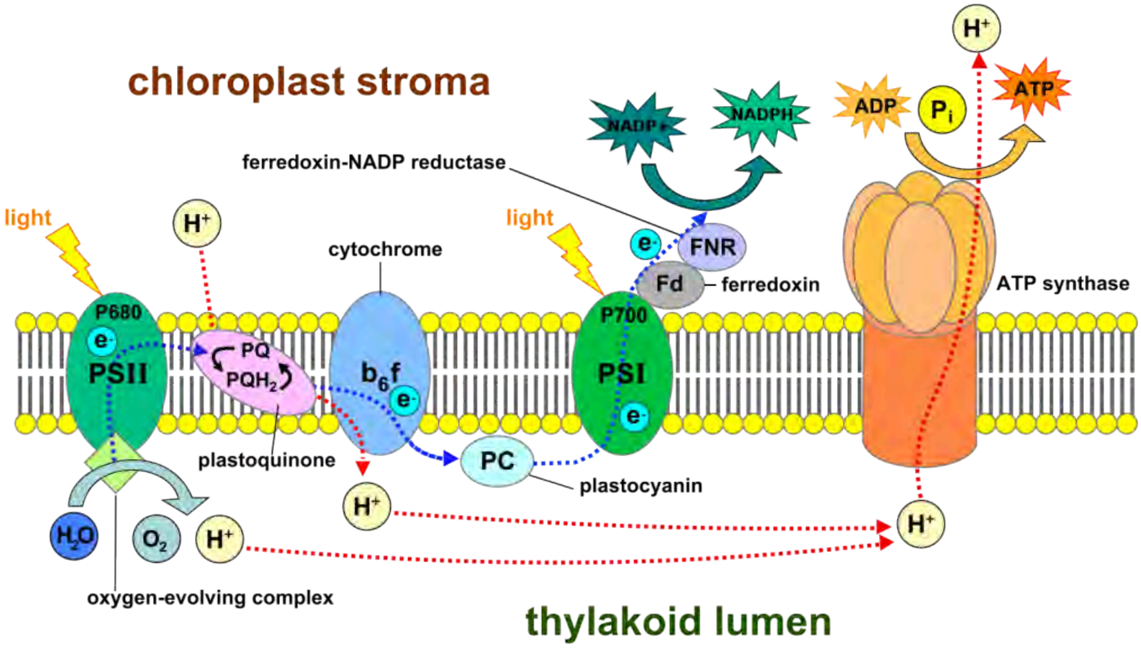

Fig. 3 A model of the inner chloroplast membrane showing multiple components and illustrating the flow of electrons from water to NADP+. This electron flow involves reactions that pump protons into the thylakoid lumen. These protons, along with protons that remain after electrons are removed from water, can flow through an ATP synthase molecule forming ATP.

The carbon dioxide assimilation reactions of photosynthesis

The products of the light reactions, NADPH and ATP, are used to synthesize carbohydrates from carbon dioxide, a process called carbon dioxide fixation.

Carbon fixation fundamentally involves the use of the 'reducing power' of NADPH to reduce carbon dioxide, and the process is summarized in the following equation:

$$\text{NADPH} + \text{ATP} + \text{CO2}\text{—>} (\text{CH}_2\ \text{O})_n + \text{NADP}^+ + \text{ADP} + \text{iP}$$

Note that one of the extremely important aspects of these reactions is that it regenerates metabolites needed in the light reactions: $NADP^+$, ADP and iP. Since the supplies of these metabolites are limited, it is critical that they be recycled. The reactions of carbon fixation can be summarized in three steps: carboxylation, reduction and regeneration.

Carboxylation

Carboxylation describes the incorporation of carbon dioxide into an organic molecule. Interestingly, this can be accomplished without involving any of the products of the light reaction. Carboxylation occurs when carbon dioxide is added to a metabolite called ribulose bisphosphate (RuBP), a five-carbon sugar with two phosphates, in a reaction catalyzed by an enzyme called ribulose bisphosphate carboxylase (rubisco). The resultant 6-carbon compound rapidly breaks down to two molecules of a three-carbon compound called phosphoglycerate (PGA).

Reduction

Although carbon dioxide has been assimilated, the PGA is not a very useful compound because it is too oxidized. To be useful the PGA needs to be reduced. It can then be used as a precursor molecule to make a variety of biomolecules such as sugars, amino acids, nucleic acids and many others. In addition, the reduced compound can be used to make more RUBP and thus allow more carbon dioxide to be assimilated.

The reduction of PGA is accomplished using NADPH and ATP produced in the light reactions of photosynthesis and produces a three-carbon sugar called glyceraldehyde-3-phosphate (G3P).

$$\text{PGA} + \text{NADPH} + \text{ATP} \text{ --> } \text{G3P} + \text{NADP}^{+} + \text{ADP} + \text{iP}$$

Regeneration of RuBP

In order to sustain photosynthesis the plant needs to regenerate RUBP, the 5-carbon sugar that is used to acquire CO_2. This occurs when RUBP is synthesized from G3P. Obviously, you can't make a five-carbon sugar out of a three carbon sugar. You might do it using two G3P molecules but there would be one 'fixed' carbon leftover. However, the synthesis can be accomplished tidily if one starts with five G3P molecules (fifteen total carbons) and makes three RUBP's (also 15 carbons). These reactions are called the Calvin-Benson cycle and they require one ATP made in the light reactions for each RUBP produced.

At the same time, G3P can be used to make six-carbon sugars, in particular glucose and fructose and from them, sucrose, starch, cellulose and a wide variety of polysaccharides.

Putting both these activities together, if six molecules of carbon dioxide are fixed by carboxylating six RUBP's, then 12 G3P can be produced after reduction utilizing 12 NADPH and 12 ATP. Ten molecules of G3P can be used to regenerate the six RUBP's and this process requires six more ATP. The remaining two molecules of G3P can be used to form a fructose or a glucose. This is how **all** plants carry out photosynthesis. Each carbon dioxide assimilated requires two NADPH and three ATP.

Note that ALL of the above equations are summaries of multiple reactions occurring simultaneously. There is a great deal of chemistry taking place in chloroplasts, although the net effect can be expressed simply as

$$6\ CO_2 + 6\ H_2O \longrightarrow (C_6H_{12}o_6) + 6\ O_2$$

Note that the net equation does not include ATP, ADP, iP, $NADP^+$, NADPH, RuBP, PGA or G3P. All of these reagents are produced at the same rate that they are consumed. The net equation also hides the fact that that actually 12 H_2O are needed as reactants and that 6 H_2O are products (the net effect is simply the consumption of 6 H_2O). Part of the elegance of photosynthesis is that in spite of the myriad of reactions taking place, the net effect is very simple. Another aspect of its elegance is that the product of the process, carbohydrate $(CH_2\ O)_n$, can be used to make all of the diverse chemicals that the plant produces, not just the obvious ones (starch, cellulose, hemicellulose, pectins) but the less obvious ones (amino acids, nucleic acids, lipids, lignin, etc, etc). Moreover, carbohydrates are also used as a source of energy to power these synthetic reactions: In cellular respiration. carbohydrate is consumed to produce carbon dioxide and water while producing ATP and NADH, chemicals that are needed in many of the synthetic reactions.

Carbon dioxide acquisition, problems and solutions

For terrestrial auatotrophs, the carbon dioxide needed for photosynthesis comes from the atmosphere and it is highly significant that very little carbon dioxide is present there; atmospheric carbon dioxide concentration is only 400 ppm — for every million air molecules of air only 400 are molecules CO_2. Carbon dioxide enters the leaf by diffusion. Recall the flux equation introduced in Chapter 3 that the flux of CO_2 into the leaf is dependent upon the driving force, the difference in CO_2 concentration between the inside of the organism and the outside. The outside concentration is set at a low value, 400 ppm, and the inside value for most photosynthetic organisms (for most autotrophs, i.e. plants, this is the intercellular air inside the leaf) is about 100 ppm. This is because rubisco, the enzyme that catalyzes the 'fixation' of carbon dioxide, loses the ability to function when CO_2 concentrations are lower than 100 ppm. Because the driving force for carbon dioxide diffusion into the leaf is low, the inward movement of carbon dioxide (i.e., photosynthesis) is limited. Again examining the flux equation, it can be seen that flux can be enhanced if the resistance to CO_2 entry is low. In the case of a leaf this would mean making the leaf more porous, more open to the outside air. In moist environments, where water is readily available, there is no problem with have very porous leaves (i.e., open stomates), but when water is scarce the plant must balance carbon gain with water loss. Stomatal behavior reflects this compromise: they generally close at night, when photosynthesis is impossible, and during times of drought, when acquiring water to replace that which has been lost is difficult.

The additional carbon dioxide in the atmosphere in the last 200 years probably accounts for the observation that the earth is 'greener' (increased leaf cover) now than 50 years ago. More carbon dioxide can act as a 'fertilizer' and/or allows plants to survive under conditions of low water supply.

While there are a number of features that allow some plants to survive under dry conditions there is one that directly involves the photosynthetic reactions discussed above. This modified photosynthetic pathway, called the C4 pathway, allows some plants to acquire carbon dioxide while losing less water than a normal plant would. C4 plants concentrate carbon dioxide in a relatively small portion of the leaf, called the bundle sheath cells. The pathway utilizes two carboxylations. The first occurs in leaf mesophyll cells and utilizes an enzyme, PEP carboxylase, that adds a carbon to a three carbon compound, phosphoenolpyruvate (PEP). PEP carboxylase can operate at carbon dioxide levels down to around 10 ppm, roughly 1/10th of the concentration needed for rubisco to operate. The four carbon compound produced by PEP carboxylase is transported via plasmodesmata to a sheath of enlarged cells (Fig. 4) that surrounds vascular strands of the leaf. Here the four-carbon compound is decarboxylated, releasing carbon dioxide that is subsequently fixed in normal photosynthesis using rubisco. The remaining three carbon fragment is transported back to the mesophyll cells. Using this system of two carboxylations allows plants to produce an environment (the bundle sheath cells) where there is a higher concentration of carbon dioxide. It is only in this location where rubisco is present. Because of the CO_2 concentrating mechanism, the [CO_2] can be greater than 100 ppm in the bundle sheath cells while the [CO_2] of the air inside the leaf approaches 10 ppm. Because of the lower concentration of CO_2 inside the leaves of these plants there can be a greater driving force for diffusion into the leaf. This allows the resistance to be higher (stomates more closed) while still achieving the same amount of carbon dioxide flux (photosynthesis) as a plant that didn't utilize this pathway. Thus the leaf can function photosynthetically while being much less porous to carbon dioxide, thereby losing less water in transpiration than a 'normal' plant.

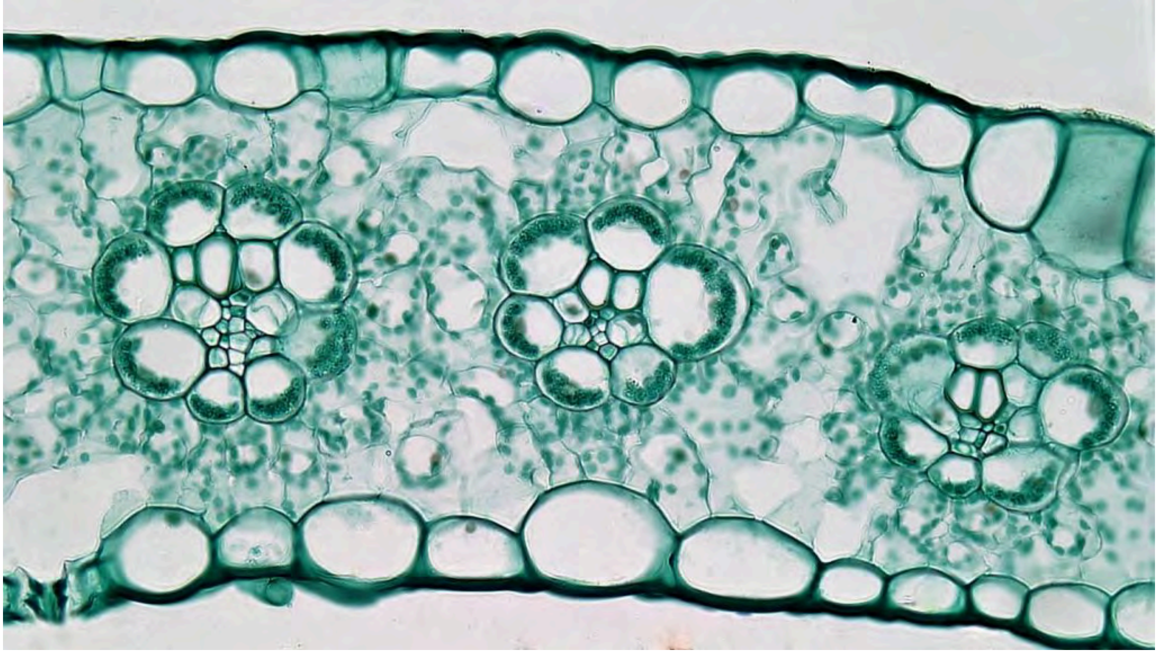

Fig. 4 C4 leaf (corn) showing enlarged bundle sheath cells surrounding the vascular bundles. Rubisco only occurs in these cells. The other cells have PEP carboxylase and transport four carbon compounds to the bundle sheaths.

Plants that utilize this dual carboxylation pathway are called 'C4 plants' because the first carboxylation produces a four carbon compound as opposed to the pattern in most plants, called C3 plants, where carboxylation produces a three carbon compound. The C4 pathway is outlined below:

- in the mesophyll cells of the leaf a three carbon compound, PEP, is carboxylated by PEP carboxylase, to form a four carbon compound
- the four carbon compound is transported to the bundle sheath cells that surround the vascular bundles (the veins of the leaf)
- the four carbon compound is de-carboxylated, releasing CO_2 and pyruvate, a three carbon compound

- the pyruvate is transported back to mesophyll cells where it is converted by into PEP in a process that requires energy in the form of NADPH and ATP
- the CO_2 that was released in the bundle sheath is fixed utilizing rubisco in the normal pathway

Note that C4 requires all the machinery and reactions of C3 photosynthesis, it is just that there is an additional set of steps prior to the C3 pattern. C4 photosynthesis is less efficient than C3 photosynthesis because it requires more ATP energy. However, it is more efficient in terms of water use and this is of greater significance in drier regions. Also, for reasons that we won't go into, C4 photosynthesis is favored at higher temperatures.

Fig. 5 Jade plant, an example of a succulent plant with thick, fleshy leaves. Most succulents carry out the CAM photosynthetic pathway.

There is a second group of plants that utilize the dual carboxylation pathway but in a modified way. They are called CAM plants. CAM refers to crassulacean acid metabolism because the pattern of behavior shown by this group was first discovered in succulent plants in the Crassulaceae family. CAM plants have several peculiarities: they are usually succulent, i.e., have thick fleshy leaves (Fig. 5), or no leaves and a thick, fleshy stem (e.g. cactus). They typically show a marked daily pattern of tissue acidity with the highest acidity at dawn and decreasing acidity during the daylight hours and increasing acidity during the nighttime. Most peculiar is that they open their stomates at night, not during the day whereas most plants only open their stomates during the day when they can photosynthesize.

Basically, these plants operate just as C4 plants do but instead of having a spatial separation of the two carboxylations as C4 plants have (mesophyll vs. bundle sheath), they have a temporal separation (daytime vs. nighttime). The initial carboxylation occurs at night when stomates are open. The four carbon compound is an acid and causes tissue acidity to increase. During the day the stomates close, carbon dioxide is provided by the decarboxylation of the four carbon acid and tissue acidity declines. The released carbon dioxide is re-fixed via rubisco to form carbohydrates.

Do these plants photosynthesize at night or during the day? It depends on how one might want to define photosynthesis: carbon acquisition is at night but sugar synthesis is during the day. CAM photosynthesis is associated, but not obligately, with succulence. CAM plants are generally found in habitats that are dry, either climatically, e.g., deserts, or because of microhabitat, e.g., epiphytes, plants that are not rooted in the ground but that grow on other plants. E piphytes are often exposed to drought because of their lack of connection to the soil. Cactus and other leafless succulents are commonly CAM plants. CAM photosynthetic rates are very low and CAM plant growth rates are also low. The association of succulence and CAM probably reflects the fact that plants in arid habitats often develop succulence to store water and that succulence is more conducive to CAM because succulent tissues can store more carbon as the four-carbon acid.

Patterns of both CAM and C4 photosynthesis reveal that these pathways have evolved multiple times, i.e., the pathways say little about phylogeny. C4, C3 and CAM are mixed within genera, families and orders. Apparently, it is relatively 'easy' for C4 and CAM to evolve.

Further Reading and Viewing

- "Early Evolution of Photosynthesis" by Robert E. Blankenship. The origins of photosynthesis.
  - https://academic.oup.com/plphys/article/154/2/434/6111499?login=true

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CHAPTER 21: METABOLIC DIVERSITY

Lessons from eccentrics

Sometimes understanding a process is aided by looking at variations on the process. We are studying how organisms satisfy their energetic and material needs allowing growth to take place. The primary material we are considering in the previous chapters is carbon, but it generally brings with it hydrogen and oxygen (in a carbohydrate molecule). We will get to other materials (elements, e.g. nitrogen) in a subsequent chapter, but carbon, hydrogen and oxygen make up 95% of most organisms. This chapter first reviews the common patterns of matter and energy acquisition found in most organisms. Then we will then consider several groups of organisms whose energy and carbon processing is eccentric in various ways.

TOPICS

- Review: 'normal' patterns involving matter and energy
    - Acquiring energy — cellular respiration
    - Acquiring food — heterotrophs and photosynthetic autotrophs
    - Acquiring carbon — heterotrophs and photosynthetic autotrophs
- ' Eccentric' organisms
    - Obtaining energy when there is no oxygen
        - fermentors
        - using alternative electron acceptors
    - Chemoautotrophs, making food (carbohydrates) without light
    - Photoheterotrophs (=photoenergetic heterotrophs) , separating matter and energy

'The norm'—the most common processes

1. Acquiring metabolic energy

Nearly all organisms utilize the reactions discussed in the chapter on cellular respiration to supply their energetic needs: cellular respiration provides energy in the form of ATP as long as a supply of carbohydrates and oxygen is available. Oxygen is readily available in all terrestrial habitats due to the fact that the atmosphere is 20% oxygen and local depletions are rare because the atmosphere is continually mixed by winds. In contrast, in some aquatic situations (including soils saturated with water), oxygen may be in short supply. Present in such situations are a number of organisms, both prokaryotic (bacteria or archaea) and eukaryotic, that can obtain ATP energy in the absence of oxygen, in a manner that utilizes only the glycolysis part of cellular respiration. Alternatively, there also are organisms, solely prokaryotes, that have mechanisms to make ATP that don't rely at all on the pathways of cellular respiration.

2. Making your own food: energy flow in photosynthetic autotrophs

If you consider it closely, the energetics of photosynthetic organisms seems unnecessarily involved: the light reactions produce ATP and NADPH in order to synthesize carbohydrates from carbon dioxide. Then the carbohydrates are broken down in cellular respiration to produce NADH (for our purposes the same as NADPH) and ATP. Why bother making carbohydrates?; why not just use the light reactions to obtain 'energy currency,' ATP and NADH? To a limited extent, photosynthetic organisms DO satisfy some of their energetic needs directly off of the light reactions, i.e., not all of the ATP and NADPH produced is used to make carbohydrates, some power other processes. But for the most part, the flow of energy in photosynthetic organisms goes from light to ATP and NADPH, to carbohydrates, and then back to ATP and NADH; and the amount of energy available is diminished along the way because the energy transfers are not 100% efficient. There are several justifications to this behavior of photosynthetic organisms:

- cellular respiration evolved first and photosynthesis appeared as a means to allow organisms to avoid having to 'beg and steal for food'
- the need for energetic compounds is continuous but nighttime prevents photosyn-

thesis from happening., ATP and NADH cannot be readily be stored and, while they are constantly recycled, the absolute amounts of ADP/ATP and NADP/NADPH are small. In contrast, carbohydrates can stored and can be present in much greater amounts.

- for vascular plants, the below-ground parts need energetic compounds yet can't photosynthesize. The labile nature of ATP and NADH means that they cannot be transported, while carbohydrates can.

However, we will see that there are some organisms who use light in a strictly energetic role, not using it to make carbohydrates that are subsequently be used to obtain energy.

3. Material needs, specifically carbon

As to material needs, for the most part (or you might say 'for most of their parts' !), organisms are composed of carbohydrates, or molecules that are made from carbohydrates, e.g., the amino acids of proteins, which basically consist of a carbohydrate with nitrogen group(s) and occasionally also a sulfur group attached; or fats, which are made from carbohydrates that have had most of their oxygens removed. Thus **any** organism must obtain carbohydrates to construct more of themselves, i.e., to grow. For photosynthetic autotrophs, carbohydrate needs are supplied by photosynthesis, but note that whatever carbohydrates directed towards material needs are not available to be used for energetic needs. For heterotrophs, carbohydrate needs are satisfied by appropriating part of what is consumed to whatever 'building projects' a heterotroph may require, but, as a result, reducing the amount of energy that can be obtained. Nearly all organisms are either heterotrophs, whose consumption of organic material (coming from the bodies or parts of bodies of organisms) provides them with both energy and with carbon materials; or photosynthetic autotrophs who use light to make their own carbohydrates out of carbon dioxide and water and then, like heterotrophs, use this 'food' for both material and energetic needs. However, there are some organisms (all prokaryotic) who are non-photosynthetic autotrophs, i.e., they are able to make carbohydrates without sunlight, using chemicals as an energy supply. There also are organisms, again prokaryotes, whose dietary habits include or require some materials that are not obviously 'organic', i.e., made by organisms, e.g., formaldehyde or 'plastic' (polyethylene terephthalate). There also are some organisms that 'eat' solely for carbon nutrition and have other mechanisms, that are not based on carbohydrate food, to obtain energy.

Below are some groups of eccentric organisms, organisms that differ from the more usual patterns discussed above.

Eccentric organisms I: anaerobic organisms —use of alternate electron acceptors

Remember that oxygen's role in cellular respiration is to be an 'electron magnet', a low point to which electrons flow. Electrons obtained from carbohydrates are transferred to NAD^{+}, forming NADH, and from it electrons flow through a series of carriers of the electron transport chain. Oxygen's role is essential both because it 'drives' the electron flow that in turn allows ATP to be synthesized, and also because the process regenerates NAD^{+} which is required in order for both glycolysis and the citric acid cycle to continue. In most of the earth's habitats, oxygen is plentiful and has been ever since photosynthesis became popular roughly 2 billion years ago. But there are situations where oxygen becomes scarce, generally as the result of cellular respiration coupled with physical factors, e.g., waterlogged soils, that make oxygen replenishment unlikely (Chapter 26). One solution to an oxygen deficit is to find another atom or molecule that will serve in the same role, i.e., be a 'downhill location' to which electrons can flow.

There are a number of bacteria that do this, utilizing a number of different molecules as substitutes for oxygen. A particularly important group to plant nutrition are the denitrifying bacteria. They use nitrate (NO_3^{-}) as the electron acceptor that receives the electrons from the NADH produced in glycolysis and the citric acid cycle. In the process, they convert nitrate, a form of nitrogen that most plants can assimilate (i.e., utilize) into dinitrogen gas (N_2), a form of nitrogen that plants can not assimilate (although some can with the aid of a symbiont). Moreover, N_2 is volatile and can escape the soil; in contrast, nitrate is an ion and consequently unable to leave the soil solution, although the soil solution itself may leave the soil, taking ions with it (i.e., leaching (discussed in Chapter 23). The process of converting nitrate to dinitrogen gas is called denitrification and in some situations, it causes a substantial loss of nitrogen from soils. Another substitute for oxygen is sulfate (SO_4^{2-}), which, after accepting electrons, is converted to hydrogen sulfide. As was the case with denitrification, these reactions adversely affect plant mineral nutrition by eliminating a form that the plant can assimilate (sulfate) and putting sulfur into a form that plants are less able to acquire and also a form that is volatile and can be lost from the plant's habitat.

Eccentric organisms II: anaerobic organisms —fermentation

One solution to a scarcity of oxygen, and one that is the closest to the normal patterns, is a process called fermentation ('anaerobic respiration') which involves an addendum to glycolysis, the first stage of cellular respiration, and necessarily the elimination of the remaining parts of cellular respiration. The pyruvate produced by glycolysis does not go through the citric acid cycle but instead is used directly or indirectly to accept electrons from NADH, allowing NAD^+ (Fig. 1) , which is essential to glycolysis, to be regenerated. Significant to the fermenting organism is that this allows glycolysis to proceed, although much less ATP is obtained in the process than would be formed if the citric acid cycle and oxidative phosphorylation were able to occur. Also significant is that, while the end products of cellular respiration are water and carbon dioxide, benign substances that are easily dispersed, the end products of fermentation, commonly ethanol or lactic acid, are more toxic and more difficult to eliminate. Fermentation is extremely important in human affairs, both in the production of alcoholic beverages (generally by fungi but occasionally by bacteria) and in the production of desirable food products, e.g., sourdough (Fig. 2), sauerkraut, sour cream, yogurt, all of which are influenced by lactic acid production. Some fermenting organisms are facultative anaerobes (i.e., they can live with or without oxygen). Most of these switch to fermentation if oxygen is not present but some carry out fermentation regardless of oxygen availability. Some are obligate anaerobes, meaning that they cannot live in the presence of oxygen.

Eccentric organisms III: making food without sunlight-chemosynthetic organisms

Most autotrophs ('self-eaters') make food through photosynthesis and then eat themselves. The energy of light is what makes an unfavorable reaction, the reduction of carbon dioxide by water, more likely. A vague but common description of the process is that some of the energy of light is captured by the plant and stored as carbohydrates. A more specific description is that light is able, in the organized structure of a membrane, to move electrons in a way that NADPH is formed from $NADP^+$ using electrons derived from water. In the process, ATP is formed as a result of the electron flow. In the Calvin cycle, these products, NADPH and ATP, can cause carbon to be reduced with electrons

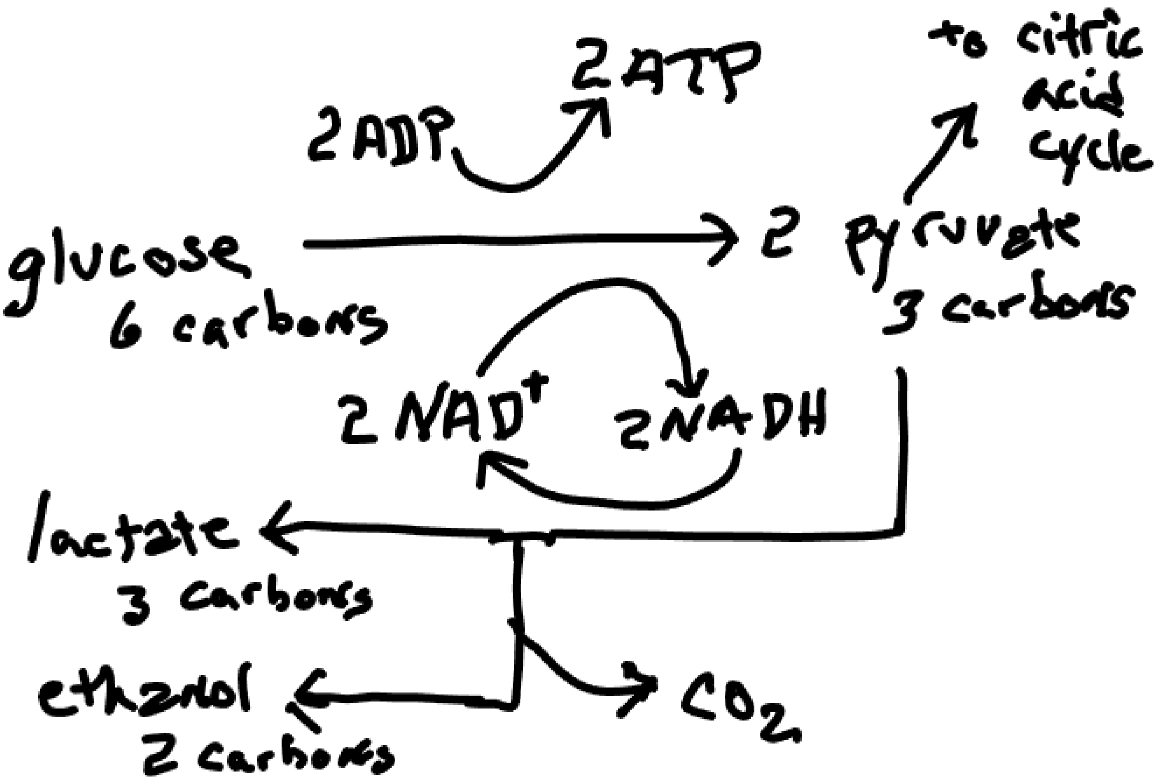

Fig. 1 Fermentation: Converting glucose into two pyruvate molecules requires two NAD+ molecules. In fermentation the pyruvate does not go to the citric acid cycle but instead is converted to either lactate or ethanol, in reactions that regenerate NAD+, and, in the case of ethanol, remove a carbon as carbon dioxide.

provided by NADPH and with ATP promoting the reactions. Light is essential to photosynthesis because it provides a mechanism to obtain NADPH and ATP. But these metabolites can be made in other ways and there are non-photosynthetic autotrophs that do exactly that. They are described as chemosynthetic organisms and they make their own food in ways that do not require light. What is needed is a chemical that can donate electrons to reduce $NADP^+$ to NADPH and a membrane system that allows ATP to be synthesized as the electrons flow from the donor to $NADP^+$. Chemosynthetic organisms are uncommon and are only found within the bacteria and archaea, but they can be very significant in certain habitats and in carrying out processes that are important to global biogeochemical cycles. Fr om a plant perspective, the most important group of these organisms are the nitrifying bacteria, a group that oxidize s ammonia (NH_3) to nitrite (NO_2^-), and a group that oxidizes nitrite to nitrate (NO_3^-). The result of the two reactions is that ammonia is converted to nitrate, which is the preferred

Fig. 2 Sourdough starter, a culture of yeast and bacteria that is used in baking. The most abundant are anaerobic bacteria (Lactobacillus, which produces lactic acid), and yeasts that produce alcohol and carbon dioxide. The carbon dioxide acts as a leavening agent, causing the dough to rise, and the lactic acid gives the familiar 'tang' of sourdough.

nitrogen source for most plants, and, unlike ammonia, cannot escape the soil as a gas. Note that both these reactions are oxidations (this is obvious in the NH_3 to NO_2^- reaction when hydrogens are removed from nitrogen, but is also true in the NO_2^- to NO_3^- conversion). The electrons removed from the nitrogen compound are used to reduce $NADP^+$ to NADPH and provide for an electron flow (through a membrane) that allows ATP to be synthesized. These reagents are then used to reduce carbon dioxide in the reactions of the Calvin cycle, 'fixing' it in to a carbohydrate form. The nitrifying bacteria, like photosynthetic plants, make their own food and then use it for synthetic reactions (as a building material) or as a source of energy (as it is oxidized to carbon dioxide in cellular respiration). There are other chemosynthetic organisms besides the nitrifying bacteria, including: (1) bacteria in deep-sea vents, that utilize hydrogen sulfide as an energy source to fix carbon, (2) methanogens, that use energy from dihydrogen gas (H_2) to fix carbon (and at the same time producing methane) , and (3) methane 'eaters' that oxidize methane to dinitrogen (N_2) while reducing carbon. Many, but not all, chemosynthetic organisms are archaebacteria, although most nitrifying bacteria are not.

Eccentric organisms IV: separating matter and energy

For most organisms, 'food', i.e., what heterotrophs absorb or ingest, and for photosynthesizers, the carbohydrates that they make, plays a dual role: as an energy source (producing ATP and NADH) and as a carbon source, providing 'reduced carbons' that are used in a variety of biosynthetic reactions that ultimately can make the organism bigger. The pathways for the two processes are initially the same but if the carbon is to be utilized as building material much less energy is obtained and less carbon dioxide is produced. If used for energy, 'food' i.e., carbohydrates, ends up as carbon dioxide and the amount of energy obtained is maximal; if used for material, the carbons of the carbohydrate end up in any one of the thousands of biomolecules found in the organism, in fats, proteins, nucleic acids, etc., and the amount of energy obtained is reduced compared to what would happen if all the carbons were totally oxidized to CO_2. However, there are some organisms who have distinct pathways for obtaining energy, pathways that generally don't involve carbon at all and their 'eating' is solely to obtain carbon atoms for biosynthesis. The easiest group to understand is photoheterotrophs. They include both archae a and bacteria that are capable of using sunlight in a process that allows them to synthesize ATP but not in a manner that produces carbohydrates. Thus they must 'eat food' (absorb carbohydrates/organic molecules) NOT necessarily for their energetic needs (i.e., to supply ATP) but rather to satisfy their carbon needs. This lifestyle is found in a few Archaea, for example, *Halobacterium* which possesses a pigment, bacteriorhodopsin, related to the rhodopsin found in vertebrate eyes. Bacteriorhodopsin is a membrane-spanning protein that can acquire protons in the cytosol, change conformation due to the absorption of light, and release protons on the outside of the membrane (Fig. 3). Protons then flow into the cell, down their electrochemical gradien t and, as is the case in the light reactions of photosynthesis and oxidative phosphorylation in cellular respiration, the proton movement causes ATP to be synthesized from ADP and inorganic phosphate. Most of the photoheterotrophs (= photoenergetic heterotrophs) are bacteria that use a form of chlorophyll to absorb light energy and again create a proton gradient that can be used to synthesize ATP but require a source of reduced carbon for material needs.

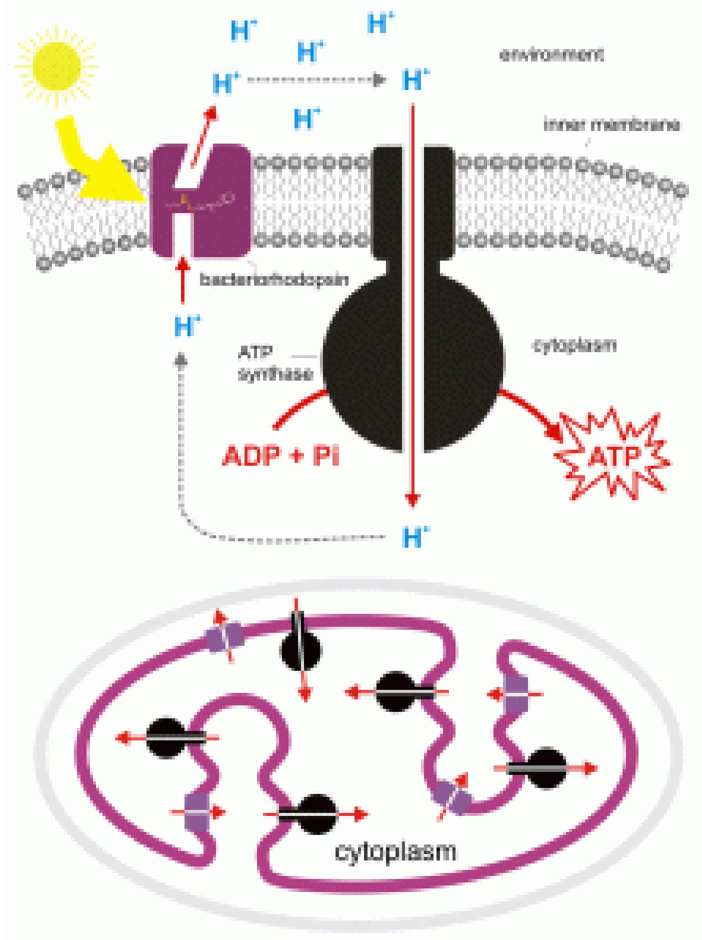

Fig. 3 ATP synthesis in Halobacterium utilizes a pigment to pump protons. These then flow back into the cell allowing ATP to be produced. No reducing power (NADH) is produced and consequently, carbohydrates are not synthesized.

In a similar manner there are chemoheterotrophs (=chemoenergetic heterotrophs), this includes some nitrifying bacteria and some methanogens. These are organisms that 'eat' for their material (i.e., reduced carbon needs) but generate ATP by chemical means that does NOT involve the cellular respiration and oxidation of carbohydrates.

Table 1 below summarizes the different modes of acquiring matter (carbon) and energy (reducing power and ATP). It introduces a new terminology. Unfortunately there are already too many but this one emphasizes the distinction between matter and energy with the former being obtained either by eating oneself (autotroph) or eating others, or the remnants of others (heterotroph), and the way that energy is obtained either from sunlight (photoenergetic) or from chemicals (chemoenergetic)

Table 1.

	energy	**carbon source**	**groups**
heterotroph (obtains matter and energy by eating others)	energy (reducing power and ATP) from oxidation of collected biomolecules	carbon (reduced) from collected biomolecules	all animals, all fungi, slime molds, water molds, some dinoflagellates, most bacteria, most archea
photosynthetic autotroph = photoenergetic autotroph	energy (reducing power and ATP) from oxidation of self-made biomolecules	carbon from carbon dioxide reduced in photosynthesis and used to synthesize biomolecules	all plants, green algae, red algae, brown algae, diatoms, some dinoflagellates, cryptomonads, cyanobacteria, green sulfur bacteria
chemosynthetic autotroph = chemoenergetic autotroph	energy (reducing power and ATP) from oxidation of self-made biomolecules	carbon from carbon dioxide reduced in photosynthesis used to synthesize biomolecules	some, but not many, bacteria (nitrifying bacteria, sulfur-oxidizing bacteria, iron-oxidizing bacteria, some methanogens) and some archaea (methanogens).
photoheterotroph = photoenergetic heterotroph	energy (some reducing power but mostly ATP) from light-driven reactions	carbon (reduced) from collected biomolecules	Some, but not many, archaea (*Halobacterium*), some green non-sulfur bacteria, some purple non-sulfur bacteria.
chemosynthetic heterotroph = chemoenergetic heterotroph	energy (reducing power and ATP) from electron flow driven by inorganic sources of electrons	carbon (reduced) from collected biomolecules	some, but not many, bacteria (*Beggiatoa*) and some archaea (methanogens).

Further Reading and Viewing

- "Chemosynthesis" by Alex Enrich-Prast
    - https://www.sciencedirect.com/topics/biochemistry-genetics-and-molecular-biology/chemosynthesis
- "Methanogens: pushing the boundaries of biology" by Nicole R. Buan
    - https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7289024/

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CHAPTER 22: NUTRITION AND NUTRIENTS

In order to grow, an organism has to acquire materials to make itself bigger. These materials are sometimes considered ‘food’ (Fig. 1-2) or may be described as nutrients and this chapter considers what nutrients are required by organisms and how they are acquired. We have already considered three nutrients, carbon, hydrogen and oxygen, that play a role in the energetics of organisms, but they also are important materially. Organisms are built of more than just these three and need the others in order to grow. The acquisition of required materials (i.e., organismal nutrition) is something that distinguishes most of the organisms considered in this book from animals. Nutrition is highly significant, not just to the success (i.e., growth and reproduction) of organisms but also to ecology and to interactions with other organisms and specifically agriculture. For reasons that should be obvious already and that are elaborated on further in this chapter, the nutrition of organisms is strongly affected by their lifestyle, in particular, whether they are an autotroph or heterotroph, and also by their evolutionary history.

TOPICS

- Chemical (molecular) composition of organisms
- Chemical (elemental) composition of organisms
- How nutritional requirements are met by heterotrophs and autotrophs
- Mechanisms of nutrient acquisition
- Vitamins

Fig. 1 Are flies 'food' for the Venus fly trap? Are the nutritional needs of Venus fly traps different from that of other plants?

Fig. 2 What is 'plant food'? How does it differ from human food?

Chemical (Molecular) Composition of Organisms

One of the properties that define organisms is their chemical composition, both in terms of elements (e.g. carbon) and in terms of compounds (combinations of elements, e.g. carbohydrates). The compounds that make up organisms are distinctive in comparison to the world they live in, with most of the chemical compounds (biomolecules) being unique to living things, although some (e.g., silicon dioxide, calcium carbonate) can be produced in non-living situations. A general classification of the molecular composition of organisms is shown below.

Table 1. The chemical compounds (molecules) of organisms

type	chemistry	elements	examples	functions
carbohydrates	($C_6H_{12}O_6$)	C, H, O	glucose, fructose	metabolites, energy sources
carbohydrate polymers	polymers of simple sugars	C, H, O	starch, cellulose, hemicellulose, pectin	energy storage, cell wall components

type	chemistry	elements	examples	functions
amino acids	carbohydrate with an NH_2 group	C, H, O, N, S	glycine, leucine, aspargine	components of proteins, means of transporting nitrogen atoms
proteins	polymers of amino acids	C, H, O, N, S	rubisco, DNA polymerase	enzyme catalysts, structural molecules
lipids	chains of carbon and hydrogen, often with a phosphate attached.	C, H, P	fats, phospholipids, glycolipids,	partitioning the cell into compartments, energy storage in seeds
nucleiotide	nitrogenous compound attached to sugar plus phosphate groups	C, H, O, N, P	ATP, GTP	energy metabolites, components of nucleic acids
nucleic acids	polymers of nucleotides	C, H, O, N, P	DNA, RNA	information storage and processing

Elemental Composition of Organisms

The elemental composition of organisms reflects their molecular composition. Typically around 98% of the mass of any organism is composed of four elements, C, H, O, and N. But other elements are present and many of these are 'essential', i.e., the organism must have them in order to survive, grow and reproduce. Table 2 lists those elements that are considered essential for all organisms and are also found in high enough concentrations to be considered 'macronutrients'.

Table 2. Essential 'macronutrients', elements considered to be essential (with known required roles) and needed in 'large amounts', typically more than 0.1% of the dry weight of an organism.

C (carbon)	carbohydrates, lipids, proteins
H (hydrogen)	everywhere!! also important when present as protons (H^+)
O (oxygen)	carbohydrates, proteins, electron acceptor in respiration
N (nitrogen)	amino acids (proteins), nitrogenous base of nucleiotides, thus in nucleic acids; also present in metabolites such as ATP, NAD, NADP, and many others

P (phosphorus)	phospholipids, nucleic acids, ATP, and others
K (potassium)	used exclusively as a cation unbound to an anion; important in effecting changes in membrane charge and influencing water diffusion
Mg (magnesium)	present in chlorophyll, also an important ion in many enzyme reactions
Ca (calcium)	A component in cell walls often serves as a messenger in signal transmission, often plays a regulatory role within cells
S (sulfur)	found in two amino acids, and thus in proteins; also a component of several important metabolites, including some considered as vitamins
Fe (iron)	found in cytochromes and other iron-sulfur proteins important in the electron transfer processes of both photosynthesis and respiration

Note that sodium (Na) is **not** on the list. Sodium is required by animals, where it plays a role in membrane charge, electrolyte balance and nerve transmission. But it is not required by most plants and fungi. In spite of this and because sodium is common in the environment, sodium is generally present in both plants and fungi. Typical sodium concentrations in plants are high enough, in spite of the fact that it is not required, to supply herbivores and other heterotrophs with sodium sufficient for their needs.

In addition to macronutrients, organisms require additional elements but only need them in very small amounts; these are called micronutrients. Table 3 lists micronutrients known to be essential in plants and thought to be essential in all organisms. Table 4 lists micronutrients that are not essential to plants but are thought to be essential to at least some organisms.

Table 3. Essential 'micronutrients', elements considered to be essential (with known required roles) and needed in small amounts, typically less than 0.1% of the dry weight of an organism.

Cu (copper)	co-factor in multiple enzymes; in normal (oxygenic) photosynthesis, copper is involved in electron transport between the two photosystems
Mn (manganese)	a component of several essential enzymes and also in the 'oxygen-evolving complex' of the oxygenic photosynthesis process found in plants and cyanobacteria
Zn (zinc)	required by several enzymes and also is a component of regulatory proteins involved in gene expression
B (boron)	probably plays a role in several enzyme systems; also present in plant cell walls, important in the elongation of plant cells
Cl (chlorine)	important as an electrolyte; in plants, chlorine is also involved with water splitting and the oxygen-evolving complex of oxygenic photosynthesis
Ni (nickel)	involved several essential enzymes
Mo (molybdenum)	involved in several essential enzymes; in plants, Mo is essential to processes involved with nitrogen assimilation

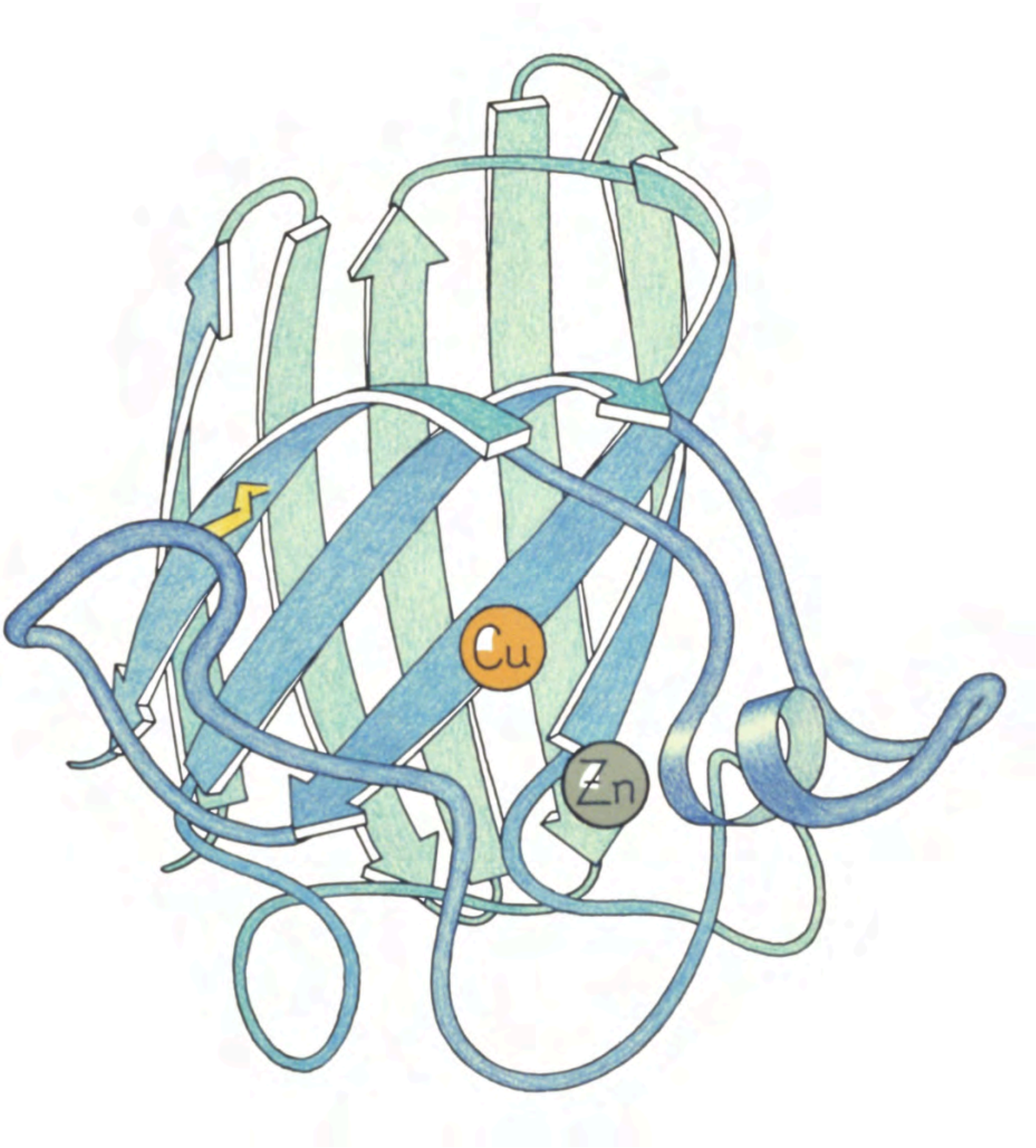

Fig. 3 Model of the bovine superoxide dismutase, one of several enzymes that have micronutrients (in this case copper and zinc) as essential components. This is the most common reason why the essential micronutrients are essential.

Table 4. Common micronutrients required by some or many heterotrophs but not required by plants. The first four (sodium, iodine, cobalt, selenium) have known roles for substantial numbers of organisms.

Na (sodium)	not required for most plants but commonly present in them; required by animals where it plays a role in electrolyte balance, membrane charge and nerve transmission
I (iodine)	a component of thyroid hormones, not required by plants
Co (cobalt)	a component of vitamin B12, which is essential for animals and many protists (including some photosynthetic protists), also required by bacteria and cyanobacteria that carry out nitrogen fixation
Se (selenium)	part of several enzymes, including some that eliminate oxidant molecules, required by few plants where it is generally is a component of antiherbivore compounds
Vn (vanadium)	component of antioxidant enzyme found in diatoms and red, brown and green algae; needed in nitrogen-fixing bacteria and cyanobacteria
Cr (chromium)	essential role debated, some cite a role related to insulin
Fl (fluorine)	essential role debated but is known to strengthen bones and teeth
As (arsenic)	essential in rats and mice; essentiality not established for humans, role not known
Sn (tin)	essential in rats and mice; essentiality not established for humans, role not known

Tables 2 and 3 list the 17 essential elements required by plants. The elemental composition of plants, and organisms in general, is not reflective of the abundance of elements in the atmosphere (80% nitrogen, 18% oxygen) or the solid earth (46% oxygen, 28% silicon, 8% aluminum, 5% iron ~ 3% calcium, sodium, potassium, magnesium) or dissolved in the water (chlorine 19.1 g/kg of seawater, sodium 10.7 g/kg, magnesium 1.3 g/kg, sulfate 2.7 g/kg). Clearly, organisms are not in equilibrium with their environment and somehow acquire elements to higher levels than found in their environment.

Acquisition of nutrients—how nutritional needs are met

Nutrition is strongly influenced by lifestyle. For heterotrophs, their chemical composition and how they acquire it are relatively easy to explain — 'you are what you eat;' the composition of heterotrophs reflects their absorption of biological molecules that are derived from the organisms that they ingest. And since all life is made of the same materials, the consumption of biomolecules by heterotrophs should allow heterotrophs to acquire the material required to make more of themselves and consequently to grow. Recall that some heterotrophs are ‘ingesters’ (e.g., lions, caterpillars, humans) swallowing organisms or parts of organisms into a tube inside their body where digestion occurs that breaks down the large biological molecules (e.g., proteins) into smaller ones (amino acids) that can be absorbed by the organism. Other heterotrophs are ’absorbers’ (e.g., fungi, many bacteria, water molds) and do the digesting outside of their body. The basic process is the same in both groups: large molecules are broken down into smaller ones that can be absorbed. Three key factors influence the nutrition of heterotrophs: food choice (what they choose to eat), digestive abilities (what biomolecules they can break down into smaller units, and absorptive abilities, what molecules they can transport into their cells. These factors vary tremendously, especially within the archaea, bacteria and fungal groups. Also note that for absorbers, digestion may be partly or largely the result of other organisms living in the same habitat. A similar situation exists within ingesters because they usually harbor organisms within their gut track that participate in digestion. Note that for heterotrophs the acquisition of the nutrients shown in Table 4 may be problematic because the element may not necessarily be in the ingested food, e.g., iodine is not required by plants so heterotrophs may not necessarily acquire it from the food they eat. The same is potentially true for sodium, but in practice, most plants contain sodium even though they do not require it because sodium is common in the environment.

The nutrition of autotrophs is very different. They need the same elements that heterotrophs do (Tables 2 and 3) but they do not acquire these in a ‘prepackaged’ form. Moreover, many autotrophs can’t utilize nutrients in a prepackaged form. While some photosynthetic protists (algae) and many photosynthetic prokaryotes do have the ability to absorb organic compounds, plants have no ability to ingest materials (i.e., no mouth and digestive tract), nor can they break down large organic molecules outside their body, or even to absorb breakdown products like amino acids, should they happen to be present. In fact, the materials that plants absorb are not ‘organic’ (= biological), they are elements or simple compounds found in the environment, such as CO_2 (carbon dioxide), NO_3^- (nitrate), SO_4^{2-} (sulfate) , PO_4^- (phosphate) or elemental ions (e.g., Ca^{2+}, Cl^-). Autotrophs have the ability, which heterotrophs lack, of transforming these elements and simple compounds into biological compounds. By far the most extensive process is the conversion of carbon dioxide and water into carbohydrates, but many other reactions are essential:

adding nitrogen groups to carbohydrate molecules to produce amino acids, synthesizing nucleotides, nucleic acids, assorted metabolites (e.g., $NADP^+$, assorted vitamins), etc. This process is made all the more challenging by the fact that the raw materials used by autotrophs are all dilute and scattered in the environment. This is in contrast to the materials that heterotrophs consume, where all the needed materials are usually found together in 'food'.

In order for autotrophs to acquire the minerals, they need these minerals must be in a form that dissolves in water and in a form that autotrophs can acquire (i.e., will pass through a membrane or through a channel/carrier protein imbedded in a membrane). For aquatic autotrophs, all of the nutrients that they acquire come from the solution they are immersed in. For terrestrial autotrophs (plants), carbon is the sole element acquired directly from the air, as carbon dioxide. All other nutrients come from the 'soil solution', the water held in the soil. Not only must nutrients be in soil solution, they also have to be in a form that the organism can assimilate. For example dinitrogen gas (N_2), readily dissolves in water, and readily enters into organisms, but it can only be assimilated, i.e., incorporated into an organic form, by a relatively small group of organisms in both the Bacteria and Archaea groups. Plants, other eukaryotic autotrophs, and most prokaryotic autotrophs cannot assimilate N_2 and need to acquire nitrogen as either ammonia or nitrate.

The role of heterotrophs in autotroph nutrition

A common bumper sticker used to be 'Have you thanked a green plant today?'— the message being that green plants are essential to all life on earth because they form the base of the food chain. A comparable message is also significant—' Have you thanked a heterotroph today?' As essential as green plants are, they in turn are dependent on heterotrophs. Heterotrophs are essential to autotrophs (and thus to heterotrophs themselves, i.e., this is circular) because heterotrophs put nutrients into a form that autotrophs can use. Without heterotrophs, green plants would be unable to acquire the carbon and other elements that they require. When viewed by autotrophs the general role of heterotrophs is decomposition, to break down organic material into simple 'inorganic' compounds that they can utilize, a process described as 'mineralization'.

Because nutrients are diluted in the environment and concentrated in organisms, absorption of elements involves accumulation — the concentration of elements inside organisms.

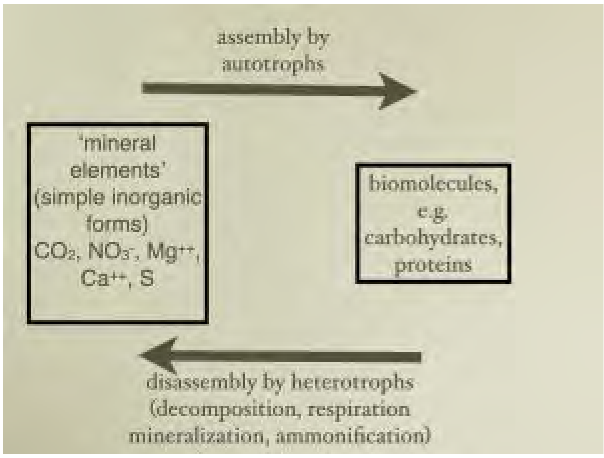

Fig. 4

And this accumulation requires energy and is an 'active' process. Some nutrients are absorbed in the charged (ionic) state. Since the inside of the cell is negatively charged relative to the outside of the cell, nutrients that are cations (positively charged) may actually be accumulated by moving down their electrochemical gradient. In such a situation the accumulation might be considered 'passive' (down an electrochemical gradient) but this is ignoring the fact that energy is required to make the inside of the cell negatively charged.

For both autotrophs and heterotrophs, a variety of cellular mechanisms account for the absorption of nutrients. They include the following:

- **diffusion across the membrane:** since most nutrients are charged and since charged molecules do not readily penetrate the phospholipid bilayer of the cellular membrane, this is relatively rare; however, occasionally it can account for the absorption of uncharged molecules, e.g., ammonia (NH_3)
- **passive diffusion through channels:** Cations are sometimes acquired by diffusion down an electrochemical gradient through protein-structured 'pores' in the phospholipid bilayer. Generally, these pores are selective and only allow certain cations to pass through them.
- **pumps**: some nutrients move across the membrane in a process that requires an energy source, typically ATP. This movement involves proteins (enzymes) whose conformation changes in response to some process that is energetically driven. Generally, pumps account for the accumulation of nutrients against an electrochemical gradient, but they could also could also account for enhanced movement of cations

down their electrochemical gradient.

- **coupled ion transport:** Since cells are negatively charged, the movement of charged molecules can be coupled to the passive movement of cations into the cell, or anions out of the cell. Most commonly, anion movement into the cell is coupled with the inward movement of protons. Coupled ion transport also involves proteins and generally is quite specific with regard to nutrients, i.e., there are separate carriers for different ions.

Absorption mechanics are significant because all of the elements required by autotrophs may actually become toxic (with levels high enough to inhibit growth) if they become overly abundant in the environment (e.g., chlorine toxicity in saline soils). It is also significant that autotrophs often take up elements that they do not require and this may be beneficial (e.g., sodium) or detrimental (e.g., arsenic) to the heterotrophs down the food chain.

Acquisition mechanisms for essential nutrients

Carbon

For all autotrophic organisms carbon is acquired as carbon dioxide, either from the atmosphere or dissolved in water. Carbon dioxide dissolves in water and then can be transformed into a variety of compounds by (mostly) abiotic chemical reactions. The most significant reactions are the formation of carbonic acid from carbon dioxide and water; the formation of bicarbonate ion as carbonic acid loses a proton; the formation of carbonate ion as bicarbonate ion loses a proton. Carbon is readily exchanged between these pools and all of them can be considered 'biologically active' forms of carbon.

$H_2O + CO_2 \rightarrow H_2CO_3$ (carbonic acid)

$H_2CO_3 \rightarrow H^+ + HCO_3^-$ (bicarbonate ion)

$HCO_3^- \rightarrow H^+ + CO_3^{2-}$ (carbonate ion)

For heterotrophic organisms, carbon is acquired in a variety of biomolecules: carbohydrates, proteins, lipids. The exact mix of compounds depends on the dietary preferences of the organism. Heterotrophs can only absorb relatively small molecules (simple sugars, amino acids, nucleotides) and therefore often have to break down polymers (e.g., starch, proteins) before absorption actually occurs. Once inside the cells of the organism, these small molecules (e.g., glucose, amino acids) may be oxidized in cellular respiration, decomposing them to carbon dioxide, water, and (for amino acids) some nitrogenous compounds like ammonia. A bsorbed nutrients may also be 'reassembled' into polymers or metabolites like NADH that are used for growth or to replace molecules that have been broken down.

Hydrogen

For autotrophs, hydrogen is is acquired in water molecules and occasionally in other compounds. For heterotrophs, hydrogen is acquired in water, carbohydrates, proteins and lipids.

Oxygen

Oxygen plays two roles in organisms: a structural role, being a part of most biomolecules (carbohydrates, proteins, nucleic acids) and a dynamic role, being an essential reactant in cellular respiration that is subsequently lost as water. For autotrophs, oxygen for the structural role is acquired as carbon dioxide that is incorporated into carbohydrates and subsequently into other important biological molecules. For heterotrophs, structural oxygen is acquired in the food that they consume. For both autotrophs and heterotrophs, oxygen for respiration is acquired as molecular oxygen (O_2) which, for terrestrial organisms, can be acquired directly from the atmosphere where it accounts for nearly 20% of the air's molecules. In aquatic systems, oxygen is obtained from the water where it usually is present as a dissolved solute. Oxygen concentrations in water are variable, depending primarily on exchange with the atmosphere, biological activity and how much the water is being mixed (circulated). Photosynthetic organisms produce oxygen but this effect is limited to the region of the water column that receives light. Throughout the water column, oxygen is consumed by all aerobic organisms. How much the oxygen levels are lowered by this action depends on the amount of living things, their rate of oxygen consumption (this is a strong function of temperature), and the rate of oxygen delivery to the system.

Nitrogen

For heterotrophs, nitrogen is obtained from the food that they eat, primarily from proteins, but also from nucleic acids and nucleotides. Some fungi, bacteria and archaea can acquire nitrogen as nitrate (NO_3^-) or ammonia (NH_3) or ammonium ion (NH_4^+). For plants, nitrogen is always acquired as nitrate or ammonia dissolved in water. Although nitrate and ammonia are considered to be 'inorganic' molecules they are almost always produced from biological molecules as a consequence of the following biological processes:

> **ammonification** is the production of ammonia and can be considered to be a type of 'decomposition'. It occurs as amino acids are used as a source of energy; the carbohydrate component of amino acids is oxidized in cellular respiration and the amino group is either directly excreted as ammonia or as some other small nitrogen-containing molecule (urea, uric acid). All heterotrophs participate in ammonification, either by directly producing ammonia, or indirectly by producing compounds like urea and uric acid that are readily converted (mostly by bacteria) to ammonia. How much a particular heterotroph participates in ammonification depends upon their diet, specifically how much protein they consume.
>
> **nitrification** is the production of nitrate. Nitrate is produced by the action of a small group of chemosynthetic organisms (previous chapter) that use ammonia as a source of energy; as ammonia is oxidized to nitrate, an electron flow is created that can result in the synthesis of ATP. Additionally, some chemosynthetic organisms use the reducing power of ammonia to reduce carbon dioxide to carbohydrate. The process first involves the conversion of ammonia to nitrite (NO_2^-) by one group of bacteria followed by the conversion of nitrite to nitrate (NO_3^-) by a second group of bacteria.
>
> Ammonia is uncommon in most soils because it is usually quickly converted to nitrate by nitrifying bacteria and also because it is volatile and can be lost from the soil by vaporization, unless acidic soil conditions transform it to ammonium ion, which is not volatile.

Most plants take up nitrate more readily than ammonia, but a few prefer ammonia. Ammonia is a toxic compound and is rapidly metabolized by plants (and other organisms) if it is absorbed.

The pools and processes of the nitrogen cycle are illustrated in the figure (Fig. 5) and table (Table 5).

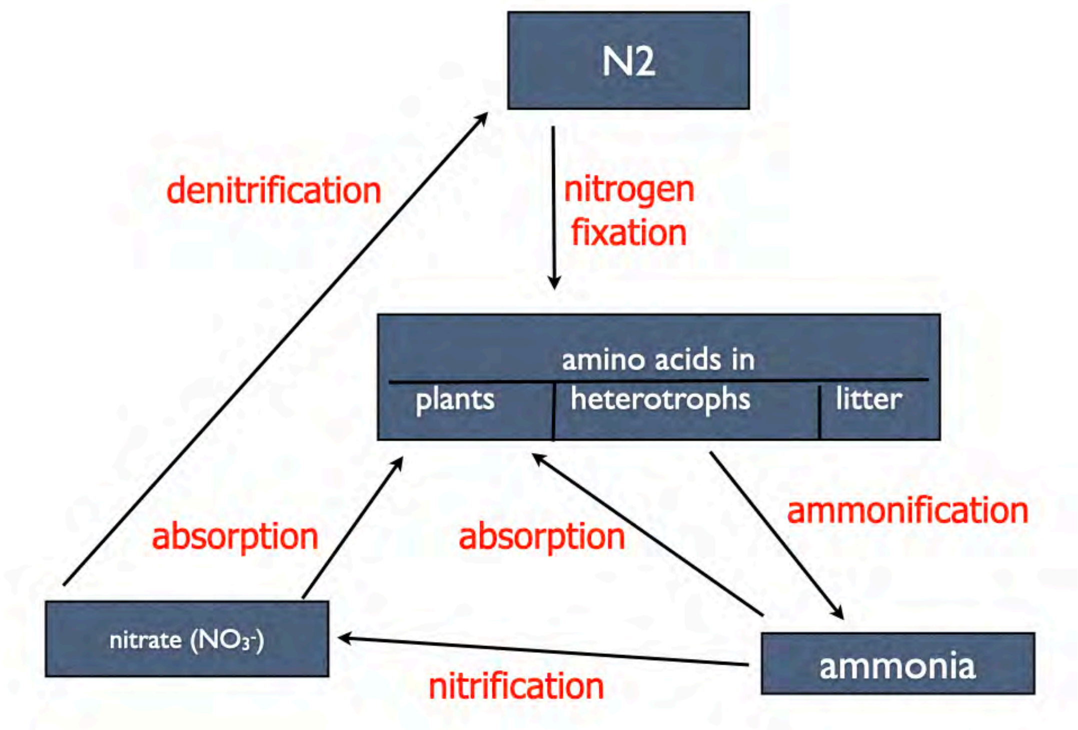

Fig. 5 Pools and processes of the nitrogen cycle.

Table 5.

	Process	Who does it?	Chemical notes
1	nitrogen fixation	only a few prokaryotes, including *Nostoc* and Rhizobium	nitrogen is reduced, electron source ultimately is carbohydrate
2	consumption	all heterotrophs	no change in chemical form; proteins broken down to amino acids

	Process	Who does it?	Chemical notes
			and then used to make more proteins
3	death	all life	no change in chemical form
4	ammonification (respiration/ excretion)	most heterotrophs, especially if they consume protein rich food	oxidation of amino acids forms poisonous ammonia which must be excreted
5	nitrification	a very small group of prokaryotes, called nitrifying bacteria	ammonia serves as an electron donor; electron flow to oxygen allows ATP to be synthesized (chemosynthesis)
6	absorption	most plants absorb nitrate, a few prefer ammonia	if nitrate is absorbed the plant must reduce it to NH2 to to form amino acids
7	denitrification	a very small group of obligate anaerobic prokaryotes, called denitrifying bacteria	nitrate substitutes for oxygen as an electron acceptor for anaerobic conditions
8	symbiotic nitrogen fixation	bacteria + plants	bacteria symbiotically associated with plants absorb N_2, form ammonia and transfer it to host plants

Phosphorus

For heterotrophs, phosphorus is obtained as phospholipids, nucleic acids and other metabolites in the food that they acquire and break down. For autotrophs, phosphorus is generally acquired as the phosphate anion (PO_4^-) which is made available by the action of heterotrophs who break down organic material and release phosphate. Phosphate is a key nutrient in aquatic systems and often regulates the amount of autotroph biomass and primary production.

Calcium, magnesium and potassium

These ions play multiple roles in organisms, generally being present as dissolved cations but occasionally being permanent parts of molecules (e.g., magnesium is part of the chlorophyll molecule). For heterotrophs, these elements are obtained as cations dissolved in the cytosol of the cells that they digest. Plants absorb Ca^{2+}, Mg^{2+} and K^+ as cations dissolved in the soil solution. These ions are generally derived from the breakdown of organic material (decompositions) and as soil minerals are weathered (dissolved) and put in solution. Fungi are unusual compared to most eukaryotes because they generally require much lower levels of calcium.

Sulfur

For heterotrophs, sulfur is obtained primarily from protein digestion releasing the two sulfur amino acids, cysteine and methionine and their subsequent absorption. While some heterotrophs can utilize either cysteine or methionine as a sulfur source, humans and some other animals cannot synthesize methionine from cysteine and therefore methionine must be obtained in their food. For autotrophs, sulfur is acquired as the sulfate anion (SO_4^-) and subsequently needs to be reduced to produce all biologically active forms.

Iron

For heterotrophs, iron is obtained from organic material, where it is a universal cellular constituent, albeit in low concentrations. Iron absorption into the heterotroph is sometimes deficient and iron deficiencies may result from an inability to absorb rather than from a lack of iron in food. For plants, iron is acquired as both the ferrous (Fe^{+2}) or ferric (Fe^{+3}) ion. The ferrous ion is much more soluble in water but is much less common under normal (high oxygen) conditions which cause iron to be in the more oxidized ferric state. In this state, the availability of iron is strongly influenced by pH, with less available iron at higher pH's (over 6). Consequently, although iron is very common in soils it is often unavailable to plants because it is not in solution, especially at high pH's. However if the soil becomes waterlogged and anaerobic, iron becomes readily available in the ferrous state and may become toxic.

Sodium

Sodium is common in most water sources, even 'fresh water' sources. While sodium is known to be essential for few plant species, in particular many CAM and C4 plants, it is not essential for most plants. In spite of this, sodium does promote the growth of a number of plants. At the sometime, like most plant nutrients, sodium is can be toxic to plants when at high concentrations. Although typical soils do not have sodium concentrations high enough to cause problems, arid regions commonly do have 'saline soils', soils with high concentrations of sodium ion in the soil solution. Additionally, irrigation can cause an accumulation of sodium, and adversely affect plant growth because irrigation delivers solutes, including sodium to farmland. Not surprisingly plants do not have active mechanisms to acquire sodium, nonetheless, especially in saline soils, it does 'leak' in. Plants do have mechanisms to excrete sodium and also to sequester it in vacuoles. As mentioned previously sodium is generally present in plants amounts sufficient to supply the needs of most heterotrophs.

Micronutrients (molybdenum, chlorine, boron, copper, zinc, manganese, nickel)

For both heterotrophs and autotrophs these elements are absorbed either in elemental ionic forms (Zn^{2+}, Mn^{2+}, Cu^{2+}, Ni^{2+}, Cl^{-}) or as simple molecules (MnO_4^{2-}), H_3 BO. Because most of these ions/compounds are not only essential but can become toxic, control of their movement is important and most, perhaps all, have specific protein transporters that control uptake, movement and sequestration.

Vitamins

A final nutritional category is 'vitamins'. These are molecules, not elements, that play a critical role in specific chemical reactions and, for a variety of reasons (inability to synthesize, inability to absorb, metabolic disorders), may be deficient in certain situations. Bacteria and archaea, whether autotroph or heterotroph, do not have vitamin requirements, generally because they make these metabolites themselves from the 'raw materials' that they require, or, less commonly, they have alternative biochemical pathways that avoid the vitamin requiring step. (There are, however, multiple bacterial strains found and/or developed that have specific vitamin or other nutritional requirements. These have been very useful tools for research). Among eukaryotes, plants, like prokaryotes, generally have no vitamin requirements, generally because they can synthesize vitamins along with the many other molecules that they manufacture. In contrast, eukaryotic heterotrophs often do have vitamin requirements, i.e., molecules that they cannot make and therefore that they must acquire from the food that they eat. For example, humans, and a few other animals, require vitamin C because they are unable to synthesize it. Plants and most animals, including cows, make vitamin C. But although cows can make the vitamin, meat provides very little to consumers, so a diet containing fruits and vegetables is important in preventing vitamin C deficiency in humans. Among other roles, vitamin B3 (niacin) is a precursor to the metabolites NAD and NADP discussed earlier. Although humans and other animals can make niacin from the amino acid tryptophan, they can develop niacin deficiencies if eating a diet low in niacin and tryptophan. Plants can make both niacin and tryptophan from mineral elements and the carbohydrates produced in photosynthesis. They therefore never have niacin deficiency and can provide these nutrients to heterotrophs that consume them. The vitamin requirements of heterotrophs apparently reflect a loss of metabolic abilities through evolutionary time, presumably the result of the fact that the vitamins are generally present in the organic matter that they consume. Plants, who do no consuming, must manufacture any required metabolite. Surprisingly, a number of autotrophic algae groups do have vitamin requirements for several B vitamins. It probably is significant that these organisms are aquatic and B vitamins are water-soluble and hence commonly found in aquatic environments, the result of decomposition of organic matter. In some cases the requirement for B vitamins in some algae may reflect their heterotrophic ancestry.

Further Reading and Viewing

- "Genlisea: A carnivorous plant acting as a trap for Protozoa" by Wilhelm Barthlott et al. Genlisea, an unusual carnivorous plant.
    - http://wolfbat359.com/genlisea.htm
- "Insights into the Evolution of Vitamin B12 Auxotrophy from Sequenced Algal Genomes" by Katherine E. Helliwell et al. Vitamin B12 requirements.
    - https://academic.oup.com/mbe/article/28/10/2921/973459?login=true
- "Algae need their vitamins" by Martin T Croft et al. Algae need their vitamins.

  - https://pubmed.ncbi.nlm.nih.gov/16896203/

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CHAPTER 23: SOILS

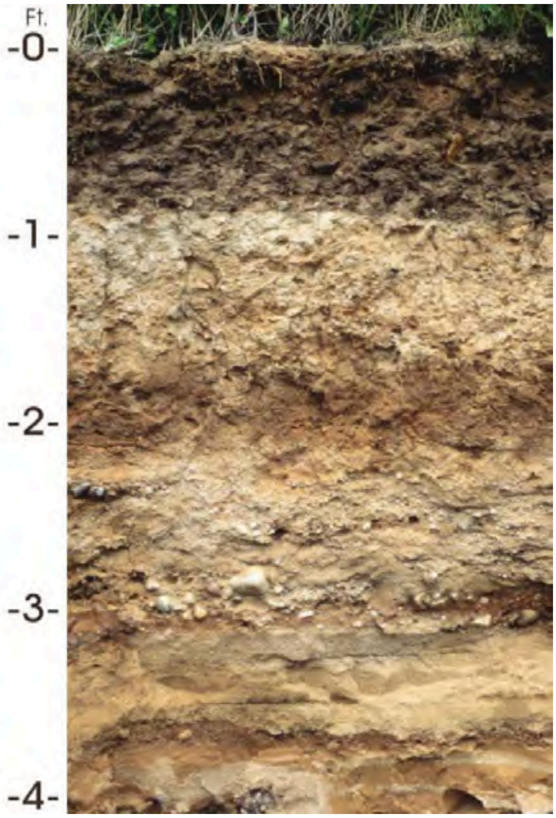

Fig. 1 Antigo, the state soil of Wisconsin. Note the layering (in color, other features besides color are layered as well). Layering is a consequence of biotic and abiotic processes.

If people had a longer life and were more observant of what is below their feet perhaps they would appreciate that soils (Fig. 1) are living things and that they demonstrate many of the properties that we associate with organisms. They are dynamic entities that develop through time in an orderly and predictable way and are characterized by a number of processes that involve matter and energy transformations. However, they do not have boundaries in space or time and, since they are not discrete, they do not reproduce. In an ecological sense, they are communities possessing a variety of living components that collectively, in conjunction with physical processes, carry out a variety of functions. Observers often consider soils to be an abiotic medium in which organisms grow, but the actions of the organisms in the soil are often so intertwined with the physical processes occurring there that it is pointless to try to separate them, other than to acknowledge that the relative importance of the activities of organisms in the soil vs. the physical processes varies greatly between different types of soils.

Although most consider soils to be an assemblage of debris (i.e., 'dirt'), soils are better understood if viewed as being composed of the four basic elements that the Greeks and other cultures described: earth, air, water and fire. The **earth** is a solid material, derived both from inorganic sources, ultimately rock, and from organic sources, pieces of material that are derived from living things. **Water** pervades the soil as its adhesive properties assure that it sticks to all the particles. Depending on the amount of water, **air** permeates the soil to a greater or lesser extent. And finally, the **fire** of the soil is the living creatures, mostly small, highly dominated by fungi and bacteria, but also including a variety of invertebrates, protists, occasional vertebrates and a dynamic population of plant roots. All four of the soils parts are critically important to plants: the solid material is the ultimate source of most nutrients and provides surfaces where significant events occur; water is needed by all plants and also is the medium from which they obtain nutrients; air provides the oxygen that plants and many other living things in the soil require; the living things in the soil carry out a variety of processes significant to plants, in particular, the degradation of large molecules into units that can dissolve in the solution and be available to plants. Each of these four components, earth, water, air and fire, interacts with the others: living things change the gas composition, the gas composition affects living things; water moves and organizes the solid phase; the solid phase controls the water content; the solid components change water chemistry; changes in water chemistry can add or subtract to the solid phase. Soils are a web of interactions, and while components can be listed, the whole is much more than the sum of the pieces and the functions of soil are hard to attribute to specific components.

The D's of Dirt—Deeds, Dynamic, Diverse

Biologists (and non-biologists!) should be aware of three key aspects of soils: what they do—their **deeds**; how they are **dynamic**, and how **diverse** they are.

TOPICS

- Deeds of the soil — what soils can do
- Dynamics of the soil — how and why soils change
- Diversity of soils

Deeds

What do soils do? A great deal more than we can enumerate here but some of the most important to organisms, populations and communities are: holding water, holding nutrients, and changing the chemistry of the water in the soil.

Soils hold water, usually very significant quantities of water, and this vastly enhances the possibilities for life outside oceans, lakes and rivers. While some terrestrial life exists in areas with no soil (i.e., on bare rock) , their activities are strongly modulated by the availability of water, and water is only available when it is raining and for a short period thereafter. Unless rain is frequent, the activity of living things is very limited because organisms require water and when it is not available they must shut down, becoming inactive and thereby able to tolerate the dry conditions. In contrast, a soil holds and stores water, greatly prolonging the time that water is available to living things and making possible a vast diversity of lifestyles and organisms that would not be present otherwise. Because the soil can absorb and store water, soils moderate the pulses of water flowing overland when precipitation occurs, diminishing the erosion and flooding that would occur without a mantle of soil. This fact is very apparent if one is in a large paved parking lot when rain is falling, or on a parcel of land once the soil has been filled to capacity and can no longer absorb water, or in a situation when rain is falling faster than the soils can absorb it.

The amount of water held by a soil is greatly influenced by the size of the particles that make up the soil. A term that describes the sizes of particles in the soil is **texture**. Most soils are composed of particles with a variety of sizes, but soils made up mostly of very small particles are called clay soils, and soils composed primarily of larger particles are called sandy soils. There are two main reasons why texture affects the amount of water held by a soil. The first is obvious but often not that significant: texture affects pore space: the total volume between the solid particles which is where water can reside. Obviously, a soil with more pore space has more volume available for water. Surprisingly, the total pore space of different textured soils is not all that different: sandy soils have about the same total pore space as clay soils. What is different between clay soils and sandy soils is the size of the spaces, and this turns out to be particularly important. Clay soils have many small spaces where water can reside while sandy soils have fewer spaces for water but they are considerably larger.

Consider two soils that occupy the same volume, both with ‘no‘ water (although it turns out to be impossible to get rid of all the water). The soil can be filled with water so that all the pore space (spaces between the solid particles) are occupied with water. A soil at this state is said to be **saturated** (Fig. 2) and one could determine the total pore space by keeping track of how much water had to be added to the soil to saturate it. A soil can only be saturated if it is in a closed container, one that gravity cannot pull water out of. If holes are opened in the bottom of the container then the force of gravity can pull out water. Significantly, gravity cannot pull out all of the water, but it can pull out some of it. It turns out that gravity can remove much more water from the sandy soil than from the clay soil. This is because water is held in small pores much more tightly than water held in large pores, and the force of gravity is only strong enough to pull water from the largest pores. A soil holding all the water that it can against the force of gravity is said to be at **field capacity (Fig. 3)**. To remove more water from the soil one needs to add plants. One could also wait for evaporation to remove more water but this is generally much slower than allowing plants to do it and allows one to see another critical point in soil moisture. Plants, like gravity, can only remove some, but not all, of the water remaining in the soil. This is because eventually the soil becomes so dry that plants cannot survive. Soil at this degree of dryness is said to be at a **permanent wilting point (Fig.4).** Plants do differ in how much dryness that they can tolerate but most plants, in particular crop species, have quite similar tolerances. Both field capacity and permanent wilting point define degrees of dryness in the soil and actually can be defined in terms that relate to the force holding water in the soil and to a thermodynamic term defined as water potential. And the amount of force present is related to the size of pores that still hold water: as soil dries the water remaining in the soil is in smaller and smaller pores and is harder and harder to remove. Knowing how much water is in a soil is not particularly useful: a clay soil with 15 grams of water per 100 grams of soil (percent moisture = 15%) is so dry that few plants could live in it. A sandy soil with a water content of 15% may be saturated and gravity could remove water from it. Consequently, the ‘wetness’ of a soil is monitored not by water content (percent moisture) but in energetic (water potential) terms.

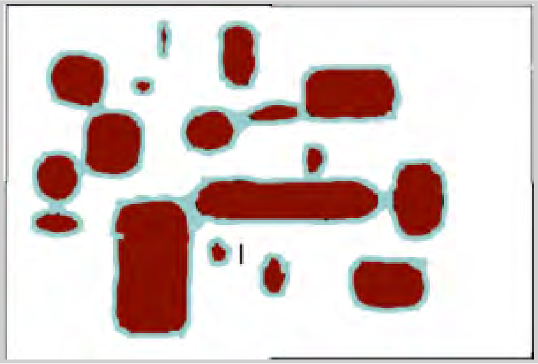

Fig. 2 This figure represents a saturated soil: all the spaces between the soil particles are filled with water.

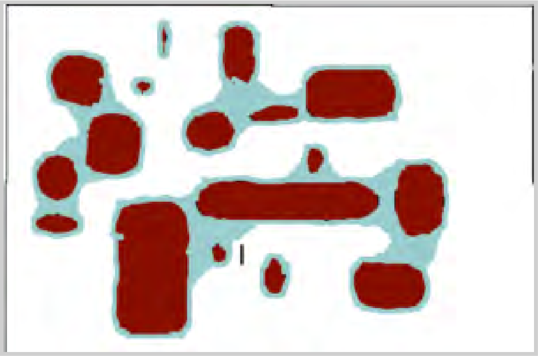

Fig. 3 If the soil is able to drain gravity will remove water from a saturated soil and the water that remains will be present surrounding the soil particles, because of adhesion, and also in spaces between soil particles, because of cohesion water sticks to itself. The amount of water that gravity can remove and consequently the water 'held' by the soil, depends on the size of the spaces, the pores, between the soil particles. Gravity can remove water from the big pores just as gravity will pull water out of

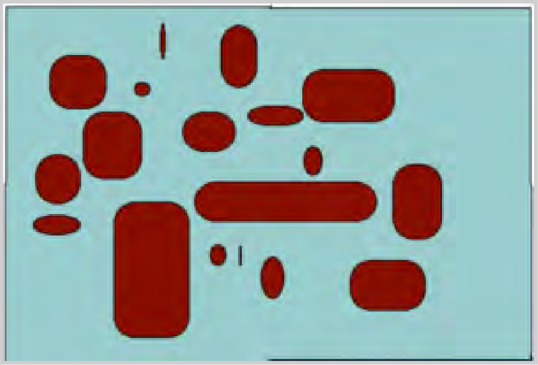

Fig. 4 Plants growing in soil can remove water from a soil at field capacity. They can exert a pull strong enough to remove water from 'medium-sized' pore spaces. But eventually, the only water that remains is in small pores and most plants cannot pull hard enough (see Chapter 24)to remove this water and they die (aka 'permanently wilt') at a certain level of soil dryness.

The amount of water held by a soil between its field capacity and the permanent wilting point is important because it represents the storage capacity of the soil that is useful to plants. Water added to a soil that is a field capacity will drain out of the soil due to gravity (how quickly this happens depends on the texture of the soil). Water held in the soil below the permanent wilting point is unavailable to (most) plants. Sandy soils dry out quickly because they store little water between field capacity and permanent wilting point. Clay soils can hold much more but because water moves slowly through the clay soils are generally not desirable for agriculture—the best agricultural soils are described as loams, with a mixture of sand and clay.

a straw. But gravity cannot remove water molecules out of small pores because the cohesive forces of water exceed the force of gravity.

In addition to water, soils also hold nutrients. Remember that all the nutrients that plants acquire, with the exception of carbon, come from the soil solution. Thus the water held by the soil represents not only a supply of water but also a supply of nutrients. Exactly how much of each nutrient (and other solutes) are present depends partly upon the amount of water but also on chemical interactions in the soil. A simple view of soil chemistry is that nutrients can be in one of two situations: solids (i.e., part of the soil particles) or solutes, dissolved in the water. There are a variety of mineral salts that can disassociate, putting ions in the soil solution, e.g., Na^+ and Cl^-. The reality is more complex. The soil is a three-phase system with chemicals not just in the solid-state (precipitated state) and in solution as dissolved ions. A third phase, in between these two, is described as an 'ion exchange surface' that is the result of solid components of the soil breaking down (weathering) and losing (generally) cations, producing a negatively charged surface that can electrostatically bind cations, forming a 'cation exchange surface'. The movement of ions from the soil solution onto this surface is less specific and more dynamic than the precipitation of ions from the soil solution into specific minerals. While precipitation to a specific minerals requires a match between cation and anion, any positively charged ion (cation) can associate with a cation exchange surface. Which cations are actually held depends on their abundance in the soil solution, their size, and the amount of charge. For plant nutrition, the key parameter is abundance in the soil solution. Consider a soil solution in equilibrium with a cation exchange surface and consequently having a certain ratio of Na^+ to K^+ in the soil solution. If plant roots remove K^+ from the soil solution, the lowering of the K^+ concentration in the soil solution increases the Na^+ /K^+ ratio and causes Na^+ ions to be exchanged for K^+ ions on the cation exchange sites. This replenishes the supply of K^+ in the soil solution. A common application of cation exchange surfaces is in water softeners, devices that remove the calcium and magnesium from water and replace them with sodium, thereby making the water 'softer '. This results in a number of favorable consequences, e.g., more effective washing with soaps. A water softener operates by moving water through an ion-exchange 'column' that has been 'loaded' with Na^+ (i.e., all the ion exchange sites are filled with Na^+). As the water moves through the column the Na^+ replaces the Ca^{2+} and Mg^{2+} in the solution. Eventually one needs to replace the ion exchange material because it has become 'filled' with calcium and magnesium ions.

Hence there are three ‘pools’ of plant nutrients in the soil: specific solid materials, both organic and inorganic, the soil solution, and ion exchange sites. Ion exchange can help buffer changes in nutrient supply and explains why soils with higher cation exchange capacity often are generally better soils for agriculture (i.e., can grow better crops). Most ion exchange surfaces are negatively charged and hence are cation exchange surfaces. The amount of ion exchange surfaces present in a soil is strongly dependent on the age of the soil. As soils age, specific minerals are produced by the weathering of the soil minerals and the decomposition of soil organic material. Remember that the soil as a whole, and the soil solution specifically, remains neutral: positive charges equal negative charges. This is also true of the solution that enters (e.g., rainfall) and exits the soil as groundwater, but the chemistry of the water flowing out of the soil may be quite different from that entering the soil.

Ultimately the supply of nutrients (e.g., K^+, Ca^{2+}, PO_4^-, SO_4^{2-}) in the soil depends upon the balance between additions and losses. Processes that add nutrients include: additions from rain, snowfall and dust; decomposition of organic material into components that are able to dissolve in the soil solution; weathering of soil minerals into components that are able to dissolve. Processes that remove nutrients from the soil include erosion, leaching (the loss of solutes in water as gravity pulls water out of the root zone), and the harvesting / removal of plant or animal material.

Dynamics of the soil

Soils are continuously changing as a result of a variety of processes. Solid material is continuously being added, primarily from the plants that shed leaves, stems, fruits and entire bodies to the soil surface and continually add roots directly within the soil. Material is also added by animals and by mass processes e.g., wind and water deposition. Some of the material is readily decomposed, disappearing into the atmosphere (carbon dioxide) and soil solution (ammonia, ‘dissolved organic matter’) within a few days. Other materials (e.g., tree trunks, large woody roots) remain for hundreds of years. Water is continually flowing through the soil, usually being deposited on the surface by rain/snow and moving down with the pull of gravity. But occasionally water moves upwards because of evaporation from the surface of the soil. As water moves, it carries material with it, mostly in solution but sometimes in suspension (if there is a mass flow). Carried materials are not necessarily transported out of the soil but may be deposited, generally in lower layers, where the physical conditions (amount of oxygen, pH, size and type of particles) may be different. While the water balance of a soil is generally zero (i.e., inputs match outputs) over the course of a year, this is generally not the case for solid material and soils may be either accumulating or losing material. Even if the solid and liquid phases are in a steady-state, with losses matching gains, activities in the soil can change its structure. While we generally think of material in the soil as breaking down because of the processes of weathering and decomposition, sometimes larger molecules are made from smaller ones and existing soil particles may fuse with each other.

Diversity of soils

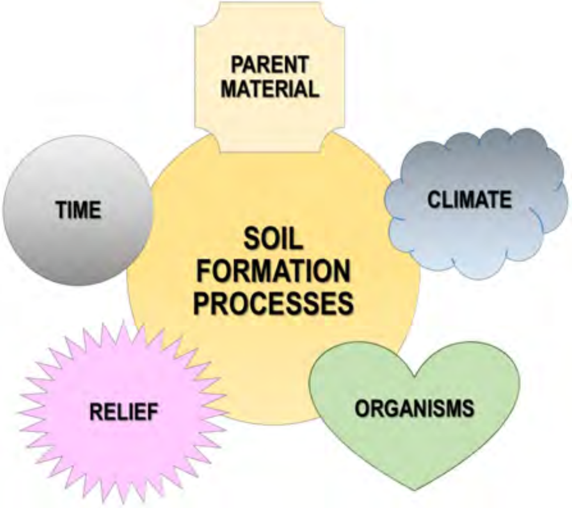

Fig. 5 Factors controlling soil development and that account for soil diversity.

Because soils are dynamic, they are diverse and change through time in predictable ways, i.e., they develop over time. Young soils will have different features than old ones. The age of the soil is one of the five key factors that determine the nature of a soil (Fig. 5). The other four are: parent material (what it is made of), climate, biota, and slope. Parent material can vary between solid rock (e.g., a lava flow), particulate mineral material (e.g., volcanic ash), or organic matter (e.g., in a bog) with a wide variety in between. Parent material affects particle size, soil chemistry and what organisms are likely to occupy the soil. Climate, i.e., patterns of rainfall, temperature and the variation in these factors, is important for reasons that should be apparent: temperature controls the rate of decomposition and weathering; rainfall also influences decomposition and weathering and also controls the amount of water percolating through the soil. Biota, the forms of life present, influences the types of organic material that are deposited and the rates of decomposition. The remaining factor of importance, slope, is perhaps is surprising until one appreciates that all of the following are influenced by it: the amount of water running through the soil, whether or not water may be stagnant on/in a soil, the amount of erosion/deposition on a site.

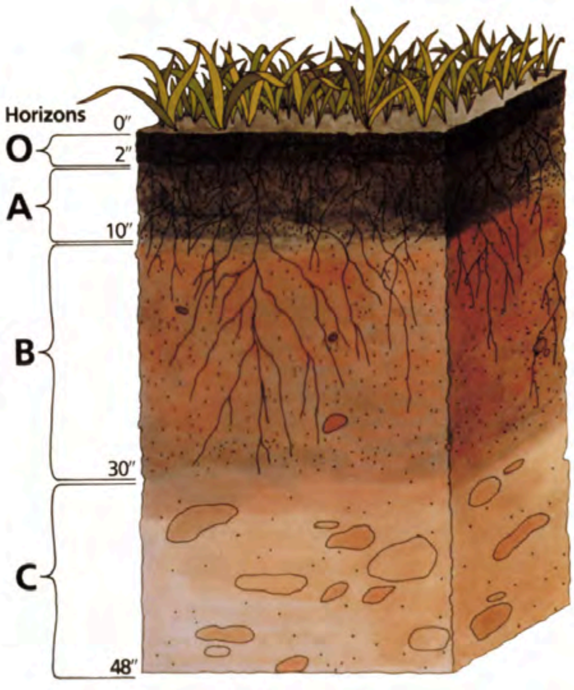

Fig. 6. The layering of soils is a consequence of the processes taking place and are a function of the five key factors shown in Fig. 5.

Because of variation in the factors described above, soils are diverse. Moreover, their features are changing continuously depending upon their age. One manifestation of this diversity is the existence of layers (horizons) in many soils. The horizons develop because of processes taking place in the soil.

In many parts of the world, including the north central and northeastern U.S. glaciers played a very significant role by influencing three of these factors: In many areas, they eliminated whatever soil was present, thus many soils are relatively young; the glaciers deposited a variety of soil materials (ranging from sands to clays) on which new soils developed; and glaciers created a variety of topographies (slopes) upon which soils developed.

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Fig. 7 A podzol, a soil type typical of areas with cool temperatures and abundant rainfall

Fig. 8 A mollisol, a soil type typical of grasslands, areas with moderate temperatures and rainfall. Mollisols are excellent agricultural soils

CHAPTER 24: MATERIAL MOVEMENT AND DIFFUSION'S MULTIPLE ROLES IN PLANT BIOLOGY

Fig 1. Redwoods in the Muir Woods. Water needs to be transported over 100 meters up and sugars need to be transported 100 meters down in order for these trees to survive.

In addition to needing materials, organisms need to move materials: materials need to be moved from where they are acquired or synthesized to other places where they are utilized; materials may need to be transported to storage sites and also retrieved from storage sites; chemical signals may need to move from a place of sensation to a place of response.

Materials are moved in three basic ways in organisms, two of which occur in non-living systems as well: (1) materials move by diffusion, which is a consequence of the fact that all molecules at a temperature above absolute zero (i.e., all molecules!) are moving in a random thermal way; (2) fluid materials (i.e., gases and liquids) move by mass flow, from high pressure to low as long as there is an open pathway that allows the fluid to move; (3) materials move as the result of forces developed as a consequence of chemical interactions unique to biological entities, for example the rotary motors of flagella that create a rotational movement that 'runs on' proton movement down an electrochemical gradient and the so-called motor proteins, which can use chemical energy (generally supplied by ATP) to do physical work (i.e., pushing or pulling a molecule, applying force over a distance) as in a muscle. Note that motor proteins are highly significant in multiple ways, not just in muscles. They can divide cells, move chromosomes and produce cytoplasmic streaming, a process that is significant to larger cells because diffusion is ineffective except over very short distances. The larger cells found in some of the algae, and especially in the coenocytic/siphonaceous cells (see Chapter 4) are highly dependent on the ability of motor proteins to transport material within the cell. Of particular importance to plants is the ability of a large, multicellular organism to move materials throughout the organism, a process that is accomplished by a combination of diffusion and pressure flow.

TOPICS

- Diffusion
    - A simple but insufficient model
    - Osmosis — the diffusion of solvents, including water
    - Effects of pressure on diffusion
    - Combining the effects of purity and pressure
- Plants and Fungi use manipulations of pressure and osmosis multiple ways
    - Structurally
    - Growth
    - Guard cell movements
    - Leaflet movements
    - Long-distance transport
        - In the phloem
        - In the xylem

- the patterns
- the mechanisms
- the problem of cavitation and trade-offs in xylem anatomy
- rare cases of pressurized xylem

Diffusion

A simple but insufficient model

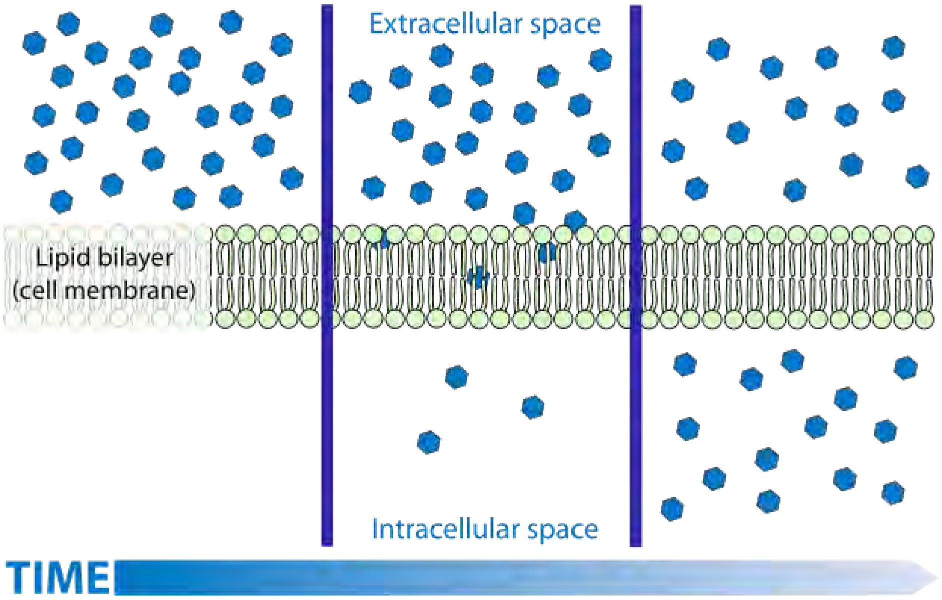

Fig. 2 Diffusion of a solute across a cell membrane—random thermal motion results in a net movement

Diffusion is a process familiar to most. While the diffusion of gases and solutes is easily understood by simplistic models, the understanding of the diffusion of liquids, in particular water, is much more challenging and is often muddled by the imprecise application of terminology. The diffusion of gases and solutes is described as a spontaneous movement from regions of higher concentration to regions of lower concentration. The explanation for this spontaneous process is easily linked to kinetic theory—molecules move in a random way because of thermal energy. As a consequence of this random movement, there is a net flow of matter from places where there are more molecules (i.e., higher concentrations) to regions where there are fewer molecules (lower concentrations). If dealing with mixtures (a gas with more than one component), each component will move independently of the others.

Liquid water diffusion (osmosis) is NOT always from 'high concentration to low '

However, this model (explanation) is not readily applied to liquid water with solutes, or to solutions in general, largely because the idea of 'concentration' varies. Concentration is not as precise a term as one might think, it can be expressed in several different ways (mass concentration, number concentration, molarity, molality, mole fraction). In the simplistic model of diffusion, the most appropriate measure would appear to be (number) concentration (number of molecules per unit volume) since random movement would move molecules from where they have more molecules per unit volume to where they have fewer molecules per unit volume. However, when considering the solvent (not the solute), the number concentration is not an accurate predictor of diffusion. For water and for most solvents the number concentration of the solvent changes very little as solutes are added, yet adding solutes can have a substantial influence on the diffusion of solvent. And while water volume changes little as solutes are added, the extent that it does change varies with different solutes. But the effect on the diffusion of water is not controlled by the specific solute added but only by how much solute (number of particles) was added. Consider that while the addition of most solutes causes the water to slightly increase in volume (the number concentration goes down — the same number of water molecules are now in a larger volume), the addition of some solutes can cause water to contract (i.e., the number concentration goes up — the same number of water molecules are now in a smaller volume). If the (number) concentration of water is what directs its movement one would expect different solutes to have different effects on the diffusion of liquid, depending upon how much they caused the solution to change volume (and number concentration). And you actually would expect that some solutions (the ones that cause water to shrink) would have water diffuse from the solution into pure water. This never happens! Keeping all other factors constant, water always diffuses from where it is pure into any solution, regardless of the solute. And, at low concentrations, there is little to no effect of the particular solute — they all have the same effect on diffusion regardless of their impact on water's number concentration. It is the concentration of the solute NOT the concentration of water molecules that is directing diffusion: all other factors being held constant, water always diffuses from where there is a lower solute concentration to where there is a higher solute concentration. From this, one can conclude that it is the purity of water, not its concentration, that drives diffusion. This may seem like a subtle difference but it actually reflects some very profound features related to the laws of thermodynamics. Purity relates to entropy, and entropy is known to 'drive' spontaneous processes. Moreover, our 'mental image', i.e., model, of what causes diffusion, doesn't work — solvent molecules do NOT go from where there are more of them to where there are less of them, they tend to go from where they are purer to where they are less pure.

The effect of pressure on diffusion

A second key reason that the description/model that describes diffusion as occurring from 'high concentration to low' is deficient is that it fails to consider the effects of pressure. Pressure is the most familiar reason that fluids move (wind, water flow in pipes, blood flow in animals) but these movements are not diffusion, they are something called 'mass flow', a movement that depends only on pressure differences, and a movement that will occur whenever there are pressure differences and an open path for fluid flow. But when mass flow is impossible (because there is no 'open path') pressure can also influence diffusional movement: water will diffuse from areas of high pressure to areas of low pressure. This is especially important for cells possessing both a cell membrane and a cell wall.

While the membrane allows there to be different purities of the solvent (water) inside vs. outside the cell, the wall allows there to be different pressures inside vs. outside the cell, and both purity and pressure are important in dictating the diffusion of water.

Combining the effects of purity and pressure

All other things being equal, water moves by diffusion from regions of higher pressure to regions of lower pressure and also from regions of high purity to regions of low purity. These two factors can 'balance' each other and it is possible to have NO diffusion between an area of low purity and high pressure connected to an area of low pressure and high purity. As an example, if you have water of low purity confined in a rigid container (i.e., a cell with a cell wall) and it is put into pure water, water will move into the cell, increasing the pressure in the cell. Eventually, a pressure will be reached where there is no more diffusion into the cell. At this point, the pressure differences between the inside and outside are matching the purity differences between the inside and outside.

Unfortunately, there is no easily conceptualized model for the diffusion of liquid water as there is for the diffusion of gases and solutes. A rigorous model of the diffusion of liquid water requires the application of concepts from a thermodynamic parameter called water potential. The basic idea is relatively simple: osmosis (the diffusion of liquid water) is a spontaneous process and any spontaneous process must result in a decrease in the amount of energy available to do work (the 'free energy'). Generally, two key factors affect the free energy of water (its water potential): the pressure (which increases its water potential) and the presence of solutes (which decreases its water potential). Liquid water diffuses from areas of high water potential to areas of low water potential just as heat flows from warm areas to cold areas.

For all organisms the cell membrane and cellular activity allow solute concentration differences to develop between the inside and the outside of the cell, resulting in differences in water purity between the inside of the cell and the outside. When purity differences develop, water will flow in or out by diffusion. As long as the purity differences are small this movement can eliminate the purity differences by making the inside less pure (if water flows out) or more pure (if water flows in). However, such water movement will also cause the cell to change volume and if the cell swells or shrinks too much it can cause irreparable damage to the membrane, thereby destroying cell functioning. As a consequence, organisms without a cell wall must either live in areas where water purity is similar to what is found inside their cells or they must have structures/mechanisms that lessen diffusion and/or have the ability to either eliminate the water that diffuses in (e.g., the contractile vacuole of *Paramecium*) or to acquire water to replace that being lost by diffusion (generally this is accomplished by acquiring the 'salty' water and eliminating the salts).

For cells with a wall (e.g., plants and fungi), the wall allows a new 'fix' to living in areas where the cell is more concentrated in solutes than the external environment (this is the normal situation for most non-marine habitats: fresh-water lakes and streams and terrestrial habitats where organisms are immersed partially or totally in soil whose water is generally quite pure, i.e., with few solutes). For these organisms, the rigid wall allows pressure to increase as water flows into the cells. This pressure acts to reduce the inward diffusion of water and eventually a dynamic equilibrium is reached where the high pressure and low purity inside the cell balance the lower pressure and higher purity outside the cell. Water moves (diffuses, i.e., moves by osmosis) in and out at the same rate.

Plants and fungi use 'osmotic systems' in a number of ways

Structurally

Water can be used as 'building blocks' when it is confined in a structure that will not expand. Living cells, with the combination of a cell membrane and a cell wall, are structurally strong and plants and fungi use them to form rigid structures that can withstand gravitational and wind forces (also discussed in Chapter 3). Evidence for the structural importance of water comes from the observation of wilting: if plants are deprived of a source of water to replace that being lost by evaporation, they loose structural integrity (Fig. 3).

Some plants and fungi produce some structures (e.g., trees, bracket fungi) that don't collapse when deprived of water, but for many plants access to water is essential to 'standing up' because it is the pressurization of cells that provides rigidity. Central to this ability is a cell wall that has high tensile strength and resists expansion and consequently allows for pressurization.

Growth

For organisms with cell walls cellular growth occurs when the internal pressures exceed the strength of the cell wall, causing it to yield to the pressure inside it. Organs (fungal filaments, roots and shoots) grow as a result of the expansion of individual cells and the internal pressure not only has to push out the cell wall but may also have to push away (compress) soil in its path. Thus for plants (both roots and sometimes shoots) and fungi, growth may require the production of a significant amount of force. The force to power this growth comes from the diffusion of water (osmosis), and very significant forces can be created as the result of the movement of water down its water potential gradient. Pressures of 2-4 bars (= 0.2-0.4 MPa [megapascals] = 2-4 atmospheres of pressure = 30-60 pounds per square inch) are common and can be quite effective, as anyone who has observed a dandelion coming up through a sidewalk may have realized.

Fig. 3 Wilted cucumber plants show loss of structure when deprived of water.

Guard cells and stomates

The opening and closing of stomates come about as a result of changes in the pressure of specialized cells, guard cells, that surround the pore. Pressurization of the guard cells, as a result of solute accumulation and subsequent water diffusion into the guard cells, causes the cells to swell and form an opening (a stomate) in between them. A decrease in solutes in the guard cells will cause a movement of water out of the cell, resulting in a drop in pressure and consequently stomatal closure. The triggers that stimulate guard cells to accumulate or lose solutes have been extensively studied and include light and the concentration of carbon dioxide. The exact controls may not be the same for all species. At least some plants are able to regulate internal carbon dioxide levels at a 'set point' that allows photosynthesis to proceed with little inhibition due to a lack of carbon dioxide, while at the same time minimizing the amount of water lost due to transpiration.

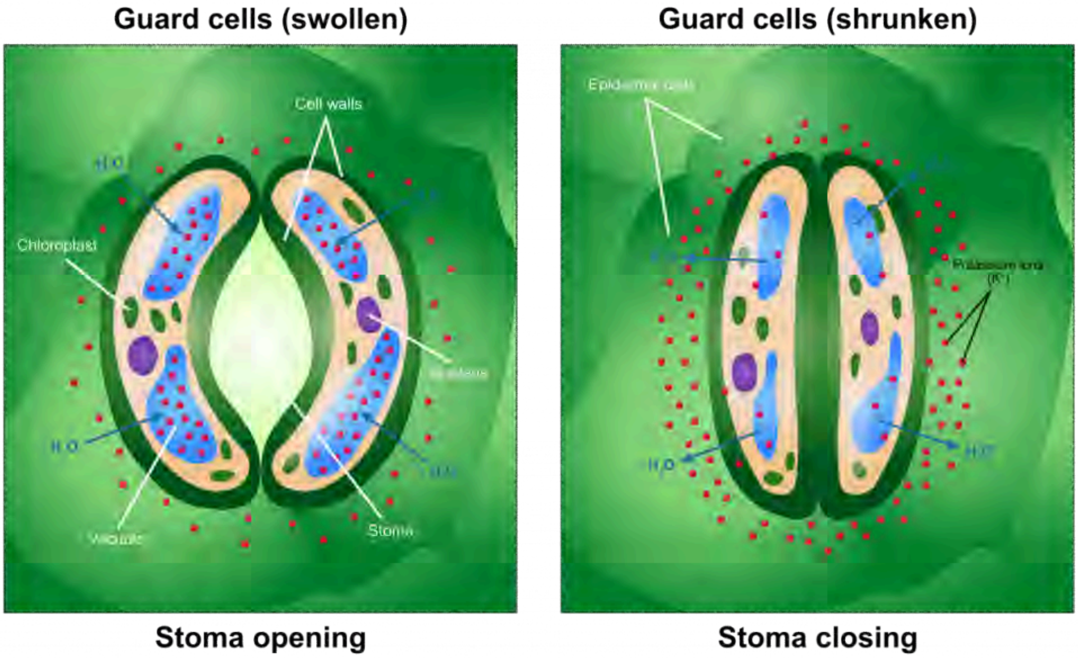

Fig. 4 Stomatal pores are formed when guard cells take on water and are pressurized.

Leaflet movement

Similar to the action of guard cells, a number of plants have leaves or leaflets that move in response to environmental cues such as light, touch and drought, resulting in leaves or leaflets whose orientation varies depending upon circumstances. A common example is 'sleep movements' where leaves are horizontal during the day and vertical at night. These movements are the results of changes in the pressure of 'pulvinar' cells, located at pivot points. Relatively small changes in the size of these cells are leveraged as a result of their location and can cause substantial changes position of organs involved. (see https://youtu.be/U-PK13JEgk8 below)

Watch

One or more interactive elements has been excluded from this version of the text. You can view them online here: https://milnepublishing.geneseo.edu/botany/?p=1214#oembed-1

Long-distance transport

Phloem

Both transport systems in plants, the xylem and the phloem, operate as the result of pressure differences created in the 'pipes' found in these tissues (see Chapter 6). The pressure differences are created as the result of the diffusion of water. In the phloem, pressures are created as a result of the addition of solutes (sugars) to the pipe cells, a process known as phloem loading, that occurs in regions of the plant called 'source' areas. As a consequence of the phloem loading, water flows into the sieve tube elements of the source area, and the pressure increases, triggering a flow in the pipes. The pressure differences and the flow are maintained because solutes are not just loaded at 'source' areas, they are also removed at 'sink' areas, the locations that solutes are being transported to; thus a continuous pressure gradient occurs in the phloem, from sources that provide sugars, to sinks that consume or store sugars. The exact locations that serve as sources or sinks can change depending upon whether a location is producing sugars (usually sucrose) or consuming them. Phloem transport can be up the plant (e.g., from storage sites in the root to shoot apical meristems) or down the plant (e.g., from photosynthesizing leaves to storage sites in the root). Loading of sucrose requires metabolic energy as ATP is used to move sucrose from where it is less concentrated to where it is more concentrated. As was the case in guard cells, water movement into the sieve tubes is passive once the solutes have been added. Because it is a mass flow, not just the sucrose but any solute that is in the sieve tube will be transported to the sink. The most common of these other solutes are amino acids, but other nitrogen-containing compounds are transported in the phloem along with some mineral elements (e.g., K^+, Mg^{2+}, Ca^{2+})

Xylem

Water transport in the xylem is also the result of 'pressure' differences but these are actually differences in tension rather than differences in pressure. While pressure compresses fluids, the tension pulls liquids apart, just as pulling on a string exerts a force that acts to break the molecules of string. Surprisingly, in certain situations, water has substantial tensile strength and can indeed be pulled. The cell walls of all the cells in a leaf are infused and coated with water because of the adhesion of water to the cell walls and the cohesion of water to itself. When water leaves a leaf by evaporation the remaining water is put under tension (sometimes described as 'stretched', but the water is not being stretched, rather it is the material that it is attached to), because the remaining smaller volume of water is covering the same original volume of cells. This tension is transmitted to the water in the conducting cells of the xylem and creates a 'pressure' difference (actually a tension difference) that can pull water up the (non-living) pipe cells. What is generally driving the water movement up the pipes (tracheids and vessels) is a tension created as water is lost due to transpiration. However, water flow up the xylem can also occur even if there is little transpiration as long as growth is occurring: the diffusion of water into expanding cells can create a tension to pull water up plants in the spring at a time when plants lack leaves and transpiration rates are very low.

Water loss from the leaf is simple diffusion: water vapor at high concentrations (high humidity of the air inside the leaf) diffuses through open stomata to where the humidity is lower outside the leaf. The humidity of the air inside the leaf is maintained because liquid water in the cell walls of mesophyll cells evaporates and replaces water that has been lost. The tensions generated by water loss causes the tracheids and vessels to be slightly compressed as the pressure outside them is 'normal' (one atmosphere) but the pressure inside is lower. Note that this is in contrast to the situation in living mesophyll cells which are pressurized because they have a membrane that allows them to concentrate solutes. If the tension in the water column of becomes too great, a phenomenon called cavitation occurs:

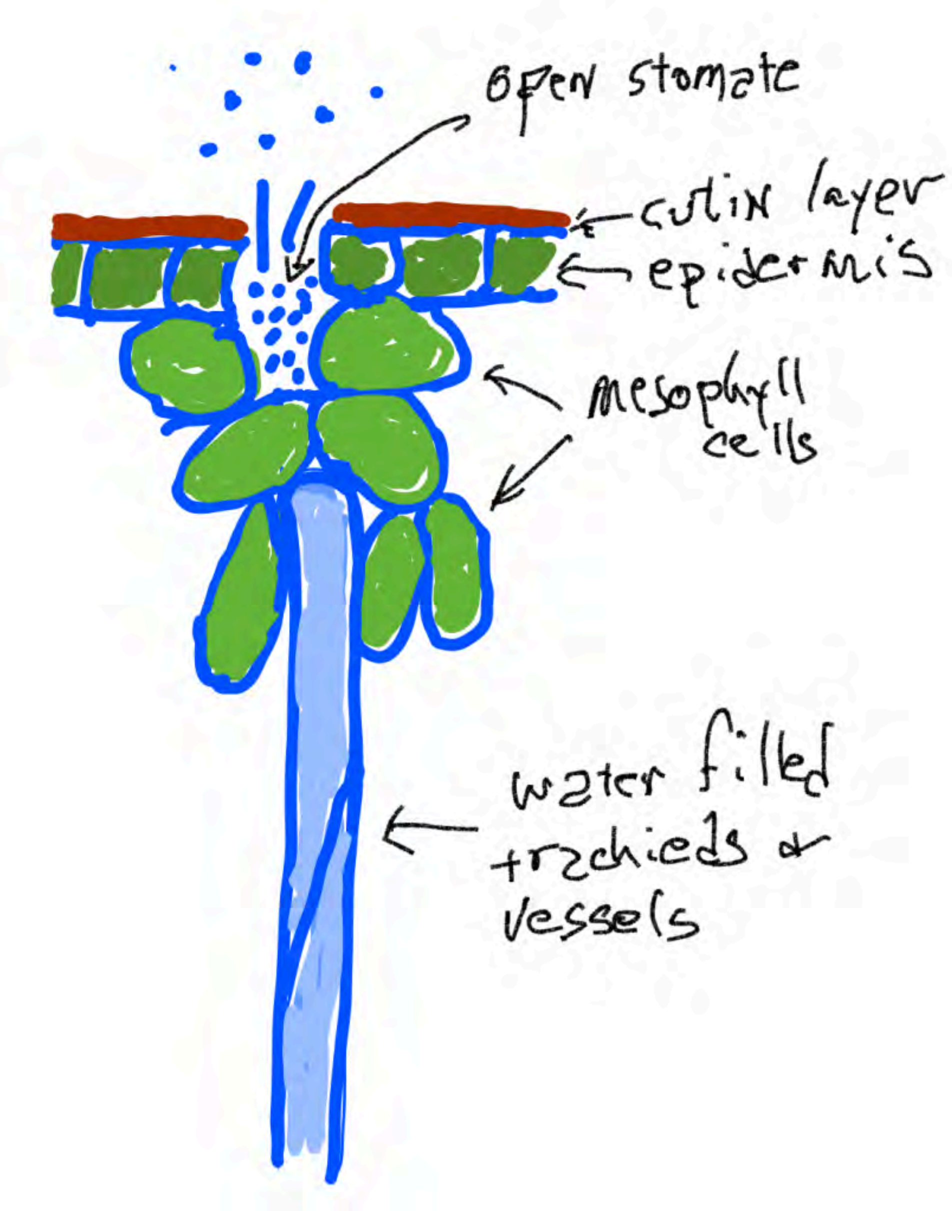

Fig. 5 Xylem transport occurs in response to water loss from the leaves or as a result of water entry into growing cells.

air bubbles form when the water column is broken or when water breaks away from the sides of the tracheid or vessel. In either case, the cell is 'cavitated' and is no longer useful for water transport.

In both transpiration-driven and growth-driven situations, and in phloem transport, there is a short-distance diffusional movement that creates a pressure difference that can result in a long-distance movement. In both the xylem and phloem the movement within the pipes is NOT diffusion, it is a much more familiar process called bulk flow. Bulk flow is a much more effective means to transport materials over long distances than diffusion, which is only effective over very small distances (tenths of a mm for liquids). Bulk flow is blocked by cell membranes and is impeded, but not prevented, by cell walls. The pits found in the cell walls of tracheids and vessel tube elements provide a relatively low resistance pathway for water to move between adjacent cells. Water flows even more readily through the perforation plates of vessels because the openings are complete (no cell walls).

In the (living) conducting cells of the phloem, plasmodesmata connect the individual cells and bulk flow of phloem sap (which is essentially cytoplasm lacking organelles) occurs from cell to cell through the plasmodesmata. Bulk flow is also significant in the soil where there are passageways for water to flow through and where both gravity and the 'pull' by movement into plants can create pressure differences.

The pressures and tensions found in vascular tissue reflect these mechanisms. If a sieve tube is penetrated, phloem sap flows out because the pressure inside the cell is greater than atmospheric, just as you will bleed if your skin is severed. Under most circumstances, if a tracheid or vessel is penetrated water does NOT flow out, rather air flows in, reflecting the fact that the water inside the tracheid /vessel was under tension. In fact, if one measures the volume of a tracheid /vessel as tensions develop, it slightly decreases because of compression from the outside. Because of this, tree trunks exhibit a measurable decrease in circumference during the day as transpiration and tensions increase and rebound overnight as the tensions are relieved and the plant is rehydrated during times of little or no transpiration.

On rare occasions the water in the xylem is pressurized.

This condition is described as 'root pressure' and only occurs under relatively rare circumstances. 'Root pressure' is demonstrated by the 'bleeding' (exudation) from a decapitated stem. Under these same special conditions, if one punctures an individual xylem vessel or tracheid it will also bleed, unlike the more normal situation described above. Root pressure occurs if the soil is moist, roots are actively growing, and transpiration is low (at night or when no leaves are present). Under these conditions solutes (mineral ions) accumulate in the xylem of the root because of the actions of root cells, and because the endodermis collectively behaves like a membrane and is a barrier that prevents solutes accumulated in the root xylem from leaking back out of the xylem tissue. Hence, like a living individual plant cell which can pressurize because the cell membrane allows solutes to be accumulated, the entire root xylem can accumulate ions and pressurize. This phenomenon is rare, because solutes typically do not accumulate in the root xylem because mineral acquisition by roots is matched by xylem transport up due to transpiration. Additionally, 'pull' from the top (created by transpiration or growth) prevents a pressure buildup from occurring.

A final situation where the xylem is pressurized is the one that causes sap to flow (out) in maple tree trunks in the late winter and early spring. 'Tapping', inserting a cylinder, into the xylem, results in the bleeding of sap that can be collected, concentrated and used as a source of sugar. Maple sap flow does NOT require root activity — it can be observed in stems removed from the root system. Maple sap flow DOES require freeze/thaw cycles because these somehow allow the xylem to become pressurized. The sugars found in the xylem sap are coming from xylem rays whose starch is converted into sucrose in late winter. Why only maples and a few other species of trees exhibit this behavior is generally attributed to aspects of their wood anatomy. Most tree species do not pressurize when exposed to freeze/thaw cycles.

Although phloem tissue is penetrated when maple is tapped and although phloem tissue is pressurized and transports sucrose, extremely little of the sap collected from maples is derived from the phloem. The living cells (sieve tube elements) of the phloem tissue are capable of rapidly plugging holes to prevent 'bleeding' and consequent sugar loss. If one could tap into the phloem tissue it would be found to have a much, much higher sugar concentration (comparable to maple syrup) than maple sap, whose sweetness is barely detected by humans until it is concentrated. Maple trees that are tapped will bleed from the xylem tissue for several months, as long as they are exposed to proper freeze/thaw and as long as there isn't a 'pull' from the top of the plant caused by growth or evaporation from leaves. Maple sap flows when leaves aren't present and growth is not occurring.

Further Reading and Viewing

- "Xylem Structure." Good discussion of xylem transport.
  - https://ib.bioninja.com.au/higher-level/topic-9-plant-biology/untitled-6/xylem-structure.html
- "Xylem feeding by spittlebug nymphs: some observations by optical and

cryo-scanning electron microscopy" by Laura J. Crews et al. What do spittlebugs say about xylem transport.

  - https://bsapubs.onlinelibrary.wiley.com/doi/pdfdirect/10.2307/2446427

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CHAPTER 25: PLANT GROWTH—PATTERNS, LIMITATIONS AND MODELS

One of the marvels of life is growth, the ability of organisms to get bigger. This is especially the case for plants since, as described earlier, plants grow ' out of thin air.' And while plant growth is a very ordinary phenomenon, its explanation is very much 'extra-ordinary,' as they are able to accumulate scattered pieces of their environment and assemble them into an organic entity. In contrast, animals need only to find pre-assembled pieces of life, perhaps still living, perhaps not, and reconfigure them to their own use. And while the controls on animal growth are straightforward, being tied to ingestion, what controls plant growth is less obvious.

Fig. 1 Germinating sitka spruce seedling. Almost all growth to this point has been supplied by nutrients stored in the seed. As the first leaves emerge they will be able to photosynthesize and provide for the material and energetic needs of growth.

When plants grow, they generally get bigger both in size and in weight and the process of growth can be linked to increases in either. However, for a variety of reasons, the growth of plants is defined as an irreversible increase in size, not an increase in weight. Part of the reason for this is because water absorption and loss can change plant (wet) weight substantially because of processes that most would not consider growth. For example, trees gain a considerable amount of water overnight to replenish that lost during the day; most would not consider the overnight weight gain to be growth nor the loss during the day to be 'negative growth.' To avoid the dynamics of water, one might monitor growth with increases in 'dry weight', a consequence of the accumulation of carbon, nitrogen, phosphorus, etc., and the synthesis of organic molecules such as carbohydrates and proteins. But defining growth by an increase in dry weight would lead to some counterintuitive results. Most would consider that trees grow in the spring when the shoots elongate and leaves appear. At this time the tree is actually decreasing in dry weight. During the summer in temperate areas, as trees photosynthesize and absorb nutrients, their dry weight increases, yet many are not getting bigger in terms of longer shoots. Similarly, a sprouting seed, which most would consider to be growing, is actually decreasing in dry weight until its photosynthetic rate exceeds its respiration rate; this generally doesn't happen until the seedling is a couple of weeks old and already of substantial size. Consequently, plant growth is typically defined as an irreversible increase in size.

TOPICS

- Growth processes
- Limitations on plant growth
- Growth models

Growth Processes

Increases in the size of plants come about as individual cells, produced by cell divisions in the meristems, expand. While this may seem at first a simple phenomenon, consider the following aspects of the process:

1. All plant cells, even small ones, are surrounded by a confining cell wall, whose most basic function is to **prevent** expansion. This allows the cell to pressurize and this is important to plant cell water balance and functioning.
2. As the cell expands the thickness of the cell membrane and the cell wall outside it do **not** diminish. In contrast, consider an expanding balloon: as you blow air into it,

the ‘skin’ of the balloon is stretched thinner and thinner as the static volume of balloon material is spread over a larger and larger volume. This does not happen as plant cells grow–consequently, the expansion must be coordinated with the production of new material for the cell membrane and cell wall; this keeps the thickness of the boundaries of the cell constant. The significance of this, especially with respect to the membrane, should be apparent; stretching the plasma membrane is not possible, only the tearing of it, and this would destroy its ability to be a selective barrier, keeping some molecules in and others out of the cell.

3. A lthough the expansion of the cell is a consequence of water absorption, this is not a simple ‘dilution’ of the cell. Similar to what is happening in the membrane and wall, the cell is adding intracellular components at a rate that keeps pace with its expansion.
4. Although the cytosol does increase its volume as a cell grows, it is generally the expansion of the vacuole that accounts for most of the increased volume of the cell. Assuming that a larger cell is beneficial to the organism (because it allows it to penetrate more of its environment, important for both roots and shoots), the large central vacuole is a relatively ‘cheap’ way for a cell to get bigger because the contents of vacuole take less energy to obtain than the contents of the cytosol. The enlarged cell is not simply a diluted and stretched version of the original one, its walls and membranes are the same thickness as before and the cytosol is the same composition as before. The cytosol has increased somewhat in volume but the majority of the increase in overall cell volume is the result of a larger vacuole, which must have the same solute concentration as the cytosol, but the solutes are different and ‘cheaper’ ones are in the vacuole.
5. The region of growth of a plant is separated, often by very substantial distances, from the source of materials for that growth. What materials are needed for growth? We can identify three basic needs: **water**, which represents the biggest component of ‘new plant’ material; **carbohydrates** which are used both in cellular respiration, to provide energy for synthetic reactions, and also as building materials to make cell walls, cell membranes, internal membranes, proteins, metabolites, vitamins, etc; and **mineral nutrients**, e.g. phosphorus for membranes, nitrogen for amino acids, etc. Water and nutrients are coming from the soil and are thus very close to the growing cells of root meristems, but must be transported considerable distances to get to the tips of shoots, up to 350 feet in the case of a redwood tree. Carbohydrates are supplied by photosynthesizing leaves, which may be relatively close to growing shoots but may be 350 feet away from an expanding root meristem.

> Carbohydrates often do not directly flow from leaves to growth points but instead may flow from leaves to storage sites and then from storage sites to growth regions.

Cellular expansion is resisted by the strength of the cell wall and expansion occurs when the pressure inside the cell, created by the inward diffusion of water, exceeds the strength of the wall. Growing cells have 'softer' cell walls, i.e., walls that yield (expand) at lower pressures than non-growing cells. And it is believed that plants control cellular growth by controlling the 'softening' of cell walls. To summarize, plant growth involves a coordinated process of the synthesis of membranes (both the cell membrane and the vacuolar membrane), (2) cell wall, (3) cytoplasmic materials (proteins, membranes, metabolites) , and (4) some vacuolar materials, along with the absorption of water and minerals. The size of a cell is determined by genetics and environmental conditions. Growth stops when the wall 'hardens' and no longer yields to the pressure generated by water diffusion. In those cells that have secondary cell walls additional cell wall material is deposited after cell expansion has ceased — note that while secondary wall materials are added the cell is not growing in size but is growing in mass.

Most of the growth of plants is a result of the expansion of the vacuole. This follows cell division, which produces new cells roughly the same as the original one, thus producing what is known as cytoplasmic growth and only a modest increase in the size of the organ. Cell division is essential to the growth process because it provides cells that have the potential to exhibit vacuolar grow. Cell division occurs in plants in isolated spots called meristems and the majority of the growth of plants occurs in areas adjacent to these meristems where the newly produced cells exhibit vacuolar growth. The expansion of newly produced cells pushes the meristematic regions further away from the main body of the plant, expanding the total size of the plant. Thus there is a spatial separation between the region of cell division and the region of cell growth (Chapter 8). This pattern is most apparent in apical growth but is also the case for secondary (lateral) growth (Chapter 9) although in both the vascular cambium and the cork cambium cell growth occurs on both sides of the meristem. Activity generally occurs simultaneously in the region of cell division and the region of cellular growth. Most growth of the organ occurs whenever the new cells produced by the meristem are allowed to expand. For some plants, growth is more or less continuous and steady as long as environmental conditions (in particular temperature, water and light) are steady. However, most plants exhibit episodic growth with bursts of cell production and expansion followed by periods of inactivity, even when conditions are constant and favorable. For many perennial plants living in areas with seasonal climates, growth is strictly seasonal, occurring for only a portion of the year. Often the growth period is only a very small portion of the 'favorable' time period. For example, many trees in north temperate areas grow only for two to four weeks in May.

The patterns described above represent the extensional growth exhibited by apical meristems in roots and shoots (primary growth) and the expansional growth produced by the lateral meristems (secondary growth). The growth of leaves and fruits is different; these determinate organs have a pattern similar to that of many animals where the entire organ has a period of cell division followed by a period of cell expansion, i.e. cell division and expansion are separated in time not in space. There may be a period of overlap where both division and expansion are occurring but usually, well before growth ceases, cells stop dividing and no more embryonic cells are produced. Growth is sustained as the new cells expand. Eventually the growth of the organ stops and a structure of unchanging size remains. However, these structures **do** continue to develop: showing senescence and abscission in the case of leaves and in the case of fruits showing ripening in ways that promote seed dispersal (and this often also includes abscission).

Two examples of growth:

> **Tree buds** Temperate tree buds are formed over the last half of the summer. The bud contains an apical meristem, a very short section of stem with several leaf primordial attached and all packaged by special leaves (bud scales) that cover the entire structure. Buds increase in size from their initiation to a time when they become dormant in early fall but the size increase is modest, producing buds that commonly range from 0.5 to 3 cm. In the spring, at 'bud break' the contents of the bud show a tremendous increase in size, producing a section of stem that may be 20 cm in length with several leaves of comparable length. As was the case with fruits, most of the cells that are present in this new section of stem had been formed earlier and most of the growth seen in the spring is the result of the expansion of these cells by vacuolar growth.
>
> **Fruits** A typical apple fruit begins its development following fertilization, typically in late April. A month later the fruit has grown to but a small portion of its eventual size, with a diameter of 1-2 cm and a volume of about about 5 cubic cm, yet all of the cells of the fruit (roughly 75 million(!) cells) are present. Over the course of the summer the apple grows to its mature size of perhaps 10 cm with a volume of 1300 cubic cm. During this time no new cells are added; there is only growth of

Fig. 2 Twig growth—the twig growth is indeterminate but occurs in yearly 'flushes.' The leaf growth is determinate. All of the structure to the right of the arrow was present in the bud produced at the end of the previous summer. And most of the cells of both the twig and leaves were present in the bud for nine months before rapidly expanding over a 2-3 week span in May.

the already existing cells. In apple and many other fruits the eventual fruit size is determined by the number of cells produced and thus is dependent of conditions in late spring, not those during the summer.

In order to sustain growth, a supply of materials is needed, not just the water that powers cellular expansion, but the materials to make more cell walls, cell membranes and all the cytoplasmic constituents as the cell expands. Not only are materials needed to construct the enlarging cells, material is also needed to supply the energy that is needed for these processes. Every peptide bond requires the hydrolysis of an ATP, as does every additional glucose unit in a growing cellulose polymer. In addition to direct 'construction costs' energy is needed for other cellular processes, e.g., the transport of molecules across membranes.

Limitations on growth

Many people are interested in making plants grow more, producing more material in a shorter period of time. What is it that limits growth? Below are listed some significant factors, several of which operate in multiple ways. Although increases in all of these factors may increase growth, this response is not constant and often tapers off with further increases in the factor, leading to the phenomenon of **saturation**, where further increases in the factor cause negligible changes in growth. Moreover, for all of these factors, there can be 'too much of a good thing' and further increases actually diminish growth (toxicity).

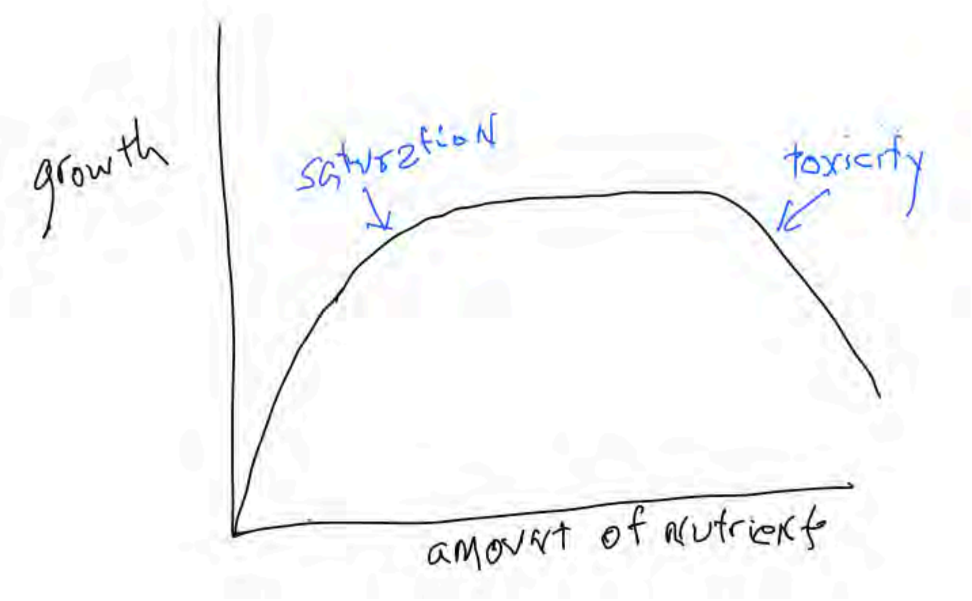

Fig. 3 Growth changes in response to increases in the amount of a nutrient. When the nutrient is at low levels it affects growth in consistent, often linear, way. But with further increases in the nutrient, the increases in growth diminish, i.e. saturation occurs and eventually growth is no longer increased as more nutrient is added. Additionally, most nutrients are toxic when at high enough levels, i.e. growth is diminished as more of a nutrient is supplied.

Nutrients

Fig. 4 Typical fertilizer contains nitrogen, potassium and phosphorus. This one is 13% of each in the order; if it listed 20-10-8 it would be 20% nitrogen, 10% potassium and 8% phosphorus.

All of the required mineral elements can potentially limit growth. The limitation can come about both because that element is lacking from the soil or because, although the element is present, it is unavailable because of soil conditions. For instance, iron is frequently unavailable in basic soils even though it may be present in abundance. The problem is that under aerobic, basic conditions very little iron is present in a form that readily dissolves.

Somewhere on earth, there are soils that are deficient in all of the 14 mineral elements required by plants and deficiencies can develop even for elements like molybdenum that are needed in very small amounts. In the early 19th century Carl Sprengel developed an idea later championed by Justus van Liebig called the 'Law of the Minimum:' that plant growth will be limited not by nutrient availability generally but by whatever nutrient is in the shortest supply relative to how much is needed. For example, although additions of nitrogen often increase plant growth, if there isn't enough molybdenum available such additions will not result in any growth enhancements. One can think of growing crops to be like baking a cake: if the cake recipe calls for five ingredients, making a cake can be limited by any of the five ingredients, and a lack of one is not made up for by excesses in others. This is a very straightforward idea that applies in many situations. But it runs counter to the common idea that response to factors will always be the constant: 'if a little bit is good then a lot must be better' is generally **not** the case!

While too little of the essential nutrients can limit growth, too many of the same elements (toxicities) can also retard growth. The most common toxicities are the result of saline soils that have high levels of K, Ca, Cl, SO_4 and Na but unique soil conditions (waterlogging) can also bring about toxicities in iron and manganese in non-saline soils.

Water

Fig. 5 Pivot irrigation in a cotton field. The system rotates around a central water source.

Water is the most important factor limiting terrestrial photosynthesis worldwide. Water plays multiple roles in plant growth: as a reagent in photosynthesis, as the main constituent of any new cell that is produced, as the transport medium which moves materials throughout the plant and in particular to the growing regions. While all of the above might potentially play a role, the effect of water comes primarily because of the interplay between water loss and carbon dioxide gain. In dry habitats, plants keep their stomates closed to avoid water loss. This lowers the carbon dioxide concentrations inside the leaf and lessens the amount of photosynthesis. Additionally, plants may reduce water loss by having smaller leaves or fewer leaves, both of which may limit growth because the total amount of leaf area determines the amount of photosynthesis that can occur. While lack of water can reduce growth, too much water is also damaging to most plants, primarily because waterlogged soils become anaerobic and the roots grow poorly and/or die.

Light

Without light, photosynthesis can't occur and without photosynthesis, growth cannot occur. Light can have a very significant effect on photosynthesis and growth, but only when other conditions are favorable to sustain growth and only when dealing with light levels comparable to those typically experienced by the plant. Too much light can be extremely harmful for a number of reasons and plants adapted to the shade usually do very poorly if exposed to high light levels. For the home gardener, the proper location of ornamental plants is strongly influenced by light considerations. The amount of light a plant receives is controlled both by the intensity of light and by the duration of light exposure; the effects do not always compensate for each other, i.e., short periods of very bright light are not equivalent to longer periods of less bright light. Most crop species are adapted to high light conditions and will do very poorly if grown under shaded conditions and it is probably the case crop growth can be reduced as a result of prolonged

Fig. 6 Satellite view of Kansas cropland. The circles reflect the use of central pivot irrigation systems where a large boom circles around the water source. The boom is motorized to allow for its circular movement; water, supplied from a well, is pumped out of the boom and used to irrigate crops.

cloudy conditions. However, such conditions are often associated with frequent rains and these might also be the cause of decreased growth if the soils become flooded.

Leaf distribution and longevity are important plant parameters that are influenced by light considerations because of problems associated with self-shading. In general, leaves are produced in ways that lessen self-shading and allow for more photosynthesis. Older leaves, that are experiencing shaded conditions, are often abandoned (i.e., they senesce and abscise) because they no longer obtain enough light to be profitable in an energetic/material sense. This is reflected in the following equation:

$$\text{Net photosynthesis} = \text{gross photosynthesis} - \text{respiration}$$

Assuming that the maintenance cost (i.e., that the amount of respiration needed for a leaf to maintain its living condition) of a leaf is constant, shading will decrease gross photosynthesis to the point that net photosynthesis is negative, i.e., the leaf costs more to maintain than it 'makes' in photosynthesis. At this point it the plant can cut its losses by eliminating the leaf.

Temperature

Plants are poikilothermic, their temperature is not regulated internally but is determined by the environmental conditions. Moreover, plants have a range of temperatures within which they can survive (often this range of tolerance shifts seasonally). All biological processes, and in particular photosynthesis, respiration, and growth, are influenced by temperature (Chapter 26) and, with a few important exceptions, the basic response is that that plant activities, including growth, increase at higher temperatures in the range of 0 to 20 C (32 to 68 F). However, all plants have an optimum temperature for growth, above which growth diminishes with increasing temperature. Part of the explanation of this is that at higher temperatures respiration is more sensitive to temperature (i.e., increases more with increases in temperature) than photosynthesis–thus although gross photosynthesis might increase, respiration increases more and there is a decrease in net photosynthesis at higher temperature (see equation above).

Interactions between water, light and temperature

These factors are often intertwined: more light increases temperature and higher temperatures increase transpiration and can lead to complications from a lack of water. How tightly these three factors are linked depends upon a variety of factors.

Leaf area

As would be expected, plants with more leaf area generally grow faster than plants with less leaf area. This is discussed in the following section.

Models of Plant Growth

What limits plant growth is a critical question, one that has a multitude of practical implications. Clearly, plant growth can be limited by adverse environmental conditions, e.g., lack of rainfall. But if conditions are ideal for growth, what limits it? Like all organisms, plants grow by acquiring material and incorporating it into their own structure. One might assume that the ability of a plant to acquire material is directly related to its size, with bigger organisms able to acquire more than little organisms. This would result in a positive feedback process of growth: acquisition of resources—>growth—> bigger plant—>greater acquisition of resources—> more growth—> even bigger plant, etc., etc. This idea can be modeled in a set of equations that are predicated on the idea that the growth rate is a linear function of plant size: more plant, more growth; more growth more plant.

In words, this idea can be expressed in two ways:

(1) growth rate is determined by plant size

(2) the growth rate, expressed per unit of plant, is a constant

In mathematical terms these two statements are:

(1) growth rate = $\Delta S/\Delta t = k * S$, where $\Delta S/\Delta t$ is the growth rate, the change in size divided by the change in time, S is the total plant size and k is a constant

(2) $(\Delta S/\Delta t) * (1/S) = k$,

For most biology students this should be familiar because: (1) it sounds like 'exponential' population growth, or perhaps 'geometric' population growth, (2) it is starting to sound like calculus, a course that is often required for biology majors (and perhaps you now see why!)

Calculus can lead to the following, putting these in differential form:

(1 a) $dS/dt = k * S$

(2 a) $(dS/dt) * (1/S) = k$

(3) size (S) at any time (t) is given by $S(t) = S_o\, e^{(k*t)}$

Note that while the jump to equation (3) requires calculus, the ideas of equation 1 and 1a, and their rearrangement in 2 and 2a, should make sense without it. Equation (3) follows from either of the first two.

Thus, one might expect plant growth to be exponential, just as you might expect population growth to be exponential. Note that the meaning of the word 'exponential' has a mathematical meaning that is not equivalent to the one in general use. Exponential growth is not necessarily 'fast', and indeed, fast is a subjective adjective. In a mathematical sense, exponential is described in equations 1-3, although only 3 has an exponent in it. One could develop similar equations based on leaf area (i.e., that the growth rate per unit leaf area is a constant), with the argument that leaf area, by controlling photosynthesis, dictates growth rates. However, a similar argument could also be made about roots since without water and nutrients photosynthesis isn't possible. It is easiest to just assume that roots, leaves and everything else are all needed and let S simply be 'total plant size' and work with the assumption that plants can acquire more materials at a rate that is a linear function of their size (i.e., equation 1).

But the growth of plants, like the growth of populations, usually is not exponential, at least not for long. Why isn't plant growth exponential? A basic answer is that growth is not controlled by the rate of material acquisition. It is an internally regulated process and it is too simplistic to assume that the rate of growth is a simple function of the ability of leaves and roots to acquire the materials necessary for growth. The internal controls of the plant, including both hormonal controls and molecular controls (e.g., which genes are activated) regulate the processes of cell division and cell expansion and thereby the growth process. In a fundamental sense, this is no different than what was discussed earlier concerning the development of unicellular organisms (see Chapter 7 on organism development). A second factor involves meristems or more generally regions of growth. If an organism only has a limited region where growth originates and this region has a finite capacity to produce growth, then growth will not be exponential. In the case of a filamentous algae that grows from a single apical cell, it is easy to see why growth might not be exponential. Similarly, an unbranched stem with a single apical meristem might not be expected to show exponential growth although one with branches, and with branches that can produce more branches, might be expected to.

An economic model of plant growth

A useful analogy for plant growth is an economic, 'business' model. Gross income is first split between expenses (the costs of running the business) and net income ('earnings', what is left behind after expenses have been paid). Earnings can be 'invested' in a variety of ways, investments that allow for more earnings, investments that protect existing structures, or in investments that are 'frivolous', i.e., with no obvious benefit. For example, a baker earns an income from the bread he sells. Some of his income he uses for 'maintenance' covering the expenses of his bakery–to buy flour, to pay taxes, to pay for the power to run the ovens, to repair broken machinery, etc. The income left after maintenance costs have been paid can be invested in a variety of ways: (1) investments in additional ovens and mixers or perhaps in a whole new bakery. These investments would increase his earnings and would produce exponential growth. (2) in defenses, such as a sprinkler system to protect his bakery from fire, or perhaps a security system that makes robbery less likely. This might not increase his earnings at all but it does provide for protection against a variety of potential problems. (3) the money could be spent on 'frivolous' items, items that do not protect the bakery. Money might simply be stored under his mattress. Theoretically, plants operate in the same way, material acquired (primarily carbohydrates but also mineral elements) is used for maintenance and what remains can be 'invested' in structures (e.g., leaves) that will allow for the acquisition of more resources, or it might be invested in structures, (e.g., anti-herbivore chemicals) , that protect existing structures, or perhaps the material acquired might not have been invested in anything 'worthwhile' at all. Note that as long as the baker (or a plant) invests a set portion of his earnings in ways that increase his capacity to earn more income (even if it is only a very small portion) , the result will be exponential growth.

The exponential model of growth is overly simplistic and usually poorly reflects reality. It does, however, give a starting point from which to analyze growth and the basic idea that as organisms (especially plants) grow, their ability to grow (growth rate) increases simply because they are bigger.

Further Reading and Viewing

- "Tree Growth Characteristics" by Jennifer Franklin et al. Tree growth.
    - https://extension.tennessee.edu/publications/Documents/W227.pdf

- “Apple Growth and Crop-load Management” by Steve McArtney. Apple growth.
    - http://umassfruitnotes.com/v76n1/a3.pdf

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- Pivot irrigation is licensed under a Public Domain license
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CHAPTER 26: INTERACTIONS INVOLVING CONDITIONS

Fig. 1 Sugar maple leaves interact with the physical environment (conditions) multiple ways: during the day they absorb light, lowering light intensity below the leaf; they also reduce the air's CO_2 concentration, increase its O_2 and H_2O levels and heat it up by radiating long-wave radiation. At night leaves decrease the air's oxygen level but increase its CO_2 and H_2O levels. If the sky is clear the leaves can significantly affect the temperature of objects below by 'shielding' them from the cold night-time sky.

A particularly significant and interesting aspect of organismal life is its interaction with its surrounding environment. As indicated by the term, interaction implies that both components affect each other: the environment affects organisms and organisms affect the environment. The 'environment' includes components that are living, i.e., other organisms (the biotic environment), and components that are non-living such as rocks, clouds, water, dead organisms or parts of dead organisms. The environment has properties, or conditions, such as temperature and oxygen concentration that are commonly considered 'the abiotic environment' or the 'physical environment'. Conditions are the consequences of physical processes such as radiation, diffusion, convection; and these processes are sometimes strongly influenced by biotic processes (Fig. 1), such as respiration (generates heat and carbon dioxide, removes oxygen) and photosynthesis (absorbs light, adds oxygen and water, removes carbon dioxide). The conditions present on a site can dictate whether or not an organism can exist and, if it exists, how it behaves. This is sometimes described as an interaction between organisms and the physical, or abiotic, environment.

Because organisms can affect conditions, they can interact with other organisms as a result. In addition to the interaction between organisms mediated through conditions, there are more direct interactions between organisms, such as one organism eating another or an insect transporting pollen from one plant to another. Interactions are fundamental to the discipline of ecology. Indeed one definition of ecology is 'a study of the interactions between living things and their environment'.

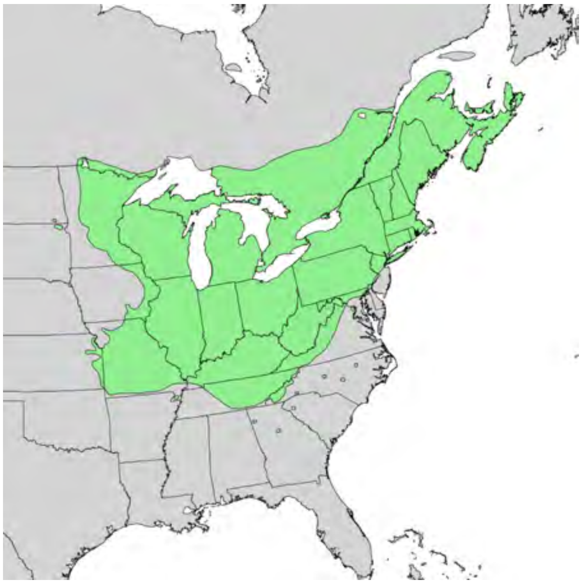

Fig. 2 Sugar maple distribution: To the North, the population is limited by lower temperatures, to the West, by lower moisture levels and to the south, by multiple factors including higher temperatures, competition with other species, and perhaps disease.

Another common definition of ecology is 'a study of the distribution and abundance of organisms' (Fig. 2). The distribution and abundance of organisms are controlled by interactions between organisms and their biotic and abiotic environment. For example, the distribution of a plant might be limited by the intensity of light. The amount of light available is a consequence of both the physical environment (latitude, degree of cloudiness, whether the site is facing south or north, etc.) and the biotic environment (presence or absence of tree species to intercept the light). The distribution and abundance of a particular plant (species 'A') might also be limited to the presence or absence of an organism that eats the plant or perhaps by an organism that pollinates the plant. In either of the latter cases, one might consider the factors that determine the distribution and abundance of the second species to be controlling the distribution and abundance of species A.

Another definition of ecology is "a study of biological organization above the level of individual." As we have seen, organisms have a structure (form, size, organization of component parts), and also organisms have functions, they do things such as develop, reproduce, and exchange matter and energy with their environment. Similarly, groups of organisms (e.g. populations) have structural and functional features that can be described and categorized, and explanations can be sought as to what determines their organization. An important point is that life is not simply organized at the level of the cell and the level of an organism; there also is an organization involving groups of organisms and this is the level of study for the discipline of ecology.

Fig. 3 A community ('northern hardwood forest') is defined in part by the presence of sugar maple. It is found in southern Canada, New England, parts of NY and Pennsylvania, and further south at higher elevations in the mountains.

Two entities that ecologists study are populations (groups of individuals of the same species) and communities (assemblages of species in a particular area). A population could certainly be considered a 'living thing' and its distribution across the landscape is a manifestation of biological organization and is a structural feature of this entity. The abundance of a species (how many individuals are present per unit of the environment) is another structural feature of a population. The fact that populations have patterns of distribution and abundance represents an organization, a structure, and the processes determining this structure are the same processes discussed above: interactions between organisms and their physical and biotic environments. Similar arguments can be made concerning the organization of communities.

The final chapters of this book examines of the role of interactions in the biology of organisms. This chapter considers the interactions between organisms and conditions, examining the key conditions that affect terrestrial and aquatic habitats, why these conditions affect an organism's function, and what factors cause these conditions to vary, including how organisms themselves may control conditions. In the next chapter, we will examine more direct interactions between organisms, trying to see fundamental similarities in the ways that organisms interact with each other. Finally, chapters 28-31 examine agriculture, an interaction that we all depend upon, and interactions that are critical to agriculture.

Our approach will be centered primarily on organisms, although many of the topics overlap with ecology and approach the topics from a broader scale.

TOPICS

- Temperature
    - Temperature's influences
    - Organism tolerances
    - Organism growth
    - Psychophiles and thermophiles
    - Fruit ripening
    - Temperature as a cue
    - Temperature's influence on other conditions
- Moisture
    - Terrestrial habitats
- Aquatic habitats
    - Salinity
    - Oxygen
    - Light
    - Currents
    - Nutrients

Temperature

Temperature is of critical importance to all organisms—it affects whether they can survive and what they do. Even for organisms who regulate their temperature at a set point, (i.e., homeotherms), temperature has significant consequences. But temperature is even more significant for the vast majority of organisms who do not regulate their temperature. For such organisms, termed poikilotherms, the thermal conditions of their environment control their metabolic activity. Although the temperature is important in all habitats, it is of relatively less importance in most aquatic systems because the thermal properties of water buffer temperature fluctuations. But organisms in terrestrial habitats are immersed in a fluid (air) that absorbs very little heat energy and has a low heat capacity (i.e., little buffering ability). This makes the temperature of terrestrial systems much more dynamic in time and space than in most aquatic systems. One of the key reasons why temperature is important in terrestrial habitats is because it affects evaporation and moisture levels. While there are some terrestrial habitats where temperature is not a key determinant of activities, from a global perspective temperature and moisture are the major factors controlling what organisms are present and what they are doing.

Temperature's Influences on Organisms

All organisms have a range of temperatures in which they can carry out the functions that define and sustain them. Temperatures above and below this range alter their structure and functioning in several ways. The most important alterations are listed below.

Membranes and temperature

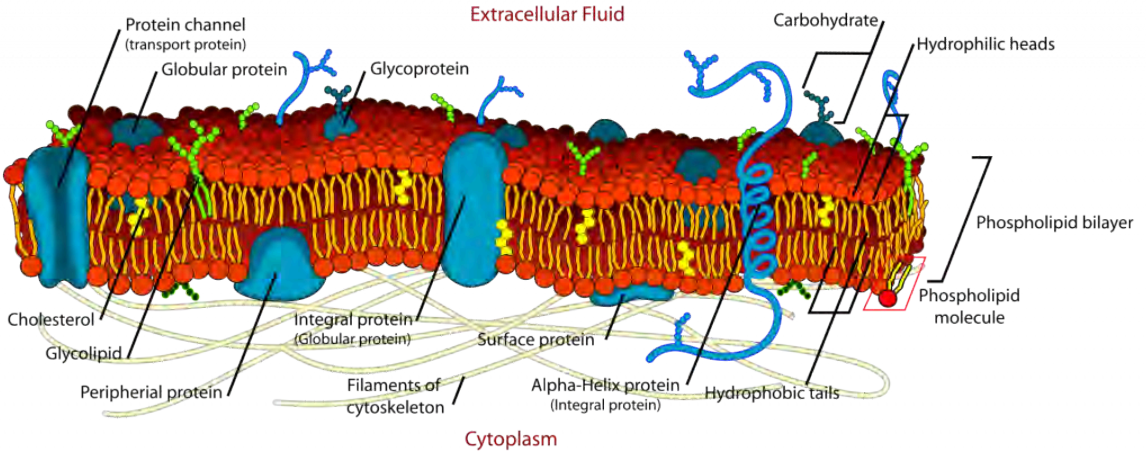

Fig. 4 A model of a membrane, discussed in more detail in Chapter 3.

Membranes are essential for life, they regulate molecular movement and perform a variety of other functions. The physical nature of membranes is between a solid and a liquid; they can be described as " liquid crystals" because part of their nature is rigid and ordered while other parts are fluid-like (Fig. 4, discussed also in Chapter 3). This duality of structure is important to their function; they need to be partly rigid because much of their functioning depends upon the organization of its parts; if these parts are out of place, functioning is disrupted. At the same time, membranes need to be able to change shape and membrane components do need to be able to move laterally; this is only possible because of membrane fluidity. Temperature disrupts the balance between fluidity and rigidity—high temperatures make membranes more fluid and low temperatures make them more rigid (crystalline). Shifts in either direction are damaging. Membrane characteristics of organisms found in habitats of different temperatures are different in predictable ways that relate to the maintenance of a certain degree of 'fluidity'. In organisms living at higher temperatures, the lipids are more likely to contain longer chains of hydrocarbon and these chains are more likely to be more saturated. Both of these features make the membranes that they are found in more 'solid-like' at any particular temperature. Along the same lines, it has been found that some organisms that experience yearly variation in temperature adjust their membrane chemistry in a way that maintains a constant degree of fluidity in spite of changing temperatures. Thus, the range of temperature tolerance is partly determined by the chemical nature of an organism's membranes.

Coordinated chemical reactions and temperature

A second factor involved in both high and low-temperature disruptions of organism function is the balancing of the myriad chemical reactions that are taking place inside cells. The rate of nearly all chemical reactions is strongly influenced by temperature, with the rates going up as the temperature goes up. Most of these reactions are in some sort of a balance so that, in general, there is no build-up or depletion of metabolites. This balance can be upset at both high and low temperatures because the temperature sensitivity is not the same for all reactions—thus reactions that are 'in balance' at some temperatures may not be at higher or lower temperatures. The biochemistry of cells is such that control process (e.g., feedback loops) can operate to achieve balance in metabolic pathways, but there are limits to these control processes, and at least some of the problems with high and low temperatures may be attributed to problems with reactions becoming 'unbalanced'.

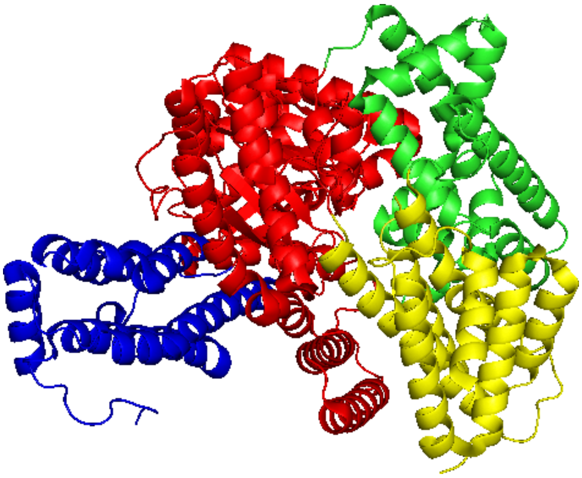

Fig. 5 A model of enzyme structure. In order to perform its functions this three-dimensional structure needs to be maintained.

Enzymes and temperature

Enzyme functioning is dependent upon a three-dimensional structure. This structure can be disrupted by high temperatures in a process called denaturing because the thermal motion becomes sufficient to break the relatively weak bonding that accounts for certain aspects of the enzyme structure. The temperature at which denaturing occurs varies with proteins but is in the range where temperatures become lethal to most organisms (25-40 C).

Problems with freezing

Not surprisingly, freezing causes a variety of problems for living things. The expansion associated with freezing can burst cells, destroying membranes and walls in the process. For plants and fungi, which have a substantial volume of their structure (the apoplast) that is outside of the membranes, freezing (especially if it occurs slowly) generally occurs first outside the cytosol, i.e., in the apoplast, because of its substantially lower solute concentration. The freezing outside causes the diffusion of water from the inside to the outside, resulting in desiccation damage on the inside. Because of these effects, a wide group of plants and fungi have their lower thermal limit at 0 C, or slightly below it.

In spite of this, plants and fungi do live in habitats where freezing occurs. For some, survival is the result of an overwintering part that is below-ground where temperatures are more moderate and never go below freezing. For others, e.g., trees and shrubs, the existence of perennial above-ground parts reflects an ability to withstand prolonged periods of sub-freezing temperatures. Tissues/cells may avoid freezing through two mechanisms, one involving freezing point depression and the other involving supercooling. Freezing point depression is one of the four 'colligative properties of solutions' — changes in the properties of a solution that occur with the addition of solutes, regardless of what solute is added. Although the presence of solutes in the cytosol does lower the freezing point, the effect is relatively small (up to -2 C at the concentrations of solutes typically found in the cytosol) , and protection against freezing by this mechanism is not significant for most organisms. Supercooling can result in much more substantial drops in the temperature at which freezing occurs. Supercooling describes a situation where liquid water exists at temperatures where it is usually frozen. Although supercooling can occur in pure, or nearly pure, water, especially if there are no sites for ice nucleation (e.g., under certain atmospheric conditions that cause supercooled raindrops), in living systems supercooling appears to be a consequence of specific antifreeze solutes, proteins or glycoproteins, that somehow prevent crystal formation. Such compounds are found not only in plants but also in fish and insects. The lower limit of supercooling is around -40 C (which is also -40 F!!!!), but for many species the limit of supercooling is well above this, in the range of -10 C.

Other problems caused by freezing are particularly significant to vascular plants and relate to water transport. Water cannot flow in the xylem if it is frozen, and, as mentioned above, the lower solute concentration of the apoplast, and particularly the xylem transport cells, means that water transport becomes impossible when the temperature falls below zero. Since water loss to the atmosphere is almost always occurring because the air is drier than the plant, desiccation will result. This probably accounts for a common linkage between freezing tolerance and drought tolerance. An additional problem related to water transport is that when water freezes dissolved air is excluding from the ice, creating bubbles of air in the ice. Upon thawing, these bubbles remain. This is potentially a problem for xylem transport because the tensions that develop during xylem transport will cause expansion of the bubbles and cavitation (air locking) of vessels and tracheids, disrupting xylem water transport. This problem may be avoided by the production of new water-conducting cells in early spring, by a pressurization of the xylem ('root pressure') that occurs in at least some species as a result of solute absorption in the spring, or as a result of physical processes that can eliminate the bubbles.

Tolerances

All organisms have high and low thermal limits; if an organism reaches that temperature it dies. Chronic exposure to more moderate temperatures can also be lethal, in a manner connected to the length of exposure. Some plants will be killed by a short-term exposure at 38 C, but 36 C is lethal if exposure is longer than 60 minutes.

Extreme tolerances

Fig. 6 Emerging from the inflorescence of wheat is a fungal sclerotium, a modified hyphal mass that is inactive and tolerant of extremes

The majority of organisms have high-temperature tolerances of around 40 C and low-temperature tolerances of 0 C but there are stages of many organisms that have a much wider range of tolerance. This tolerance is often associated with a stage in the organism's life cycle that is devoted to dispersal, e.g., spores, seeds. These structures serve to perpetuate the organism through a time of unfavorable conditions. Along with tolerance to temperature extremes, there typically comes a tolerance to desiccation and to a number of 'insults' that would normally kill cells (e.g., ultraviolet radiation, extreme pH, lack of oxygen). This tolerance is a consequence of an altered cellular structure that simultaneously increases tolerance and decreases metabolic activity. In short, the structure of the cell(s) becomes more and more inanimate and less and less affected by extreme conditions. Usually this state of 'suspended animation' involves several or all of the following: accumulation of materials such as starch or oils that serve as reserves of energy and reduced carbon, changes in membrane structure, changes in protein structure, changes in organelles (in eukaryotes), reduction in cytoplasmic volume, desiccation, and, for certain cells, a thickening of the cell wall (or sometimes the addition of a wall to a cell that previously lacked one).

Generally, these tolerant structures are single cells but in some organisms tissues or the entire organisms undergo comparable changes in structure and function. In the plant kingdom, such tolerant tissues are usually present in seeds and sometimes present in apical meristems. Such tolerance can occasionally be found in other structures and can also be found in entire plants, especially those found in freezing environments or deserts. The table below lists prokaryote, protist, fungal and plant structures that are particularly tolerant of extreme conditions. Although the table only tabulates low-temperature tolerances, it is important to realize that, in general, high-temperature tolerance, as well as desiccation tolerance, correlates with low-temperature tolerance. For example, most seeds readily tolerate prolonged exposure to frozen conditions; they also tolerate desiccation and exposure to high temperatures (e.g., 50 C) that would normally kill plants.

Table 1.

group	structure	notes
some bacteria	endospores	most are very resistant to high and low temperatures and survive for prolonged periods
most bacteria	microbial cyst (=exospore)	bacterial cells increase the thickness of the cell wall and contract the volume of the cytoplasm
cyanobacteria	akinete	an akinete is a specialized spore found only in some cyanobacteria
euglenoids	cyst	cyst formation is often triggered by changes in nutrient levels
dinoflagellates	cyst	cysts have no flagella and produce a cell wall with cellulose, features that are NOT normally present in dinoflagellates
diatoms	resting cells and spores	spores have thickened silica walls, resting cells do not; these structures may have requirements for germination. Spores of marine forms may be important components of the fossil record
zygomycetes	spores, zygospores	the zygospores that are associated with sex and are multinucleate have a much thicker cell wall and are more tolerant of abuse than normal cells
basidiomycetes	both asexual and sexual spores	in addition to spores, some forms produce sclerotia, desiccated and modified hyphae that are inactive and tolerant of extremes
ascomycetes	both asexual and sexual spores	(see above description for basidiomycetes)
mosses	whole plants, spores	the spores of most species are tolerant of a variety of treatments; in addition, the entire gametophyte plant of many mosses tolerates both freezing temperatures and desiccation

group	structure	notes
ferns and other seedless vascular plants	spores, rarely whole plants	unlike mosses and like most seed plants, ferns generally canNOT tolerate desiccation, although spores of ferns tolerate this and other extreme treatments. Relatively few species have above-ground parts that overwinter in sub-freezing conditions.
conifers	pollen grains, seeds, whole plants	as a group, many conifers are more tolerant of freezing than most flowering plants, evidenced by the presence of conifers at high latitudes and elevations; however, spores are NOT especially tolerant; they generally only occur in hydrated tissues;
cycads	seeds only for most species	only a few can tolerate temperatures below freezing, most are restricted to warmer areas
gnetophytes	seeds only	only *Ephedra* tolerates freezing temperatures
ginkgo	pollen, seeds, above-ground parts	the tree is tolerant to the USDA's zone 3, which has temperatures down to -40
flowering plants	pollen, seeds, above-ground parts of some species	quite a number of flowering plants have adapted to temperatures well below freezing; there are also a number of species that can tolerate temperatures above 40 C

Temperature's Influences on Growth

Because temperature affects the rate of chemical reactions and because chemical reactions determine what an organism does, and in particular the **rate** at which things are done, temperature has a profound effect on organism functioning. The combined effects of an organism's chemical activity are termed metabolism and metabolic rates commonly double to triple with a 10 C (18 F) rise in temperature. While most students generally assume that the opportunity to 'do more' as a consequence of a higher metabolic rate is a desirable thing, this isn't always the case. Higher metabolic rates require more food because an organism's metabolism runs on cellular respiration. To a certain extent, poikilotherms survive periods of low temperatures because it costs very little to maintain them under these conditions. Lower metabolic rates mean lower oxygen needs; consequently, many plants can survive low oxygen conditions (typically brought about by flooding) much more readily if temperatures are low.

Growth and growing degree days For any organism one of its most significant activit ies is growth, the acquisition of materials, and subsequent utilization of matter and energy to make the organism larger and ultimately coupled with the production of new organisms. The effect of temperature on growth is nicely seen in the concept of **growing degree days**, a statistic that integrates time and temperature and is used to predict the progress of a wide variety of crops during the season. While the details vary between crops, and even between different varieties of a specific crop, the basic idea is that you can predict the growth stage of a crop species by keeping track of the number of days that the crop has spent at different temperatures. For example, if the daily temperatures had a high of 86 F and a low of 70 F, corn might take 100 days to reach maturity (i.e., the time to harvest); if the temperatures were cooler, with a daily high of 80 F and the low of 60 F, it might take 140 days. Agronomists have developed models to predict how long the crop will take to reach maturity based on the accumulation of something called a 'growing degree day'. Based on its temperature, each day is assigned a certain number of growing degree days (GDD' s), with warm days earning more than cold ones. A typical formula that calculates growing degree days is the following:

$$GDD = [(Tmax + Tmin)/2\ ] - 50$$

Given the days listed above, the warmer day is worth (86+70)/2 – 50 = 28 GDD, and the cooler day is worth (80+60) – 50 = 20 days. If corn needs 2800 GDD days to reach maturity it will do so in 2800/28 = 100 days at the warmer temperatures and 2800/20 = 140 days at the slightly cooler temperatures.

This is an example of an 'empirical model', one that attempts to predict things based on observations but not necessarily based on an understanding of how a system operates. The fundamental basis for the model is the observation that crops grow faster when it is warmer. The model is successful in spite of the fact that it has a fairly crude approach to the relationship between growth and temperature. There are a number of features of the model that are useful to appreciate:

- a GDD represents a unit of growth and the basic idea is that plant development can be represented as an accumulation of these units of growth.
- a GDD also represents the product of time and temperature; although this is represented in its units ('degree-days'), it isn't obvious in the equation above because the time factor is always 1 day and is not included; the equation might be written:
    - GDD = [(Tmax + Tmin)/2 -50] degrees * [1.0] day

- the temperature term has two components, the first represents a type of average, a representation of a dynamic (changing with time) variable, in this case, temperature. This particular average (sum the extreme values and divide by 2) is convenient and it is commonly used by meteorologists to reflect daily temperature. Although it is a crude type of average, based only on two values, it works well. The other temperature term (50 in the above equations) might be described as a 'base temperature', the minimum temperature at which no growth occurs. Although the equation potentially predicts an impossible 'negative growth,' if the average temperature is below the base temperature, this prediction is rarely the case because in most situations crops aren't planted until after average temperature daily temperature exceeds the base temperature.
- the GDD concept has been used successfully for a wide variety of crops and also with insects, generally with modifications of the 'base temperature' and/or changes in the average temperature term (e.g., letting the maximum temperature never exceed 86)

If one tried to devise a 'mechanistic model', one that operates based on the mechanisms of growth, it would be much more challenging. Growth is a complex process that is a consequence of a variety of chemical reactions occurring simultaneously. Most of these are clearly affected by temperature but predicting the net effect of temperature on all of them would be particularly challenging. Certainly, the processes associated with growth are controlled by temperature, but the interrelationships associated with growth would be difficult to elucidate.

Variation in the temperature ranges for growth While the vast majority of fungi, plants and protists have an optimum temperature for growth in the range of 25-35 C, there are some exceptions. A number of plants have maximum rates of growth well below 35 C. Not surprisingly, these plants grow in cooler habitats. While there are a number of possible reasons for this, including the possibility that these organisms have membranes that function more appropriately at lower temperatures (see above), or the interaction between temperature and moisture (see below), another explanation involves the temperature sensitivity of photosynthesis and respiration. As mentioned above, respiration is closely tied to temperature and for most plants reaches a maximum in the 30-35 C range. The response of photosynthesis is different: it is generally less responsive to changes in temperature and, for C3 plants, it generally reaches a maximum at temperatures below 30 C, sometimes well below (Fig. 7). The reason that photosynthesis is less responsive to temperature is partly due to the fact that some of the key chemistry is photochemical and photochemical reactions are not strongly dependent upon temperature. An additional factor is that carbon dioxide, a reagent in photosynthesis, must dissolve in water to make it to the site of photosynthesis (the chloroplast) and the solubility of carbon dioxide decreases as the temperature increases. Because of this, C4 plants, which have mechanisms to concentrate carbon dioxide, generally have higher temperatures for peak photosynthesis than C3 plants.

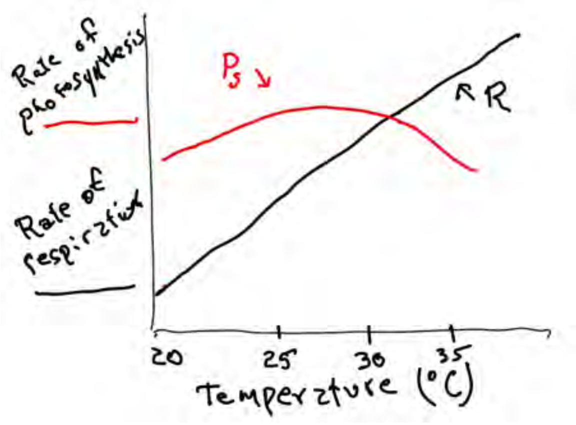

Fig. 7 The influence of temperature on the photosynthetic and respiration rates of a typical C3 plant.

When considering the effects of temperature on photosynthesis, respiration and growth, one can consider photosynthesis as 'making food' and respiration as 'eating food'. As temperature increases in the 25-35°C range, plant appetite continues to increase rapidly while the rate of food production levels off or declines. The net effect of this is that at higher temperatures there is increasingly less food to power new growth. Consequently, plant growth often tails off at temperatures lower than one might expect.

Psychophiles, Cryophiles and Thermophiles

A number of organisms, in particular certain bacteria but also some fungi and protists, are termed 'psychophiles' or 'cryophiles' because they do best at low temperatures, sometimes at temperatures below freezing. While the basic pattern of increased activity with increased temperature holds, the range of activity is shifted to much lower temperatures: 0 to 10°C and sometimes -10 to 0°C. These organisms have modified membranes and, for the ones that operate below freezing, antifreeze compounds that allow them to operate at such low temperatures. Since a very common mechanism of food preservation is low/freezing temperatures, these organisms may pose problems for the food industry. A cryophilic fungus has turned out to be the culprit in the 'white-nose disease' of bats (Fig 8) , a disease that has recently decimated populations of bats that overwinter in caves with temperatures in the 5-15°C range. The bat's behavior of lowering body temperature during the winter (in order to save energy) has provided these fungi with perfect conditions for growth.

Fig. 8 A dead bat with the characteristic 'white beard and mustache' caused by the hyphae of a psycophilic fungus.

At the other end of the tolerance range are thermophiles, who operate well above the normal activity range of 0-35°C. As with psychophiles, the vast majority of thermophiles are prokaryotes, most often archaea, but there are some thermophilic eukaryotes, all of them fungi. Several of these thermophilic fungi are important components of large-scale composting operations important to the production of commercial mushrooms where the metabolic heat generation of the compost can elevate the temperature of the mulch to 80°C.

Fruit Ripening

One additional process affected by temperature will be mentioned because of its commercial significance: fruit ripening. In addition to the influence of temperature on the growth of fruits, the temperature continues to affect fruits after growth ceases, in the developmental process we describe as ripening. This process brings about important changes in characteristics (aroma, color, taste, texture) that are of significance to both consumers and producers. This developmental process is often controlled in various ways by temperature, and temperature can have a significant impact on the commercial value of a variety of fruit crops by influencing the appearance of both desirable and undesirable traits. In a more general sense, the temperature can influence the ecologically significant characteristics of fruits that affect their role in seed dispersal by influencing their attractiveness to frugivores.

Temperature as a Cue

For many plants, and some fungi and protists, temperature provides an important cue that is used to coordinate growth and other activities with seasonal changes in conditions. Just as gravity organizes plant activity in space, the temperature can coordinate plant activity in time. In this situation, the temperature is not just a condition that the organism responds to, it is a signal that conveys information about what conditions will be like in the future, similar to the way that daylength (photoperiod) can provide information about the coming seasons. However, since the noise in the temperature signal is substantial, using it to predict future conditions is more complicated: a return to warm conditions after cold ones could be a January thaw or it could be a real (spring) thing. For many plants, spring is sensed as a warm period after a measured period of cold. An example of this is seen in the germination patterns of many seeds. The seeds of most plants are shed in a dormant condition. Although some seeds don't have specific germination requirements, they simply need a few weeks and they are able to germinate (this has been selected for in many crop species), many seeds require specific conditions or a series of specific conditions in order to germinate. Especially in temperate habitats, it is often a cold temperature treatment that will 'break' dormancy, i.e., allow the plant in the seed to resume growth (Fig. 9). This pattern is beneficial because it would prevent seeds from germinating and thereby becoming susceptible to cold until after the harsh conditions of winter. Because the original horticultural practices developed to break seed dormancy involved layering seeds and keeping them moist and cool, such treatment is termed 'stratification'. The key part of the treatment is the temperature treatment, not the layering. Contrary to the normal metabolic pattern, where activity is promoted by warmer temperatures (i.e., warmer temperatures produce more response than lower ones), in the stratification response, activity is promoted by lower temperatures, with colder temperatures having greater effects than higher ones. Typically temperatures need to be below 50°F

(10ºC) to be effective and become more effective as the temperature decreases down to 0ºC. Temperatures below 0ºC, and temperature treatments when the seed is dried out, are not effective, indicating that metabolic activity is essential for the response. The process can be modeled in a manner similar to growing degree days, except in this case what is accumulated, termed '**chill units**', requires temperatures below a certain threshold (typically 10ºC), and more chill units are accumulated as the temperature decreases down to 0ºC. When a seed accumulates enough chill units its dormancy is broken; at this point, the embryo's behavior is typical of most organisms, and activity (growth) is promoted by warmer temperatures.

Besides breaking the dormancy of the embryos in seeds, cold treatments are also a very important cue in breaking the dormancy of shoot apical meristems (buds). Home gardeners often bring shoots of flowering trees and shrubs (e.g., apple) indoors to 'force' them to flower early (Fig. 10). This practice works as long as the shoot has been exposed to cooler temperatures for a long enough length of time prior to warming it up. Shoots often will not force in December but will in February. The exact amount of 'chill time' that a shoot needs before it will respond to warmer temperatures varies. This phenomenon is a reason why certain trees may not be able to be grown in southern latitudes: they never receive enough cool temperatures to cause them to emerge from dormancy.

Accumulation of chill units is also a cue for some plants to flower, a process termed '**vernalization.**' In some situations the cold treatment itself is the trigger for flowering; in other situations, the cold treatment simply flips a switch and allows the plant to flower in response to a second signal (e.g., photoperiod) that previously would not elicit any response.

Temperature's effect on other conditions

Temperature is also important because it interacts with a number of other conditions. In terrestrial habitats the most significant interaction is between temperature and moisture. Temperature affects evaporation, and occasionally condensation, rates. Evaporation occurs when an individual water molecule is moving fast enough to escape the cohesive forces of its neighbors. Since the velocity of molecules is a function of temperature, the warmer it is the more likely evaporation is to occur. The tendency of a substance to evaporate is reflected in a property called vapor pressure, which measures the amount of the substance (in this case water) present in the vapor state when the liquid and air are in

Fig. 9 Germination of osage orange seed following cold

temperature treatment

Fig. 10 A stem from an apple tree that typically becomes active (breaks bud, starts growing, and producing flowers) in April can be induced to flower if stems collected in February are put in a warm environment. But twigs collected in January will not flower because they have not accumulated enough chill units.

equilibrium. Figure 11 shows the very strong effect temperature has on vapor pressure, reflecting temperature's ability to influence evaporation.

Under certain circumstances, evaporation will be directly related to vapor pressure and consequently would roughly double with each 10°C rise in temperature. In environments where lost water is difficult to replace, temperature can be of great significance to desiccation rates and the survival of organisms. For plants and fungi, the combined factors of temperature and water availability are of utmost importance in determining species abundance and activity. Note that although the temperature has a major influence on evaporation, other factors are also important including the humidity of the air, the sur-

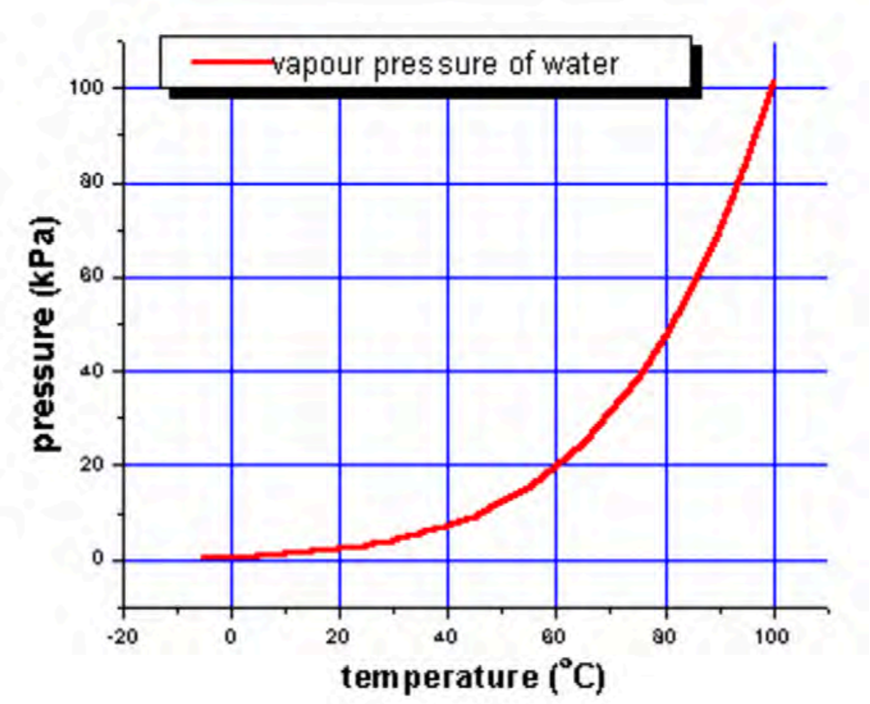

Fig. 11 The effect of temperature on the vapor pressure of water, its tendency to evaporate.

face area of contact between the air and the water, and the degree of mixing (convection) of the air above the hydrated surface. Finally, although temperature affects evaporation, evaporation, in turn, affects temperature. In the case of plant leaves, evaporation can cause leaves to be significantly (over 2° C) cooler than the air temperature.

Temperature also affects the availability of certain compounds by affecting their solubility in water. While the solubility of many solids in water increases with higher temperatures, the opposite is true for gases, and in particular for carbon dioxide and oxygen. This is particularly significant for photosynthesis and, as described above, is part of the reason why the response of photosynthesis with increasing temperature is not comparable to that for respiration even though both involve a host of enzyme-mediated chemical reactions that generally are enhanced at higher temperatures.

Another situation where the decreased solubility of gases at high temperatures can be a problem is flooded soils. The effect of flooding is more damaging at high temperatures than at low ones. Several factors contribute to this: (1) decreased solubility of oxygen at higher temperatures, (2) increased rates of soil respiration (carried out by the sum of organisms present in the soil—plant roots, fungi, bacteria, protozoans, etc.) at higher temperatures. Increased respiration means decreased oxygen (3) increased oxygen requirements for plant roots because of the higher metabolic rates associated with higher temperatures.

Water and Terrestrial Habitats

Along with temperature, moisture is a key environmental variable dictating the distribution of organisms on terrestrial habitats. The reasons for this should be clear:

- water is an essential component of living tissues and a reagent in many essential reactions, including photosynthesis and ATP hydrolysis
- in terrestrial habitats, water is nearly always lost to the atmosphere in the process of evaporation
- for terrestrial autotrophs, who obtain carbon dioxide from the atmosphere, evaporation is all the more likely to occur since these organisms must expose themselves to the atmosphere to acquire carbon
- for plants and animals, water is the medium in which materials move when transported and, for animals, water is the basis for excretion

Tolerance to drying

The vast majority of organisms maintain their moisture conditions at a particular level through the familiar process of homeostasis. Most plants (and most organisms in general) would be considered **homiohydric**, i.e., they maintain their water levels at a 'set point'. To do this requires that an organism adjust either water gain or water loss. To a limited extent, plants adjust water gain: when they get drier, the driving force for water absorption is increased and this can result in an increased flux (remember the flux equation!). However, plants have only a fairly limited ability to 'get drier,' and when they start to desiccate their most significant adjustments involve reducing water loss rather than increasing water gain. When plants experience water deficits their response is to reduce water loss by: (1) reducing the permeability of the plant to water by closing stomates, and (2) reducing the surface area for loss, generally by shedding leaves. Again, remember the flux equation and how these changes relate to it. Leaf loss is especially obvious in seasonally dry habitats where woody species lose all their leaves and herbaceous species spend the dry season as bulbs or other underground parts, both groups producing and possessing leaves only when conditions are mesic.

These measures to reduce water loss come at the price of reducing a plant's ability to feed itself. The very significant effect that moisture has on plant distributions reflects the fact that individual, population and species success involves balancing water loss and carbon gain. In some situations, a species may be successful by being able to acquire 'its own' water source. Alfalfa and mesquite roots often penetrate deep enough to tap groundwater sources unavailable to other plants. However, a majority of plants in an area share a common water source, the soil, i.e., the roots of many species are occupying the same volume of soil as other species, making the supply of water uniform for most species living in an area. Consequently, conservation by one species or individual only leaves water that can be taken by other species. Species are successful by manag ing their overall growth and patterns of growth. This represents an area of diversification between different species.

Homeohydric organisms are intolerant of desiccation and die if their water status drops below a certain level; most plants cannot recover from a loss of 10-15% of their water. Probably the main reason for this in vascular plants is 'catastrophic xylem dysfunction' which is a consequence of cavitation and positive feedback loops related to cavitation. Recall that individual vessels and tracheids may cavitate if the water in them is pulled too forcefully, the result of water loss at a time when there is a restriction of water acquisition as the soil dries. Cavitation results in a loss of part of the xylem conducting system and this makes cavitation more likely in the remaining conducting elements (see the flux equation): increased resistance to flow as a result of cavitation means that there has to be a greater pull (higher tensions) in order to acquire the same amount of water. Thus there is a positive feedback loop: cavitation makes more cavitation likely which will make more cavitation likely. Catastrophic xylem dysfunction (no ability to transport water) may result quickly after the first cavitation event, leaving the plant with little to no ability to rehydrate itself.

There are a small number of organisms, including a very few animals (tardigrades), some protists, and a few plants, that are poikilohydric: their water status is not strongly regulated but is allowed to assume the level dictated by the environment that they are in. Obviously, these organisms can only be successful (assuming that they live in an environment that dries out at least some of the time) if they are tolerant of desiccation, a phenomenon that is very rare in organisms, although they may produce parts like spores and seeds that are tolerant. Poikilohydric organisms can lose up to 90% of their water yet are still able to revive themselves when water again becomes available. The only plant groups where desiccation tolerance is common are in the non-vascular plants, in many mosses and some liverworts (ironically groups that are often considered to be restricted to moist environments). Desiccation tolerance is also present in a few clubmosses (Fig 12, 13) and ferns (Fig 14, 15) and in a very few seed plants.

Fig. 12 A dehydrated 'resurrection plant', a type of clubmoss the rolls up into a ball when tolerating extreme drought.

While there are some mosses that are restricted to moist habitats, most are desiccation-tolerant and many are particularly prominent in arid situations, both arid habitats (deserts) and arid portions of more mesic habitats, e.g., growing on rocks that have no ability to store water. Some of these species do have features to lessen water loss, e.g., a drying response that involves coiling of 'leaves' around the stem, lessening the surface area exposed to the atmosphere. Nonetheless, many mosses are capable of tolerating extreme desiccation and the whole organism, not just a select part,   can remain viable after undergoing repeated cycles of desiccation. They are inactive during dry periods but are able to quickly resume activity when moistened.

Fig. 13 The desert clubmoss after greening up and opening up..

Tolerance of flooding

At the other extreme, terrestrial organisms can be affected by excesses of water. Generally this is an indirect effect of a lack of oxygen that was discussed above when considering the interactions between temperature and oxygen.

Water in Aquatic Environments

Salinity

One might assume that there are no problems associated with water in an aquatic environment since water is abundant. However, water does play an important role in dictating the organisms present in any particular aquatic environment, primarily because of the process of diffusion. Because water tends to diffuse from regions where it is purer to

Fig. 14 A desiccation tolerant fern shown in dry conditions

regions where it is less pure, living things are strongly affected by the purity of the water that they live in, and this is primarily determined by the water's salinity. All life has the ability to both accumulate and to generate solutes, and therefore the water in organisms is decidedly impure. Consequently, if organisms are placed in pure water, water diffuses into them. The influx of water has two potential results: one is chemical, the cell solutes become so dilute that normal functioning is impeded; the second is mechanical, the influx of water can cause the organism to swell and ultimately burst. However, if the organism is enclosed in a rigid container the influx of water pressurizes the organism and the flow of water ceases with only modest changes in volume. Another possibility that allows organisms to live in 'fresh' (i.e., pure) water is to have mechanisms that allow water to be expelled from the organism at the same rate that it enters.

The problems associated with the diffusion of water into organisms are eliminated if the purity of water is the same outside as it is inside the organism, and there are a number of organisms (many marine animals, some protists) that only live in such an environment, where the purity of the cytosol is comparable to that of seawater.

Fig. 15 The same location as figure 14 but now under moist conditions.

There also are habitats, termed saline ('salty', although the salt need not be NaCl) habitats that have a water purity even less than that of most organisms. Most forms of life are excluded from such saline environments because diffusion causes them to lose water and they cannot tolerate the decrease in the internal water content that results from water loss. Organisms that are able to tolerate such environments do so by having more than the normal concentration of solutes in their cytosol, generally adding unique solutes that are typically not found in living things.

The problems of life in saline environments are not restricted to reduced water content. Additional problems stem from toxic concentrations of the solutes that make the habitat saline. Generally, this would be sodium and chloride ions but there are habitats where other solutes (e.g., potassium, calcium) are damaging. With the exception of sodium, which most plants don't require, these elements are essential for living things, but at high concentrations they can interfere with normal cellular or organismal functioning and become toxic.

Oxygen and Aquatic Environments

Oxygen is of key importance in aquatic environments. Oxygen readily dissolves in water but its solubility is such that oxygen is generally less available than in terrestrial habitats. More significantly, its abundance varies much more in aquatic habitats than in terrestrial ones. In terrestrial environments the oxygen levels of the air rarely change much because of convectional mixing (winds), due to the much lower density of air compared to water, and, to a lesser extent, due to the much more rapid rate of diffusion in gases. Processes (primarily biotic ones) may increase or decrease oxygen levels slightly but rapid mixing with the huge reservoir of oxygen in the atmosphere as a whole maintains the concentration of oxygen in the air at the normal values of slightly below 20%.

In contrast, liquid water is much denser, its movement is much more sluggish and consequently, the possibility of localized areas in aquatic habitats with varying oxygen concentrations is much more likely. Under certain situations aquatic habitats will be saturated with oxygen, i.e., holding all the oxygen that can dissolve in water, an amount that is temperature-dependent and decreases with increasing temperature. As would be expected, water is saturated with oxygen when the air and water are in close contact (i.e., the surface of bodies of water) or in situations where photosynthetic rates are high, thus increasing oxygen levels (generally these areas are also close to the surface). However, there are lots of aquatic situations where the amount of dissolved oxygen is not at saturation. Generally, this is due to the depletion of oxygen by living things and the lack of mixing with water that is in contact with the air, a situation found at the bottom of lakes, in slow-moving streams, and waterlogged soils. Impediments to mixing will make oxygen depletion more likely. One of the most common impediments are water density gradients, the result of temperature differences. Less dense water 'floats' on more dense water and this will reduce oxygen transfer from surface waters to the denser water below. The density of water decreases as the temperature increases from 4 C; hence, in this range, warmer water is less dense than cooler water and a consequence of this is that the water is layered ('stratified') during the times of the year that it is being heated from above, during the summer in northern latitudes, all year round in the tropics. The wind may cause turbulence in the water column and mixing but the penetration of mixing is limited by the density differences. The greater the temperature differences between the top and bottom, the more resistant the lake is to mixing. Because of this stratification, the bottom layers of a lake may become depleted of oxygen because they do not mix with the oxygenated water at the surface. In tropical areas, low oxygen levels at the bottom of lakes occur year-round, but in temperate areas, mixing, and as a result aeration of the bottom layers, becomes increasingly likely during the fall. This is because, unlike the heating of the summer, which reinforces the stratification by making the top warmer, cooling breaks down the stratification by making the surface denser. As long as the lake is in a location that cools enough, the lake will eventually become 'isothermal', i.e., the same temperature throughout the water column. Being isothermal also makes the lake the same density from top to bottom and, as long as the wind blows hard enough (how hard depends on the depth of the lake), the lake will 'mix', bringing aerated water from the bottom to the top. This is significant from a nutritional standpoint because organic material settles to the bottom of the lake and decomposes there. Minerals released by decomposition are only distributed throughout the water column when the lake is mixed. Further cooling of the lake in late fall (northern hemisphere) once again results in stratification, as the density of water decreases (and the colder water floats on top) when the temperature drops from 4 to 0 C. If the lake freezes, the addition of an ice layer eliminates any wind-driven mixing whatsoever and oxygen levels at the bottom of the lake once again drop if respiration exceeds photosynthesis. This is usually the case (although some photosynthesis does take place in ice-covered lakes, it is relatively low because of decreased light penetration). In the spring (in the northern hemisphere) heating of the surface first eliminates the ice and then eliminates the stratification, making the lake uniform in temperature and density at 4 C, and again allowing for mixing by the wind. Further heating causes the lake to again become stratified. Thus lakes in temperate habitats have an annual cycle that includes two brief periods in the fall and spring where mixing is very likely, so long as the wind blows and the lake is not too deep. This situation, termed spring and fall 'turnover', is highly significant because it allows for mixing of the water column, bringing oxygenated water to the bottom of the lake (and also bringing minerals to the top of the lake (see below).

Another hindrance to water mixing is material that restricts water movement. Sphagnum bogs usually have oxygen -depleted water at very shallow depths of a few centimeters, depths that usually receive ample oxygen from the close contact with the atmosphere because of mixing caused by even slight winds. However, a sphagnum mat hinders the movement of the water column and although the oxygen-rich atmosphere is centimeters away, oxygen levels drop to nearly zero at very shallow depths. A similar thing can happen in ponds that are covered with a thick 'pond scum' of algae. The low oxygen conditions hinder decomposition and result in an accumulation of organic material ('peat') and low levels of nutrients.

Light and Aquatic Environments

As is the case in terrestrial environments, light plays an important role in dictating the distribution of photosynthetic organisms. It is even more important in aquatic environments because significant differences in oxygen concentrations can develop within the water column, depending upon the balance between photosynthesis and respiration. Light intensity is influenced by the depth and transparency of the water, the latter often being strongly influenced by the number of living things living in the water. Since aquatic photoautotrophs need light to survive, they need to be in the upper levels of the water, or, in the case of some flowering plants, float on the surface or even emerge from it. Phytoplankton (small photosynthetic organisms that 'float' in the water column) need to have features that prevent their settling. Features that are sometimes significant are large surface area to volume ratios (i.e., not spheres), oil or air bodies that decrease density, flagella and phototaxis (movement towards light, see cryptophytes). Some phytoplankton are known to migrate up and down diurnally, moving up to gain more light during the daylight hours.

Currents and Aquatic Environments

Currents are very significant in some aquatic environments and can have a strong influence on community structure. Currents are significant because they can mix portions of the water column, in particular, they can bring oxygen from the upper layers to the lower layers and nutrients from the lower layers to the upper layers. This is significant because oxygen may be limiting in the lower layers and nutrients may be limiting in the upper layers. Consequently, the current can substantially change the activities taking place.

Nutrients and Aquatic Environments

Nutrients are often limiting primary productivity and consequently total activity in aquatic situations. This is a result of the fact that most aquatic environments have two distinct parts: the upper layers where photosynthesis occurs and where inorganic nutrients are incorporated into biomass, and the bottom region, where there is typically little photosynthesis, but where biomass from the upper layers tends to settle, decomposition occurs, and nutrients are released. In such a system the activities of both the top and bottom can be limited by a lack of interaction between the two parts: the upper layers are limited by a lack of nutrients, hence little accumulation of biomolecules occurs; the bottom layer becomes limited by a lack of material to eat.

Nutrients transported into aquatic systems can be very important. Nutrients can be carried into aquatic systems by runoff from the surrounding land, especially agricultural land where nutrients are added through fertilization. Nitrogen and phosphorus often play key roles in determining the amount of primary production occurring and the total amount of biological activity taking place. However, as was the case in terrestrial systems, there are circumstances where other nutrients can play key roles.

Further Reading and Viewing

- “How Does Deep Water Rice Solve Its Aeration Problem” by Ilya Raskin and Hans Kende. How rice solves its aeration problems.
    - https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1066254/
- “Mushrooms as Rainmakers: How Spores Act as Nuclei for Raindrops” by Maribeth O. Hassett et al. Mushrooms as rainmakers.
    - https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0140407
- “Deciduous Trees Allow Higher Seasonal Water Yields: Flowering Plants” by Leon Wang. Deciduous tree influence on water storage in forests.
    - https://asknature.org/strategy/deciduous-trees-allow-higher-seasonal-water-yields/
- “Hydraulic lift: a potentially important ecosystem process” by JL Horton et al. Hydraulic lift, an interesting plant induced water flow.
    - https://pubmed.ncbi.nlm.nih.gov/21238277/
- “Horizontal transfer of an adaptive chimeric photoreceptor from bryophytes to ferns” by Fay-Wei Li. An amazing evolutionary story of horizontal gene movement related to adaption in low light environments.

  - https://www.pnas.org/doi/10.1073/pnas.1319929111

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CHAPTER 27: BIOTIC INTERACTIONS

Interactions between individual organisms

Organisms interact with each other and these interactions can have significant consequences to the participants. Most students are familiar with the classification scheme below which organizes interactions into types based on the consequences of the interaction on the two participants:

		effect on the ‘larger’ organism		
		(-) negative	(0) neutral	(+) positive
effect on the ‘smaller’ organism	(-) negative	competition	amensalism	predation, herbivory
	(0) neutral	amensalism	‘neutralism’	commensalism
	(+) positive	parasitism	commensalism	mutualism

There are multiple problems with this scheme and the definitions that stem from it. Larger vs. smaller is sometimes an arbitrary distinction. It is not clear what level, organism or population, it is focused on or how effects might be measured. At the level of individuals ‘ positive’ might be monitored by organism size, growth rate, longevity or reproductive success. But at the level of populations one might monitor population density or population growth rate. Sometimes what is ‘positive’ and what is ‘negative’ may not be obvious. A bird eating a poisonous butterfly is negative to both the individual butterfly and the bird, but at the population level one could argue that it is good for both the bird and butterfly populations. Some fungi living in plants (endophytes) substantially increase the growth of plants that they infect (positive effect), yet at the same time reduce or eliminate the likelihood of producing offspring (negative effect). Nitrogen-fixing bacteria infecting roots may benefit plants (faster growth, bigger plants) if soil nitrogen is low, but harm plants (slower growth, smaller plants) if nitrogen levels are high. Pollinator visits may benefit plants if they transport pollen to other members of the same species but not if their next visits are to different flower species.

Fig. 1 Do wolves harm or benefit prey?

Perhaps the most significant biological context for the terms would be evolutionary (positive = enhanced reproductive success) but this may depend on circumstances that are difficult to evaluate. Predators (Fig. 1) would generally be thought to have a negative on prey populations, but in a number of situations, predators are thought to 'benefit' prey populations by preventing overpopulation. Seed predation (e.g., Clark's nutcracker eating pine seeds, Fig. 2)) is clearly harmful to the individual pine organisms (i.e., the embryonic pine individual present in a seed) but apparently benefits the pine populations by allowing for dispersal. In short, the terms defined in Table 1 are not always useful.

Another way to organize biotic interactions is not based upon arbitrary considerations of what 'benefits' or 'harms' the organisms/populations involved, instead, it is based upon the medium through which the interaction occurs:

- trophic interactions—one organism eats another or part of another, obtaining material (carbohydrates, proteins, fats) that can be used both for energy (i.e.,

Fig. 2 Do individual pine seeds benefit from their interaction with Clark's Nutcracker? Obviously some don't (the ones eaten), but a few do.

burned in cellular respiration) or partially broken down and reformed into molecules of the consumer

- resources/conditions interactions—Resources are materials (e.g., oxygen) that an organism either produces, making them available for other organisms, or depletes/ consumes, making them less available for other organisms. Conditions are physical parameters, e.g., pH, temperature, humidity, light intensity. Conditions influence organism behavior, and organisms can change conditions and thereby affect other organisms. Resources and conditions are combined here because several can be considered both as a resource and a condition. Oxygen can be considered a resource because oxygen can be produced or consumed but it also is a condition that has physical consequences, e.g., oxygen concentrations affect the solubility of ions in the soil solution. Similarly, light is a resource that plants 'consume', reducing its availability to the shaded plants below, but it also is a physical condition that influences all organisms in a number of ways.
- work interactions—one organism does work for another organism (work in the

sense of physics and chemistry, a process that requires the expenditure of energy, e.g., moving material from one place to another, or producing a particular chemical or a physical structure).

TOPICS

- Trophic interactions
    - Predation
    - Grazing
    - Parasitoids
    - Parasites
    - Leftovers
- Interactions involving resources and conditions
- Work interactions

Trophic Interactions

Although all trophic interactions are 'organism A "eats" organism B', resulting in a transfer of material from A to B, the way the eating is done varies greatly—most familiar organisms (i.e. animals) ingest into an internal tube where digestion occurs and the products of digestion are absorbed across membranes and into the eater. Most fungi digest outside and then also absorb digestion products. For both familiar animals and some fungi the process of killing of prey releases nutrients that can be absorbed with relatively little digestion. And a few organisms, e.g. blood parasites, tapeworms and some fungi, manage to get to and live in a place where nutrients are available without digestion.

As will be seen in some of the examples below it may be the case that the most significant consequences of the trophic interaction do not involve material gain and loss.

Below are four categories of trophic interactions. The categories are based on the manner of the interaction between the two 'players': the organisms doing the eating ('eater') and the organism being eaten (the 'eatee'). In two categories, predation and parasitoids, the eatee is killed because of the interaction, while in the another two categories, grazing and parasitism, the eatee is not necessarily killed. And in a final category, ('saprophagy') the eatee was killed prior to the eating event. An assumption that holds most but not all of the time is that the eater always benefits. However, sometimes the material ingested is toxic or contains pathogens. As for the eatee, in predation and parasitoids it is clear that the individual is harmed, but, as mentioned above, the consequences may be different at the population level.

Predation

Fig. 3 Red crossbills have a specialized bill that allows them to open the cones of conifers and predate on the seeds inside.

This trophic interaction kills prey (the 'eatee', the organism being eaten) and the eater, the predator, consumes multiple prey items during its life (Fig. 3). All forms of life (even predators) are subject to predation but for plants this most commonly occurs when the eatee is small: when they are pollen (tiny haploid male plants), seeds ('seed predation'), or in the consumption of seedlings. The materials found in a pollen or seeds are particularly nutritious per unit weight because, compared to larger plants, they have relatively less structural material (i.e., cell walls) and relatively high concentrations of minerals and vitamins. Similarly, fungal spores as prey items are more nutrient rich than the hyphal strands. Predation is very important in aquatic systems where the base of the food chain are typically phytoplankton (unicellular photosynthetic autotrophs: cyanobacteria, diatoms, cryptophytes and unicellular green algae) that are preyed upon by zooplankton.

In predation the eater benefits from the nutrients and energy obtained (assuming that eatee does not contain toxins that the eater cannot handle) and the eatee is eliminated. For as long as seed plants have existed this interaction has driven evolutionary changes involving chemical, physical and phenological (timing) changes in plants, and consequent changes in predators. Particularly significant to plants is the fact that this interaction has developed into a means of dispersal, e.g. the consumption of pollen led to the development of pollination, with the eater transferring pollen from one plant to another. Although not as ubiquitous, a similar situation has developed into a mechanism of seed dispersal, utilizing an eater's mobility and perhaps its caching behavior (see the reading on pines and the Clark's Nutcracker). Both of these interactions are discussed below as 'work' interactions. Similarly, seed predation also was a driving force in the development of fleshy fruits as a means of seed dispersal: plants developed features that would reward the eatee in a way that did not involve (permanently) consuming the seed and killing its embryo. Seed predation also accounts for some fruit structures that protect the seeds inside (e.g., nuts), although seed predators have responded by developing structures (sharp teeth of saki monkeys or beaks of goldfinch, Fig. 4) and behaviors that allow them to open seeds, or digestive systems that grind the seed coat or fruit coat away.

Although one hears of 'carnivorous' or 'predatory' plants, the names are misleading. These plants certainly do kill 'prey' but they do not obtain food from them, in the sense of materials that can be utilized in cellular respiration. Predatory plants are photosynthetic autotrophs and their food (carbon and energy) requirements are satisfied by photosynthesis. For these plants 'predation' is connected to mineral nutrition. This is discussed further below as involving changes in conditions.

There are some photosynthetic organisms that are also heterotrophic (i.e. they are mixotrophs). Both the euglena and dinoflagellate groups include predatory members, some of which are also capable of photosynthesis. [Note that the adjective 'mixotrophic' can be applied both to these two groups and also to specific organisms within these two groups, i.e. both these groups have three types of organisms: solely photosynthetic, solely heterotrophic, and members that can be both depending upon circumstances.] The predatory dinoflagellates and euglenoids capture prey via phagocytosis. In addition, some dinoflagellates kill prey with toxins and then digest and absorb them. And a few of each group could be considered both parasites and parasitoids, defined below.

Considering the solely heterotrophic groups considered in this text, cellular and plasmodial slime molds are sometimes predatory and a few fungi are predators in the classic sense (i.e., they capture prey and kill them, http://www.mykoweb.com/articles/Fungal-Snares.html). Although they don't capture prey in the classic sense, plant pathogens that are described as 'nectrotrophic' (see Chapter 30) are predators that kill plants and then consume them. Examples include: *Pythium*, a water mold (Oomycete) that causes 'damping off' of seedlings; the ascomycete fungus that causes dutch elm disease; and the ascomycete fungi that cause wilt diseases in tomatoes. The pathogen may produce toxins that kill cells, and eventually entire organisms, or, in the case of the wilt diseases and of dutch elm disease, produce chemicals that plug the xylem tissue and eventually kill the plant by preventing water transport. Other pathogens of plants might be considered parasitoids or parasites, discussed below. But the majority of inanimate heterotrophs are saprophytes, also described below.

Fig. 4 American Goldfinch is commonly feed on thistle or sunflower 'seeds' (actually fruits) at feeders, but can eat a wide variety of species, including many grasses.

Grazing

The eater (grazer) does not kill the eatee, but only eats part of it, and usually, the grazer eats parts of several individuals. Most familiar examples of herbivory (eating of plants) are grazing: cows eating grass, deer eating shrubs, Japanese beetles (Fig. 5) eating ornamental plants. While most familiar grazing is on plants and on their leaves, organisms graze on other plant parts: stems, flowers, roots. And a lthough plants are the most common kind of organism grazed upon there are several other 'inanimate' groups that are grazed: photosynthetic protists ('algae', in particular ones that are 'large' by being multicellular, colonial, or siphonaceous). A few non-photosynthetic protists e.g., plasmodial slime molds, and many fungi are also grazed. Grazing is most likely to occur on organisms that have indeterminate growth.

Fig. 5 Japanese beetles damage but usually do not kill the plants that they feed upon.

Grazing affects the eatee in two ways: by the loss of structure that is used to acquire matter and energy (e.g. leaf loss in photosynthetic plants), and also because of the loss of nutrients (e.g., nitrogen and phosphorus) that are removed by grazers and are relatively hard to replace. Too much grazing can be fatal for the eatee but lesser amounts of grazing sometimes actually produce 'beneficial' (depending upon definitions and perspectives!) results; for instance, grazing of apical meristems can induce branching and produce a plant that actually produces more leaves, flowers and fruits. Artificial grazing, i.e. pruning, is a very common horticultural technique to improve yield and quality.

Fig. 6 A leaf hopper, a grazer that often spreads disease from one plant to another.

One particularly significant aspect of grazing is that it is a means of disease transmission between individuals, such as a mosquito (a grazer) spreading malaria. Leafhoppers and aphids are both insects that have piercing mouthparts to acquire nutrients from phloem tissue in leaves and stems. If they move from an infected plant to another plant they can transmit pathogens (viruses, bacteria and others) in the process, and often this is the most significant aspect of their grazing (Fig. 6).

Parasitoids

Fig. 7 Granary weevil—a seed predator of cereal grains (e.g., wheat, rice). Adult females drill through the wall of the fruit and deposit a single egg which, when hatched into a larva, consumes the seed contents and then emerges as an adult.

The distinctive feature here is that the reproduction of the eater is obligately and directly associated with the trophic event and also that the eatee dies as a result of the association. While any heteterotroph must consume food in order to acquire the matter and energy needed to reproduce, in the case of parasitoids the connection is direct because a propagule (usually a fertilized egg) is deposited on the eatee. Another feature of parasitoids is a determinate life cycle where the final stage of development involves reproduction and the demise of the host (cf. to parasites, discussed below). The vast majority of parasitoid interactions involve insects, one as the eater and another as the eatee. But there are a number of cases from the realm of inanimate life. Some dinoflagellates could be considered parasitoids on nematodes. And a number of fungi that are described as 'entophagous' (= insect eating) are parasitoids. Probably the most famous one of these is *Entomophaga maimaiga*, that is used as a biocontrol agent for gypsy moth. Spores of *Entomophaga* germinate on the caterpillars of gypsy moth, grow through the cuticle and produce a mycelium that consumes the entire caterpillar and eventually produces condidia that are dispersed through the air to other caterpillars. In addition to being predators on nematodes there are some fungi that could be considered parasitoids on nematodes, the distinction being that predators capture and kill prey and parasitoids 'enter' and then kill prey. There are also some chytrids that might be considered parasitoids, with some attacking both pollen and unicellular algae (phytoplankton). Interestingly, the zooplankton that normally feed on phytoplankton may switch to eating chytrids, thus there appears an additional link in the food chain (phytoplankton–>chytrids–>zooplankton). Another fungal group that could be described as parasitoids are some of the smut fungi. It should be noted, however, the range of lifestyles present in fungi makes the predator/parasite/parasitoid distinctions challenging.

A final parasitoid interaction to mention, because it is sometimes economically significant, involves insects eating seeds e.g., granary weevils (Fig. 7) and acorn weevils, where adult insects deposit their eggs in seeds (see this short video by National Geographic on the acorn weevil: https://vimeo.com/38056185).

Parasites

Fig. 8 The orange strings are dodder, a parasitic plant that connects to the phloem tissue of its host to acquire nutrients.

In parasitism, as in grazing, the eater generally does not kill the eatee, but in contrast to grazing, the eater generally only feeds upon one host and thus is not typically a means of spreading disease from one eatee to another. Evolutionarily, one might argue that parasites (and perhaps some grazers) adopt a strategy of keeping their host alive in order to assure a food supply for a longer time. Going one step further, it may be beneficial for the eater to make the eatee more vigorous, which is the case with mycorrhizae where fungi feed off their hosts but somehow allow them to grow more vigorously. Thus, although the eater in parasitic relationships always benefits because of the material gained, the effect on the individual eatee can range from increased longevity and vigor, through indifference (with no apparent influence on the longevity of the host), to definite adverse effects resulting from lost material and sometimes ultimately resulting in death. Looking at the classic scheme (Table 1) the bottom line depicts the multiple consequences of this type of trophic parasitism. The term parasite is also applied to situations that do not involve feeding (see the work interactions discussed below). Parasitic interactions abound and nearly all of the inanimate groups covered in this text are at times both the eatee and the eater. A few of the interesting cases are discussed below.

Red algae parasitize other red algae, often the parasitizing a close relative, a situation that is also common in insects. There are brown algae that parasitize other brown algae. There are green algal parasites of insects and dinoflagellate parasites of crabs. It is also interesting to note that the apicomplexa, a group that includes *Plasmodium*, the causal organism for malaria, along with other significant parasites of humans, are considered to be derived from a group of pigmented ancestors that also gave rise to the red algae and the dinoflagellates. Fungi are often parasites on a variety of hosts, notably plants and other fungi. And even some plants are parasites, both on other plants as well as on fungi, examples below.

There are a number of fungi called biotrophic fungi (see Chapter 30), including the important plant pathogens powdery mildews and rusts, that feed off of living plant tissue and would be considered parasites. They produce structures called haustoria that penetrate the cell wall and interact with the plant cell plasma membrane, providing them with access to materials (e.g., sugars, amino acids) present in the cytosol. Dodder (Fig. 9), a non-photosynthetic flowering plant, also produces haustoria. These penetrate into the phloem tissue of their hosts and provide them with nutrition. T he fungal component of mycorrhizae would be considered parasites, as would be the nitrogen-fixing bacteria that form galls in some plants. Indeed, most gall-forming organisms (insects, fungi, mites) would be considered parasites. The gall is an abnormal growth induced by the presence of the parasite. The parasite is fed by its host and ultimately exits the gall.

As an example see “The Amazing Tale of Sagebrush Galls” by Susan Ballinger at www.wenatcheenaturalist.com/sagebrush-galls/ or “Inside the Goldenrod Gal” on the Finger Lakes Land Trust blog at www.fllt.org/inside-the-goldenrod-gall/. Most of these interactions are similar to parasitoids in that the reproduction of the eater is dependent on the interaction; however, the host is not killed. In most instances, the eatee suffers because of a loss of nutrients, and the eater benefits because it is provided with nutrition and often with protection as a result of the structure of the gall.

Fig. 9 Galls on a sugar maple leaf. These galls are triggered by mites.

Saprophytes, i.e., eating 'leftovers'

All organisms are a source of food after they die and thereby represent an 'easily captured' prey item. Heterotrophs that consume material (plant, animal, fungal and others) that is already dead (i.e., they did not kill it) are termed saprophytes. Because plants are continually shedding leaves and roots (and in many cases stems), these discarded items are often abundant and provide food for a number of organisms. The nutrient quality of these discarded items is generally substantially below that of living tissues because the plant, in the process of senescence, recycles materials, retrieving much of the material present in the soon to be discarded item before it is actually shed. Leaf protein, nucleic acid and mineral concentrations all decline drastically before leaves are shed and the remaining material is much less digestible both because most of the molecules that remain (e.g., cellulose, lignin) are more difficult to degrade and because of the lack of nitrogen makes it hard to build up substantial populations of saprophytes. Organisms (especially larger ones. e.g., earthworms, insect larvae) feeding on dead organic material often obtain nutrition, perhaps most of their nutrition, from the consumption of much smaller organisms (e.g., bacteria, amoebae, fungi) that are present on the decaying material and not from the organic material itself, i.e., they are really getting their nutrition from being predators, not saprophytes. Bacteria and fungi are the most significant saprophytes in the soil but other groups (cellular slime molds, plasmodial slime molds and heterotrophic forms of euglenoids) may also be saprophytic. In aquatic systems, a significant amount of organic material can be broken down to the point that it dissolves and is present as dissolved organic material, which some organisms are able to assimilate.

Conditions/Resources Interactions

All organisms change the resources and conditions around them. The extent to which this affects other organisms depends on: how big the organism is (big things have more of an effect than small ones), how plentiful they are (i.e., their population size) and precisely what changes they bring about. Any organism is a 'producer,' i.e., it grows and produces a resource (i.e., biomass) that some other organisms can eat. Therefore all organisms must provide resources. Plants (and more generally autotrophs) are particularly important in a resource sense because, being the base of food chains, their activity represents how many trophic resources are available to entire communities. Also, except for autotrophs (who are 'self-feeders') all other organisms, i.e,. heterotrophs, eat something and can influence other species by depleting that resource. But there are many other ways that organisms interact with each other besides affecting trophic resources. Here are some examples:

The trees of a forest substantially change the conditions below them. Temperatures are moderated (cooler in the daytime, warmer at night). Wind is moderated. Rainfall/snowfall patterns are changed. For deciduous forests the annual deposit of leaves covers the ground surface and acts like insulation, keeping the soil warmer in the fall and cooler in the spring. In evergreen forests, leaves layer the ground but the fact that they do not come all at once alters the dynamics. Leaf litter affects soil chemistry. Thus different species can have different effects. The tipping over of a tree root system that occurs when trees are blown over changes the topography and exposes lower mineral layers. And some species (e.g., yellow birch) germinate best in mineral soil because the roots of seedlings are unable to penetrate a blanket of leaf litter.

Oxygen consumption by organisms in terrestrial habitats generally has little impact because the oxygen levels in the air are high (~20% of the air is oxygen) and because winds keep the air well-mixed and localized depletions are unlikely. In contrast, oxygen depletion in the soil and in some aquatic situations can have very significant consequences. In waterlogged soil, oxygen consumption by roots, fungi and a host of soil organisms, coupled with reduced oxygen movement in because of the soil's water-filled pores, can make the soil anaerobic. Similarly, unless there are processes promoting mixing of the water column, respiration by heterotrophs at the bottom of the lake, where organic matter settles, significantly lowers the oxygen levels, potentially affecting all organisms living there.

Fig. 10 Red bog moss (Sphagnum capillifolium) is a common species in bogs. Note the densely packed stems.

A globally significant example of organisms changing oxygen availability and consequently affecting other organisms involves Sphagnum moss and areas known as bogs. Sphagnum moss can develop high population densities and this, coupled with their pattern of growth, creates a dense mat of stems elongating at the top but with an extensive layer of dead stem and ‘leaf’ material below. The stems and leaves hold substantial quantities of water and water is also held in the spaces between plants, producing what is essentially a giant sponge. This creates a habitat of stagnant water, where there is little mixing of the surface layer of water with the water below. Consequently, at a very shallow depth, the water becomes anaerobic because of oxygen consumption by saprophytes feeding on the dead plant material. In addition, the chemistry of sphagnum cell walls causes the water to become acidic. The acidic conditions, combined with lack of oxygen, greatly reduce the decomposition of plant material, thereby reduc ing the supply of nutrients (remember that nutrients become available to plants because of decomposition), and cause peat (un-decomposed plant material) to accumulate. The soil conditions prevent a large number of species (e.g., trees) from existing in the area or causes them to have stunted growth. Instead, bogs have a characteristic group of species, often members of the blueberry family, that are tolerant of the soil conditions.

One of the types of plants found in the nutrient-poor conditions of a bog are 'carnivorous' plants including pitcher plants, which nicely demonstrate the nutritional distinction between autotrophs and heterotrophs. Heterotrophs obtain both 'food' (a carbohydrate supply for cellular respiration) and nutrients (e.g., nitrogen) from the material they consume. Carnivorous plants obtain energy through photosynthesis just as most plants do, making food in photosynthesis and then eating it. The significance of their 'predation' is that it provides carnivorous plants with nutrients (not 'food') that are otherwise hard to come by because of the habitats where they dwell. There are a wide variety of devices for capturing prey (generally insects), including pitchers, snap traps, flypaper, bladders and lobster traps (see more carnivorous plants at https://earthsky.org/earth/lifeform-of-the-week-carnivorous-plants-are-out-for-blood).

Pitcher plants have a highly modified leaf whose petiole serves as a container for rainwater. The pitcher also possesses features that attract and capture insects who eventually drown there. The water develops a decomposition community of bacteria, fungi, water molds, amoebae, insect larvae and others. As a result of their activity, nutrients become available in a forms that the plant can absorb. In contrast, nutrients do not become available to the roots due to the lack of decomposition in the waterlogged peat that pitcher plants are rooted in.

Dense growth of algal (usually cyanobacteria but sometimes green algae) can 'seal' the top of ponds, creating a situation comparable to sphagnum bogs because the wind is not able to induce mixing of the oxygen-rich top layers of the water with the lower layers. Because no light can penetrate the dense algal layer on top, no photosynthesis is possible except at the surface. These factors, coupled with the magnitude of dead plant material that is created by the algal growth and the decomposition of this material by heterotrophs below, cause the lower water levels to become anaerobic, eventually drastically altering the species present and limiting the rate of decomposition.

Fig. 11 An Ontario bog. The stunted trees are mostly larch and white pine. The red shrub is probably huckleberry. All of the plants are growing out of a waterlogged bed of Sphagnum.

Resources /conditions represent significant avenues whereby species can interact with each other. In particular, two species requiring the same resource can affect each other by making the resource less available for other organism/species. Plants interact with other plants by their consumption of light, nutrients and water. This is the classic explanation for an interaction described as 'competition' although there are other reasons besides resource depletion that might explain why the presence of one species might deter the growth of another species (or at the population level, where the presence of one population lessens the population density of a second population).

Globally, two of the most important biotic consequences involving resources are the addition of oxygen to the atmosphere by photosynthetic organisms and the addition of simple mineral forms of nutrients into the soil or aquatic systems as a result of the decomposition carried out by heterotrophs.

Plants provide resources in other ways; their physical structure is important to many other other species: birds nest in trees; many spiders use plant structures as a base for their webs; parts of plants and pieces of lichens are often used as building materials for nests.

Fig. 12 Plants don't just provide building materials (lumber) for humans, they provide them for a wide variety of organisms including osprey (above) and hummingbirds (below). The materials utilized include twigs, bark, vines, bits of leaves, parts of lichens. Many squirrels utilize branches and leaves to make their nests. Both birds and mammals utilize holes in tree trunks as nesting sites.

Work Interactions

A number of species interact with each other by providing services, i.e., doing work, for other species. For plants, the most significant of these results from organisms that provide mobility, mobility for male gametophytes in pollination and mobility for seeds. A nimals transport seeds both 'passively', when seeds or fruits stick to fur, and 'actively' when the plant attracts animals to a trophic reward (generally fruits, but sometimes seeds, Fig. 14) with the mobile animal then transporting the seeds and depositing them (often by defecating) some distance away. For the most part, pollination is active with the plant adver-

Fig. 13 A female ruby-throated hummingbird on its nest which has an outside coating of lichens.

tising a trophic reward, which may be nectar (a sugar secretion) and/or may be pollen. In the case of pollinators, not only are some species capable of moving pollen but they can do it in a very directed way, transporting it to members of the same species of plant, thereby allowing cross-pollination and cross-fertilization to occur. This specificity (i.e., mobility to a specific, favorable location) occasionally is the case for seed transport, e.g., Clark's nutcrackers transport seeds to sites that are particularly favorable for the growth of the pines whose seeds they are transporting; certain ant dispersed species bring about movement of seeds to sites (ant nests) that are particularly favorable for seedling establishment (Fig. 14).

While the common interaction is a 'quid pro quo' with food provided by the plant 'in exchange for' work by the visitor, occasionally the plant is providing a non-food reward. Some orchids provide specific chemicals that serve as pheromones for the insects that acquire them. The Yucca plant provides not only food but also a shelter for larval yucca moths that develop from the eggs that the yucca moth deposits as it is pollinating the plant. Ficus trees provide food and nesting sites for pollinators.

Two excellent sites that consider these interactions are:

- Yucca moth: https://www2.palomar.edu/users/warmstrong/ww0902a.htm
- Ficus: https://www2.palomar.edu/users/warmstrong/pljune99.htm

Fig. 14 Seeds of bloodroot have appendages called elaiosomes that are appealing to ants that collect the seeds and take them to their nest.

[Both these links come from an outstanding website ('Wayne's Word') that is an excellent source of botanical information. Take some time to explore it.]

There are a number of examples of 'cheating' by both the visitor and the plant. Some visitors can consume the food reward without picking up pollen and consequently without providing the plant with a service. Plants may attract visitors with visual displays but give them no rewards. And, in the case of pitcher plants, the attraction may lead to the demise of the visitor.

'Protection rackets' describe a relationship where the plant provides food and another species does work by protecting the plant from herbivores. This relationship is particularly well developed in some Acacia trees and shrubs where the plant not only provides food rewards but also provides nesting spots for colonies of ant defenders. Additionally, while the typical food reward (for pollination, seed dispersal and defense) is nectar, a compound that is cheap to produce, some Acacia species provide more complex food rewards, Beltian bodies, packets that are much more rewarding nutritionally because they contain lipids and proteins. These are much more expensive for the plant to make. An extension of this interaction is the three species interaction of plants, aphids and ants. Aphids are insect herbivores (grazers, sometimes parasites) that tap into the plant's phloem tissue using their stylet. Since phloem sap has abundant sucrose but scant amino acids, the aphid eats a lot of phloem sap to acquire the amino acids it needs and the excess sucrose is excreted as 'honeydew', aka 'frass' (insect excrement). Ants have developed a relationship of defending the aphids from predators while acquiring the honeydew that the aphids produce.

Fig. 15 The small insects on the top part of the leaf petiole are aphids whose stylets have penetrated into phloem tissue and are having phloem sap pumped into their mouth by the plants. The ants collect aphid frass and feed the ant colony with it. The ants also protect the aphids from potential predators.

Nitrogen-fixing bacteria do chemical work, the reduction of nitrate to ammonia, for their host plants, in exchange for food and a protected habitat. In nodule forming plants the protected habitat are galls on the roots. The aquatic fern *Azolla* forms small cavities on the surfaces of leaves that the nitrogen-fixing cyanobacterium *Anabaena* colonize. This relationship is utilized by rice farmers who encourage the growth of *Azolla,* a small aquatic plant that lives on the surface of bodies of water. Nitrogen fixed by the cyanobacterium becomes available to the rice when the *Azolla* dies and is decomposed.

A more 'one-sided' work interaction in volves insects acquiring and utilizing chemicals that the plant synthesizes. Monarch butterflies acquire a poison from the milkweed plants that they eat. The plant is grazed by the Monarch caterpillars and gains nothing, but the insect acquires a chemical that deters predation. A similar situation occurs with poison dart frogs. The frogs become poisonous because of the insects that they consume, with yet-to-be-determined plants eaten by the insects providing the specific chemicals. Plants can also be on the receiving end of defensive chemicals as is the case with some fungal endophytes (parasites) who produce toxins that can affect herbivores.

In a number of interactions the 'work' is the production of a particular structure (note that producing any biological structure requires material and energy). For example, vines utilize the structure of other plants and thereby avoid the costs associated with producing structural cells (sclerenchyma fibers) that are needed to produce a rigid stem that can withstand the forces of gravity and wind. Another example involving plants are what are called '**hemiparasites**'. These are plants that attach to the roots of other plants, connecting to the xylem, not the phloem. Hence it is not a trophic relationship, food is not transferred from host to 'parasite', rather the 'parasite' is utilizing the structure produced by its host, the root system, to acquire water and minerals. These move passively from the host's roots into the stem of the hemiparasite.

At least some of the benefits of mycorrhizal associations may involve a similar type of relationship, with the fungus providing structure to explore the soil to acquire water and nutrients. However, in mycorrhizae the plant fosters the relationship by providing food for the fungus. In endomycorrhizae (vesicular-arbuscular mycorrhizae) that involve Glomeromycota fungi, the arbuscules can be considered a type of haustorium that facilitates transfer of food from the host plant to the fungus. In ectomycorrhizae there are no arbuscules and but the plant 'leaks' sufficient food to sustain the fungus. In both types of mycorrhizae the fungus does additional 'work' besides simply producing structure. The fungi are producing enzymes that mobilize mineral elements that can be them to their host.

Finally, some of the well-known 'symbiotic' relationships involve structural features. One might consider the role of coral animals and lichen fungi to be providing services (structure) for the dinoflagellates and algae that live inside them.

Further Reading and Viewing

- "Botany Blog – Dispersal of Trillium seeds by ants."
    - http://botany.thismia.com/2009/09/

- “Australian Museum – Herbivory: eating plants.”
  - https://australian.museum/learn/animals/insects/herbivory-eating-plants/
- “Mycoloop: chytrids in aquatic food webs” by Maiko Kagami. Chytrids in food webs.
  - https://www.frontiersin.org/articles/10.3389/fmicb.2014.00166/full
- “The Battle Below – Saprophytes and Mycorrhizal Fungi Compete for the Same Substrate.” Fungal interactions below ground.
  - https://www.slu.se/en/ew-news/2016/6/the-battle-below–saprophytes-and-mycorrhizal-fungi-compete-for-the-same-substrate/
- “Fungal Haustoria Absorb Nutrients from Living Plant Cells” by Helga George.
  - https://www.plantsrule.com/fungal-haustoria-absorb-nutrients-from-living-plant-cells/
- “How radioactive carbon from nuclear bomb tests can tell us what parasitic orchids are eating.” What are parasitic orchids eating?
  - https://www.indefenseofplants.com/blog/2020/1/27/how-radioactive-carbon-from-nuclear-bomb-tests-can-tell-us-what-parasitic-orchids-are-eating?rq=how%20radioactive
- “Parasitism finds many solutions to the same problems in red algae (*Florideophyceae, Rhodophyta*)” by Jillian M Freese. Red algal parasites.
  - https://pubmed.ncbi.nlm.nih.gov/28427949/
- “The Microbial World: Biotrophic plant pathogens” by Jim Deacon
  - http://archive.bio.ed.ac.uk/jdeacon/microbes/biotroph.htm

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- Ants crossing

CHAPTER 28: AGRICULTURE

Fig. 1 Van Gogh's Fields of Auberge, showing 19th century French agriculture.

What is agriculture? It is an activity whereby an organism actively cultures/cultivates/cares for other organisms with the intent of somehow utilizing these organisms directly or indirectly. While we are focused on the agricultural interactions involving humans, other organisms, specifically numerous ant species, carry out agriculture, culturing fungi, aphids and other organisms. Agriculture generally involves the 'domestication', a genetic modification of organisms, both plants and animals, allowing them to be better utilized.

Agriculture involving humans and plants is certainly one of the most significant biotic interactions, an activity that influences vast expanses of land, roughly 12% of the earth's land surface. Although there is much less agricultural activity in aquatic/marine systems, there is some, and secondary effects from terrestrial activities, e.g. fertilizer run-off, also has an impact. Like all interactions, agriculture involves modifications of both partners. And while we will focus on the non-human component, generally flowering plants, it is important to keep in mind that agriculture has brought about tremendous changes in humans, with probably the most significant ones coming about as agriculture originated and humans altered their patterns of activity, movement and social interactions. It is significant to note that relative to the existence of humans, agriculture is a recent innovation, starting roughly 10,000 years ago. For most of their 200,000 year existence, humans were not involved with agriculture, although they certainly did influence specific plants by their activities. It is also significant that agriculture apparently developed separately in multiple regions. Authorities now list eleven sites of agricultural origin, including the Middle East, Africa, the Far East, and North, South and Central America. In each of these regions distinct species were utilized. The table below lists some of the earliest crops along with their region of origin:

Table 1.

crops	**site of domestication**
wheat, peas, lentils, flax, figs, chickpeas	Middle East
potato, tomato, pepper	South America
corn, squash, beans	Mesoamerica
banana, sugarcane, taro	New Guinea
rice, mung beans, soy beans	China
millet, sorghum,	Africa
eggplant, mungo bean, pigeon pea	India

The majority of crops, and certainly the crops associated with the origin of agriculture, were wild plants that humans had already discovered to have desirable features (most commonly features related to eating but sometimes the features were mechanical, e.g. cotton, or chemical, e.g. a waterproof latex from tree bark). The next step was the appreciation that the plant could yield more product if it were somehow cared for, e.g. planted, pruned, etc. For most crops, the practice of collecting and planting seeds was crucial to crop development. Through time, many plant species were genetically modified by humans through selection and planting of seeds from plants with particularly desirable traits, e.g. large seeds. Genetic modification of agricultural organisms (Darwin called this 'artificial selection') was most rapid when dealing with annual plants that could be selected for yearly. This chapter examines the histories of several crops that reveal interesting biological features.

TOPICS

- How do crops come to be?
    - Wheat
    - Strawberry
    - Naval oranges
    - Banana
    - Corn
    - Brassica
- Generating variability

Wheat

Fig. 2 Bread wheat, the tip of the stem had multiple flowers that now have developed into fruits.

The plant known as ' wheat' actually includes three distinct species in the *Triticum* genus: einkhorn wheat, emmer wheat, and bread wheat. Each of these species has wild relatives that may be considered separate species or may be lumped with the domesticated form. These species are related evolutionarily in what is known as a polyploid series. Einkhorn has a diploid chromosome number of 14 and produces haploid gametes with seven chromosomes. Emmer wheat has 28 chromosomes, 14 of which came from Einkhorn wheat and 14 of which came from a related, but separate genus (*Aegilops,* although some workers have lumped *Aegilops* and *Triticum).* Bread wheat has 42 chromosomes, 28 of which come from emmer wheat and 14 from another species of *Aegilops.*

Polyploidy is common in plants and is an aspect in the history of multiple crops. It can come about several ways, the most common being a hybridization event where gametes of two separate species are combined. Viable gametes cannot be produced in the hybrid because meiosis is thwarted by the fact that there are no homologous chromosomes to pair, the chromosomes from one parent do not have 'matches' because the second parent was a different species with different chromosomes. Consequently, the hybrid is sterile; this is what causes the two parents to be considered separate species, they are reproductively isolated.

However, hybrid sterility can be overcome in several different ways. One is to produce functional gametes (i.e. cells that can fuse with other cells) without going through meiosis, i.e. to produce 'unreduced gametes'. If these 'unreduced gametes' find each other and fuse then a new species is created, one that has twice the chromosome number of its either of its parents. In the case of emmer wheat the new species has a diploid chromosome number of 28, 14 (seven pairs) coming from einkhorn wheat and 14 (seven pairs) coming from *Aegilops.* Another possibility is that the cells within the hybrid replicate their chromosomes (mitosis) but the cell does not divide, leaving a cell with double the number of chromosomes of its parents, and significantly, producing a cell that has a match for each chromosome. Such a cell (or derivatives of this cell) could go through meiosis because it does have pairs of chromosomes. In both of these situations a new 'polyploid' species like emmer wheat is produced. Polyploidy is also discussed in Chapter 31.

Bread wheat was produced by the same polyploid mechanism following hybridization, this time between emmer wheat and another species of *Aegilops*. Hence, bread wheat possesses three genomes (sets of chromosomes), one from einkhorn wheat and two from two different species of *Aegilops.* Each set consists of seven chromosomes, thus dipoid cells of bread wheat have 42 chromosomes, two copies of each of the three sets of chromosomes. The origin of bread wheat is quite recent, less than 10,000 years ago, and after both einkhorn and emmer wheat had been domesticated.

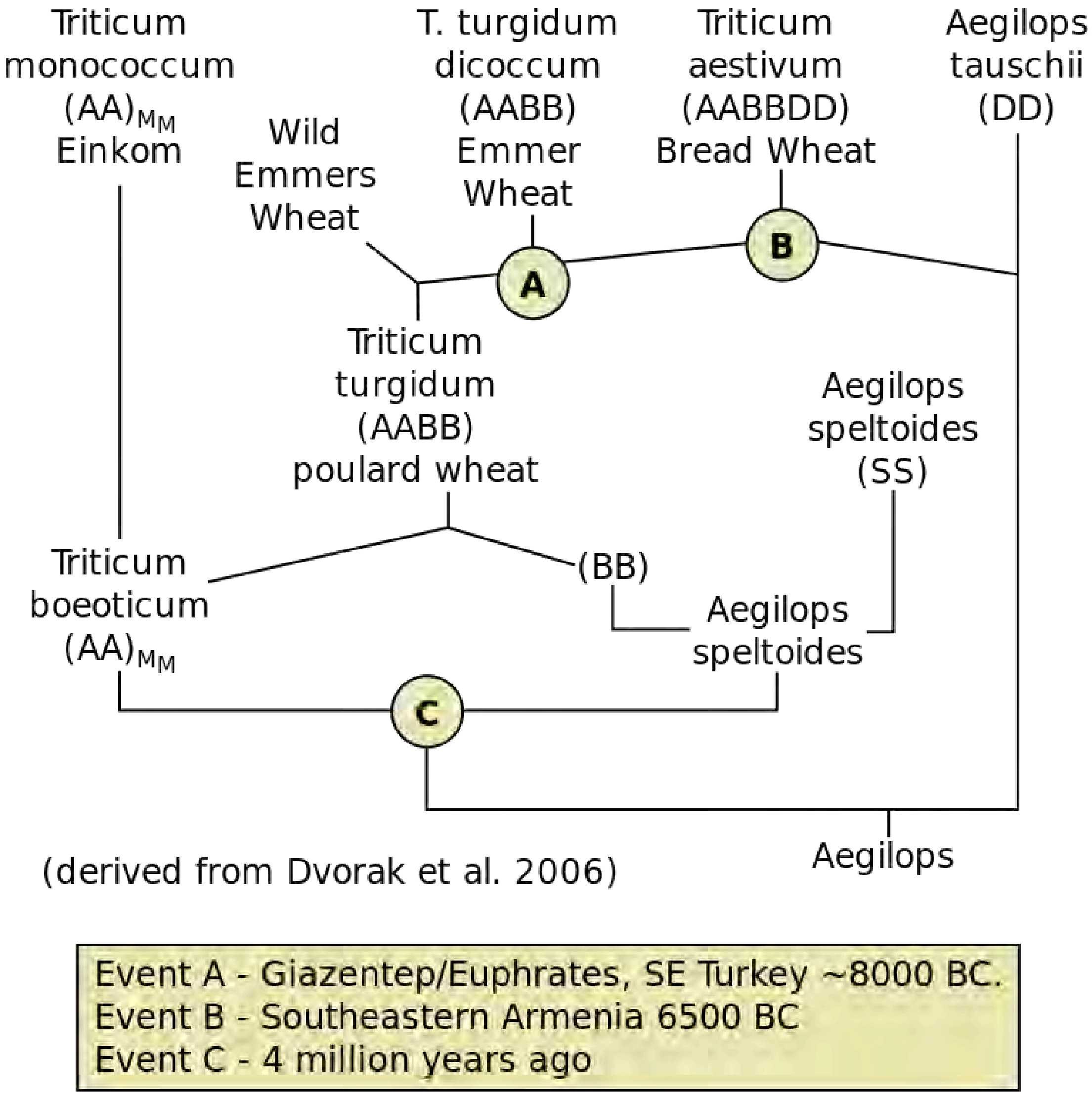

Fig. 3 Evolution of wheat (Triticum) showing two diploid wheats (genome AA), three tetraploids (genome AABB) and one hexaploid (AABBDD) along with the approximate dates of origin. Note that the event A is before event B.

Strawberry

Fig. 4 The commercial strawberry is a hybrid between two American species on from North America and one from South America.

The strawberries found in grocery stores have a very interesting heritage involving Chile, eastern North America and France. Strawberry is in the genus *Fragaria* and there are over 20 species occurring primarily in temperate regions of North America, Europe and the Far East. Most of these species have seen very limited agricultural utilization but are harvested in the wild. Although it has very limited commercial production, one European species, *F. vesca,* especially some clones with particularly large fruits, has been cultivated for over 500 years, primarily in parts of Turkey. A South American species with white fruits, *F. chiloensis,* native to the west coast of North and South America was cultivated by native tribes in what is now Chile. In the early 1800's six specimens of *F. chiloensis* were transported to France and propagated in several gardens alongside specimens of *F. virginiana*, a North American species. The two species hybridized, forming what is called 'garden strawberry', *Fragaria x ananassa* (the 'x' in the name indicates that it is a hybrid). It is this hybrid that is now widely cultivated throughout the world, generally being propagated through cuttings.

Navel oranges

Another crop with a 'chance' origin is the navel orange. It occurred as a 'sport', a mutant branch, on an orange tree growing in Brazil. Remember that branches originate from lateral buds, meristematic tissue left behind by the elongating shoot apical meristem. Occasionally, some of the lateral bud meristems possess mutations that cause them to produce a branch that grows abnormally or one that produces leaves that are unusual (a common manifestation is a branch that produces variegated leaves, leaves that are not uniformly green but are colored a variety of ways). In the case of the navel orange the branch was unusual because its flowers, which normally occur singly, occured as pairs, with a second flower produced very close to the 'normal' flower. The proximity of the two flowers is manifested in an altered fruit development, producing not two distinct fruits but rather a single fruit with another fruit inside it. This is what produces the navel for which the plant is named. If one peels and opens up a navel orange, the second fruit is very evident at navel end. This fruit does not possess a skin and is much smaller than the normal fruit, typically less than an inch in diameter. But, like the normal fruit, it is composed of wedge-shaped sections. A second abnormality of navel oranges is that the pollen is sterile and consequently cannot fertilize flowers. Because of this, the fruits produced by navel oranges are seedless.

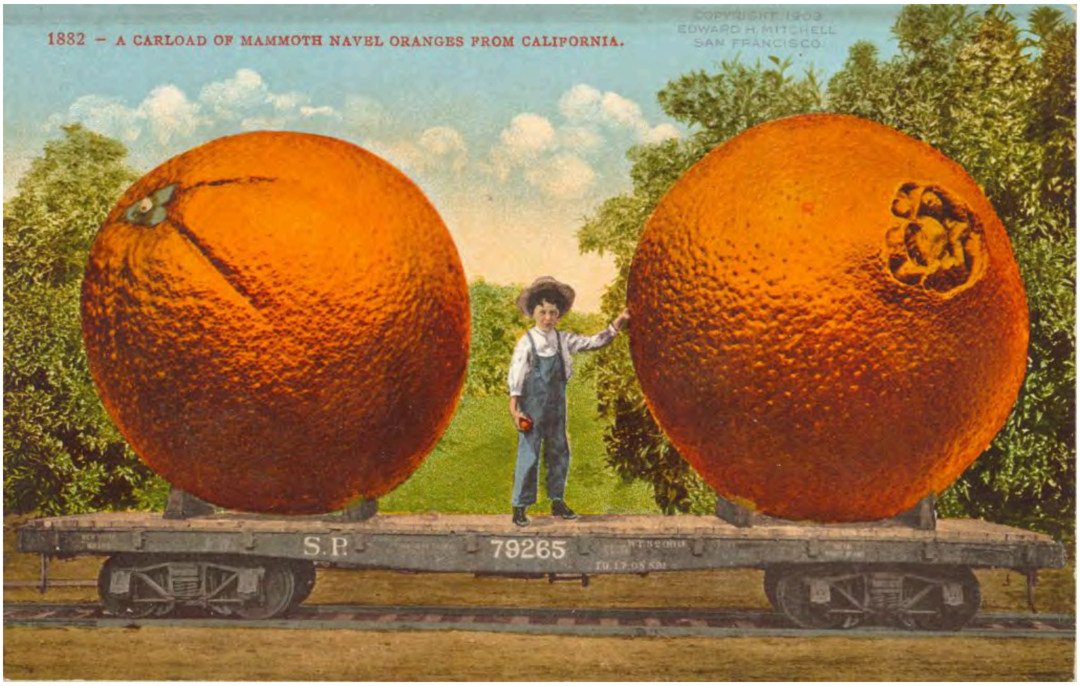

Fig. 5 Navel oranges showing the characteristic 'navel' at the end opposite of the stem that attached it to the plant.

Navel oranges are perpetuated by cuttings, and all the navel oranges grown world-side are ultimately derived from to the original branch produced on the tree in Brazil. A cutting can be rooted to form a naval orange tree but are more commonly cuttings are grafted on to an existing root stock. A variety of species, generally close relatives, can be used as rootstocks and rootstocks can be selected for, and developed for, favorable characteristics, e.g. temperature, drought and pathogen tolerance.

Banana

Unlike naval oranges which are propagated by grafting branches (called scions) on to a variety of rootstocks, bananas are propagated by the cloning of whole plants, i.e. taking a cutting, usually a branch, and having it form roots. Cloning from cuttings is much less 'technological' than grafting and the utilization of cuttings as an agricultural technique goes back to the time when agriculture was developing. There are a large number of banana varieties and it is thought most appeared in the wild and were selected because of favorable features, in particular large fruits that lack seeds. Obviously a lack of seeds makes propagation by seed impossible, but cloning allows these favorable characteristics be perpetuated. Modern studies indicate that the many banana varieties are derived from two species and polyploid derivatives of these species. Most bananas grown commercially are triploid, with a genetic constitution of AAB meaning that they possess two chromosome sets of one type and one chromosome set from another. Such a triploid may be the result of a tetraploid (AAAA, that produces gametes that are AA) hybridizing with a (normal) diploid (BB, that produces gametes that are B). The offspring of this cross are sterile because meiosis is impossible, but cloning allows the plant to be perpetuated. Moreover, the sterility brought about by hybridization has created a favorable feature — no seeds. Triploids may also arise by the the union of an unreduced gamete from a diploid species (the species is AA but produces gametes that are AA instead of A) combining with a normal gamete from another species, e.g. a diploid species BB producing haploid gametes, B. The offspring is triploid, AAB, and sterile.

Fig. 6. Ripening banana fruits, each origination from a unisexual female flower.

For most plant species the production of fruits is a consequence of the production of seeds, with the initiation of seed development triggering the initiation of fruit development. The production of fruits when seeds are not developing at all, or when seeds are initiated but soon aborted, is called parthenocarpy. It is generally considered to be evolutionarily unfavorable since the basic function of fruits is to promote seed dispersal and producing fruits without seeds is a waste of resources. Parthenocarpy can appear 'spontaneously', but it generally will not be perpetuated, unless of course it is selected by (early) agriculturalists. More recently, parthenocarpy may be developed in breeding programs. An example is the seedless watermelon, which, like most bananas, is a sterile triploid, but it was produced by plant breeders crossing a tetraploid plant with a (normal) diploid plant. Seedless watermelons do have seeds but they are small and not fully developed. Seedless watermelons do require pollination to initiate the seeds but they soon abort. In some crops (e.g. some varieties of tomato) parthenocarpic varieties produce fruits even if pollination is lacking.

Corn

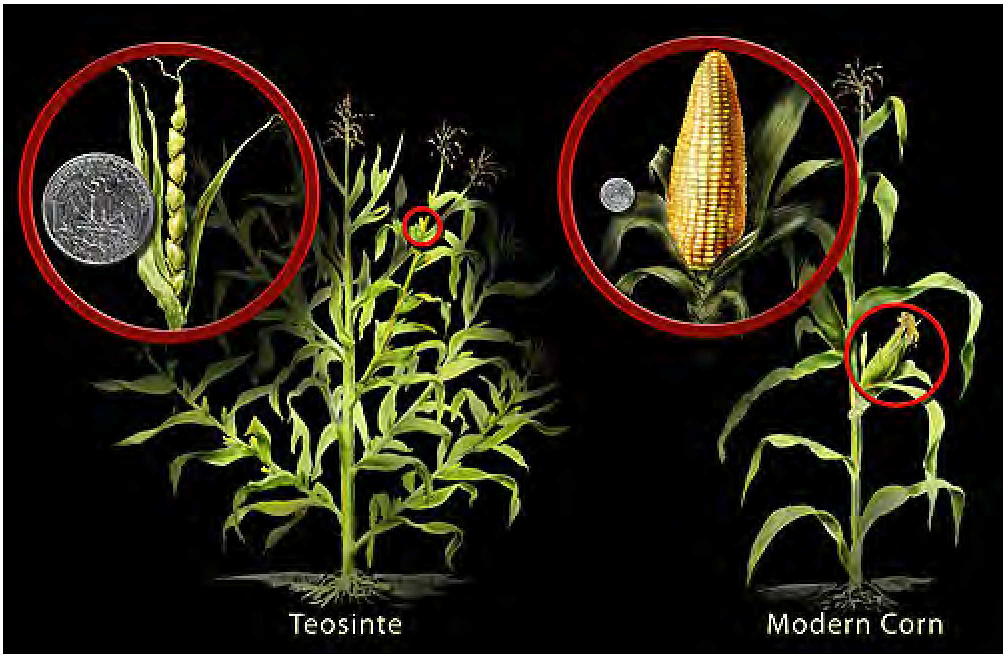

Fig. 7 Teosinte, the ancestor of corn, compared to corn.

Corn's origin as a crop has been a mystery because there had been no obvious ancestor, i.e. a species that looks like corn and could be considered to be something that primitive agriculturalists might manipulate to produce the entity that we know as corn. Research over the last 75 years has revealed that there is a close relative, called teosinte, but its proximity to corn is obscured by the fact that it 'looks', i.e. has a morphology, that is substantially different from corn. Studies have revealed that corn and teosinte are actually the same species — they readily interbreed. The morphological difference between the two are actually the result of changes in only a few (less than 10) genes. It is now thought that selection on teosinte developed the variety (subspecies) that we now consider to be corn, a plant that unlike teosinte: does not branch, has much larger 'ears' (clusters of female flowers), and has seeds that are not enclosed in a rigid container but are relatively easily removed, allowing easier access to an edible structure.

Corn was responsible for dramatic changes in agriculture, in particular the development of seed companies, commercial entities that provide seed to individual farmers. Up until early in the 20th century most farmers provided seeds for themselves by storing seed from the previous crop. When storing seed for the next year's crop, most farmers, passively or actively, selected for increased yield by saving seed from plants that were disease resistant, pest resistant and generally higher yielding. Early in the 20th century agriculture changed drastically in a number of ways, one of them being that farmers started to purchase seed from companies because they could provide seed that was better than what farmers had on hand. This better seed was the result of agricultural research occurring both in 'land grant colleges' (who were charged with improving agriculture) and also in private companies when it was realized that that money could be made by supplying seeds to farmers. Corn was instrumental to this process because it is amenable to producing what is known as 'hybrid seed', discussed further in Chapter 31.

The amazing Brassica group

Plants in the genus *Brassica* reflect a wide variety of interesting topics that intersect agriculture and biology.

Brassica is a genus in the mustard family that has a long history of cultivation and manipulation that has allowed the group to be widely utilized in numerous forms. Below is a partial list of cultivated plants in the *Brassica* genus, along with their uses::

Fig. 8 Kohlrabi, a variety of Brassica oleracea that has a very thickened stem, which is the part that is eaten.

- white mustard (spice) (*Brassica hirta* aka *Sinapsis alba*)
- black mustard (spice) (*Brassica nigra*)
- rapeseed (*Brassica napus*)—grown for oil and animal feed
- canola oil (varieties of *Brassica rapa* and *B. napus*) — grown for oil and animal feed
- leaf mustard, brown mustard (*Brassica juncea*) —grown as a vegetable
- Ethiopian mustard, Ethiopian rape (*Brassica carinata*)—grown as a vegetable
- bok choy, rapini (aka brocoli rabe), turnip, napa cabbage (*Brassica rapa*)— grown as vegetables
- cabbage, kale, broccoli, brussels sprouts, cauliflower, kohlabi (*Brassica oleoraca*) — grown as vegetables
- rutabaga (*Brassica napus*) — grown as vegetable

As was the case with wheat, polyploidy is significant in the relationships of these crops. The crops come from three diploid species, (*B. nigra, oleracea* and *rapa*), and three polyploid (tetraploid) derivatives, *B. carinate, juncea, and napus*), produced from hybridization with pairs of the three diploids.

Another similarity to wheat, and to several other crops (e.g. sunflower) is that these species are 'weedy' (see Chapter 29), i.e. they thrive in 'ruderal' (disturbed) habitats. Hence the progenitors of most of these crops probably grew in the disturbed habitats that ancestral humans created by their behavior. Domestication followed from this. In fact,

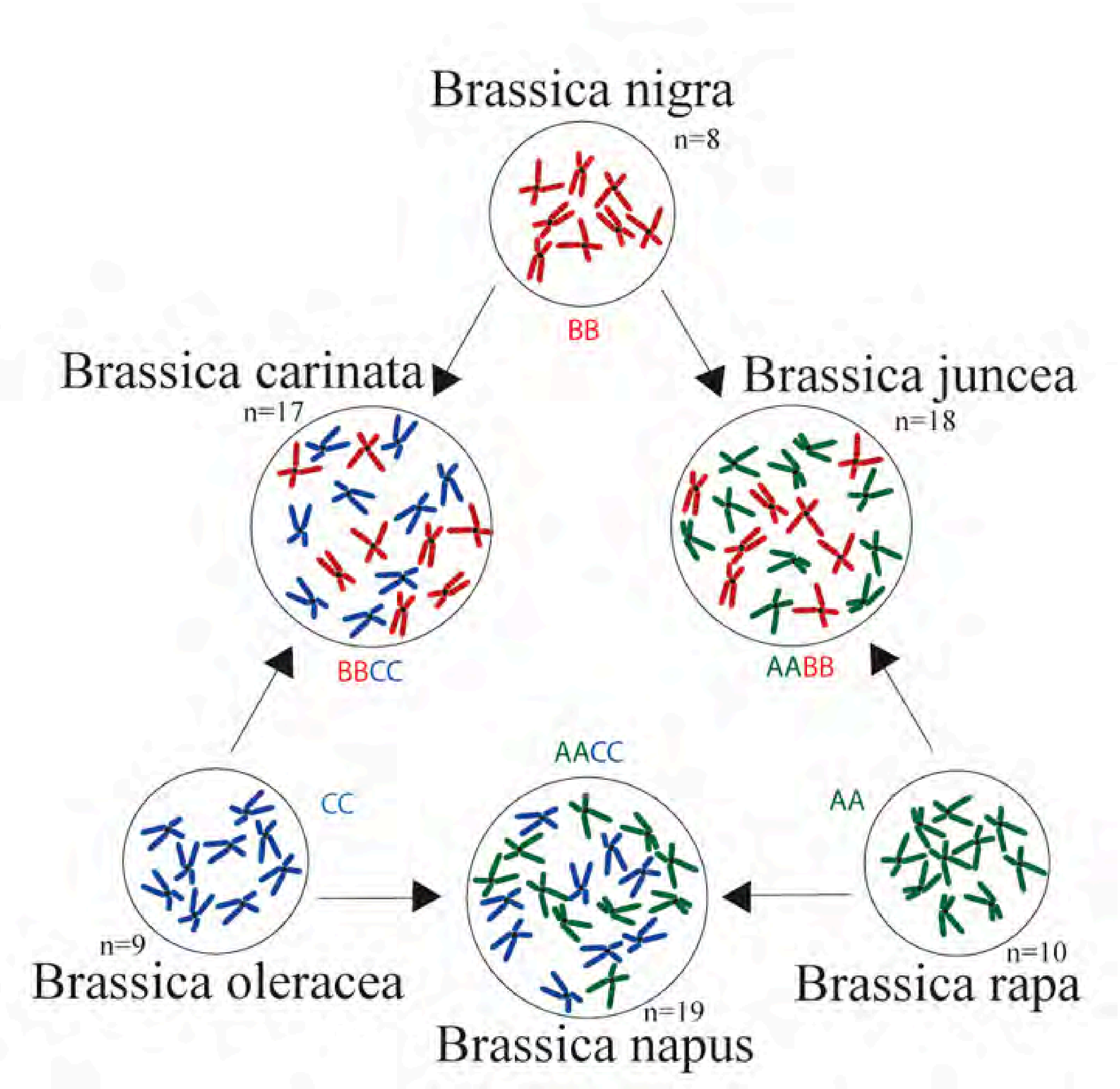

Fig. 9. Relationships in the genus Brassica.

while black mustard is grown as a crop, it is also a significant weed in many parts of the world.

Unlike wheat, a polyploid group whose members all look very similar, the Brassica group shows remarkable morphological variation, especially the ones used as vegetables, where the edible part may be leaves (kale, collard greens, leaf mustard, Ethiopian mustard), roots (turnips, rutabagas), enlarged stems (kohlrabi), shortened stems with overlapping leaves (cabbage, see Chapter 10), lateral buds (brussel sprouts, see Chapter 10), and thickened inflorescence meristems (cauliflower, broccoli).

All of these crops were developed thousands of years ago by selection for plants that had favorable traits; i.e., 'primitive' agriculturalists noted favorable features and perpetuated plants that had these features. A challenge to these early genetic engineers is that most of these crops are biennials, meaning that some of the crop must be allowed to overwinter and in the second year transform into a flowering form from which the seeds are collected, i.e. these farmers needed to be aware that flowers and seeds are only available in the second summer after planting.

Another interesting feature of these plants is their chemistry. They produce a group of chemicals called glucosinolates, that, if cells are ruptured, are converted into chemicals called isothiocyanates. It is these chemicals that give members of this group (also closely related radish, horseradish and wasabi) a peppery and sometimes 'hot' taste. Glucosinolates release isothiocyanates as a result of the action of the enzyme myrosinase. This enzyme is sequestered separate from the glucosinolates, and only acts to release isothiocyanates when herbivory is occurring, crushing cells and breaking open cellular components, thereby allowing myrosinase to be in contact with glucosinolates. Although many humans find isothiocyanates desirable, many insects do not and the system acts as a chemical deterrent to herbivory (although, as is often the case, some insects specialize on mustards and are attracted by the chemistry). A comparable sequestering system operates in some plants (e.g. apple seeds) where cyanogenic glycosides are stored separate from enzymes that can cleave a sugar group to release cyanide.

Generating variability

Whether or not one is utilizing hybrids, crop development requires variability followed by selection of plants with favorable features. Open pollinated crops generate variability both through naturally occurring mutations and also by chance shuffling of genes in the sexual process. Although there had been suspicions on the existence of sex in plants and the roles of pollen and pollination, the observations of Rudolf Cameraius late in the 17th century revealed the role of pollen and made possible the generation of variability by the intentional crossing of two related species. Often these efforts were stimulated by the botanical explorations and the collection of 'new' plants, e.g. the production of commercial strawberries described above. This allowed closely related plants to be grown together and crossed. Early in the 20th century, workers discovered that they could generate variability with treatments that induce mutations: specific toxic chemicals or harsh radiation. And most recently, modern molecular techniques allow for the most precise modifications of plant characteristics through the introduction, or occasionally removal, of specific genes. Although the later process is the only one described as 'genetic modification', one should appreciate that crops have been genetically modified once they started to be cultivated. One should also appreciate that modern techniques are by far the most specific, meaning that the modifications are the most targeted, with the least amount of disruption of non-target genes and features (see Chapter 31).

Further Reading and Viewing

- "A Brief History of the Seed Industry" by SeedStory.
  - https://seedstory.wordpress.com/a-brief-history-of-the-seed-industry/
- "Date update: Methuselah gets six siblings" by The History blog. Date palm.
  - http://www.thehistoryblog.com/archives/57817
- "The extraordinary diversity of Brassica oleracea" by The Botanist in the Kitchen. Brassica crops.
  - https://botanistinthekitchen.blog/2012/11/05/the-extraordinary-diversity-of-brassica-oleracea/
- "Domestication, Genomics and the Future for Banana" by J. S. Heslop-Harrison and Trude Schwarzacher.
  - https://academic.oup.com/aob/article/100/5/1073/137119?login=false
- "Domestication of the banana" by ProMusa.
  - https://www.promusa.org/Domestication+of+the+banana
- "George Beadle's Other Hypothesis: One-Gene, One-Trait" by John Doebley
  - https://academic.oup.com/genetics/article/158/2/487/6049579?login=false
- "Strawberry: A Brief History" by David Trinklein.
  - https://ipm.missouri.edu/meg/2012/5/Strawberry-A-Brief-History/
- "Domestication of Plants in the Americas: Insights from Mendelian and Molecular Genetics" by Barbara Pickersgill.

  - https://academic.oup.com/aob/article/100/5/925/137339?login=false
- “Here’s what 9,000 years of breeding has done to corn, peaches, and other crops” by Brad Plumer.
  - https://www.vox.com/2014/10/15/6982053/selective-breeding-farming-evolution-corn-watermelon-peaches
- “Pirates of the Carob Bean” by The Botanist in the Kitchen.
  - https://botanistinthekitchen.blog/2018/01/28/pirates-of-the-carob-bean/
- “Explaining Gluten” by Cooking Science Guy.
  - http://www.cookingscienceguy.com/pages/wp-content/uploads/2012/07/Explaining-Gluten.pdf
- “The Difference Between Waxy and Mealy Potatoes” by Cooking Science Guy.
  - http://www.cookingscienceguy.com/pages/wp-content/uploads/2012/07/The-Difference-Between-Waxy-and-Mealy-Potatoes1.pdf
- “The Unfortunate Sex Life of the Banana” by Matt Castle.
  - https://www.damninteresting.com/the-unfortunate-sex-life-of-the-banana/
- “Vanilla Mania” by Bernd Brunner
  - https://www.thesmartset.com/vanilla-mania-2/

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- Navel Oranges © Edward H. Mitchell is licensed under a Public Domain license
- Banana © Chris 73 is licensed under a CC BY-SA (Attribution ShareAlike) license
- Teosinte and modern corn © National Science Foundation is licensed under a Public Domain license
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- Triangle of u simple © adenosine is licensed under a CC BY-SA (Attribution ShareAlike) license

CHAPTER 29: WEEDS AND WEED CONTROL

Ralph Waldo Emerson defined a weed as 'a plant whose virtues have not yet been discovered', but in fact a number of weeds were known to have 'virtues' and were spread by humans intentionally. Dyer's woad is a significant pest in the western U.S. but was brought to North America intentionally for its use a source of blue dye (hence the common name). Many weedy plants, e.g. purple loosestrife (Fig. 1), were intentionally introduced by gardeners who found them attractive. A large number of weed organisms of all types are similarly the result of intentional introduction in new habitats (honeybees, earthworms, gypsy moth, starlings and many more).

Fig. 1 The pretty purple flowers are purple loosestrife, a plant brought to North America as an ornamental but it has escaped to become a problem weed it wetland areas.

Is there a better definition of weed? Ecologists consider organisms to be 'weedy' if they have a suite of characteristics (high reproductive potential, extensive dispersal abilities, rapid growth rate, ability to reproduce even under adverse conditions) that would make them likely to appear and survive in disturbed habitats. Disturbed habitats, sometimes called ruderal habitats, are areas that have once been populated but some disturbance, e.g. fire, has eliminated what once lived there. Significant for terrestrial habitats, they generally are sites with developed soils, as opposed to sites that were never vegetated and have no soil. So although ecological weeds are considered 'pioneer species', they are not pioneering onto previously uninhabited land with very young soils. Ecological weeds can colonize and quickly dominate a disturbed site but may not persist because they often are unable to compete with other species that eventually arrive at the site.

But 'weed' is not used just by ecologists and its definition is both utilitarian and subjective:

> 'A plant that interferes with the management objectives at a particular location. It is a plant growing where it is not wanted. Under certain situations, the plant may not be totally undesirable.'

This definition focuses on plants but undesirable organisms come from the entire spectrum of life, including the non-plant organisms considered in this book: cyanobacteria, green algae, red algae, diatoms, dinoflagellates and fungi.

Weeds are 'pests', organisms that are undesirable for reasons that are specific to a particular situation and, as noted above, their undesirable nature depends upon situation.

- honeybees are pests when they nest in houses or perhaps when they outcompete native bee species
- earthworms are desirable in agricultural situations but are weeds in native habitats where they can alter conditions and disrupt the native community
- dandelions are weeds in lawns, where some consider them unsightly, but are useful to pollinators and to foragers who eat their leaves and flowers
- sandbur is highly undesirable on beaches because of its sharp fruits that are painful to step on and stick to clothing
- dyer's woad clearly is (was) useful as a source of dye but if one is managing land for other purposes then it is a weed
- weeping willow trees are desirable as ornamentals but their roots can clog drainage systems
- the nitrogen fixing bacterium *Rhizobium* is desirable if it invades plant roots in habitats where nitrogen is relatively scarce. When nitrogen is abundant *Rhizobium* may actually decrease plant growth because they are being fed by the plant

The last example highlights the fact that there is some overlap between 'weeds' and 'disease', something that will be considered in the next chapter.

TOPICS

- Features of weeds
- Controlling weeds

Features of weeds

As mentioned above, weedy plants typically grow fast and reproduce both rapidly and abundantly. But given the flexible and utilitarian definition of weed a key feature of weeds is that they must have characteristics that someone might consider undesirable. Here are some examples:

Fig. 2 Sandbur is a grass whose fruits have very sharp points.

- dandelions interrupt the smooth continuous texture of a lawn giving what some consider a an undesirable look.
- sandbur produces fruits that are very painful to step on or get caught in a stocking
- burdock, beggar's tickseed, stickseed and many others produce fruits that stick on clothing
- box-elder trees produce an unappealing form that readily sheds branches. Its abundant fruits clog gutters
- poison ivy, wild parsnip, giant hogweed, St. Johnswort are toxic to many humans

Fig. 3 Poison ivy, native to North America, is highly undesirable because it produces a chemical that is a skin irritant.

The foremost undesirable feature of agricultural weeds is that their presence in cropland deters the growth of whatever crops are being grown, an interaction that generally would be labelled competition, a concept that is easy to cite but is often much more difficult to pin down. The basic idea is that if two species utilize the same resources (water, light, nutrients) then the presence of of a competitor can reduce the availability of these resources and thereby diminish the growth of the crop. The phenomenon of decreased crop growth when in the presence of weeds is well established, but the exact mechanism is elusive and certainly may vary between different weeds. Note that the best competitor for any particular crop plant is another individual of the same type, because it requires the same resources and acquires them in the same manner. Thus intraspecific competition (between individuals of the same species) may be hard to separate from interspecific competition (crop vs. weed). Keeping track of resources is often challenging and other interactions might account for the pattern. C ompetition could be due to factors such as allelopathy (the weed produces chemicals that deter the growth of the crop) or perhaps because the weed attracts insect pests/disease organisms that may affect the crop. For these reasons competition is often defined without the specific requirement of resource depletion. Most agricultural weeds are plants that deter the growth of crop species for undetermined reasons.

What might make a particular plant likely to be an agricultural weed? Here there is large overlap with characteristics of ecological weeds:

- weeds seeds germinate readily with few or no specific germination requirements
- weeds grow quickly and since resource acquisition is strongly tied to plant size, growing quickly allows weeds to be very effective competitors
- weeds readily reproduce, allowing for their perpetuation on a site and producing a substantial ‘seed bank’ of seeds in the soil. Although most of their seeds germinate readily, not all do, and some seeds remain viable for tens of years, meaning that ungerminated weed seeds remain in the soil for prolonged time periods

Fig. 4 Dyer's woad was introduced to eastern North America in colonial times. It is not a problem throughout most of the United States but is a problem in parts of the western states.

While the above apply to annual weeds, there are also perennial weeds which reproduce readily from fragmented roots which may be produced by tilling. Why till? because most crops are annuals and they would have a very hard time competing against already established plants. But note that tilling 'plays into the weed's strength': it is a form of disturbance which is generally something that weeds require.

The characteristics listed above also would be desirable features of a crop plant: germinate readily, grow quickly, reproduce abundantly. Indeed, several crops are thought to have been domesticated from weeds (e.g. wheat, sunflower, barley, carrot).

Another feature that is commonly associated with weeds is that they are non-native, i.e. they were introduced into an area where they previously had not be present, generally because of human activity (both intentional and unintentional). While some would consider any non-native to be a weed, most would require that the introduced species must be invasive, i.e. spreading from where it was introduced. Many introduced species are invasive and this is generally attributed to the fact that 'natural controls' (herbivores, disease) are not simultaneously introduced with the weed. While this certainly explains the invasive nature of some introductions, other factors come into play. Dyer's woad was introduced in the eastern U.S. and showed only a modest invasive nature as it spread westward and was restricted to repeatedly disturbed sites like the sides of roads and train tracks. Arriving in California and Utah in contaminated alfalfa seed, its behavior changed substantially, becoming much more invasive and entering habitats that are much less disturbed, replacing native plants. Part of this behavior is probably due to the fact that woad's native habitat is much more similar to the arid west than to the more mesic eastern and central part of the country.

Fig. 5 Indigo dye derived from the fruit of Dyer's woad. Most indigo is now made synthetically but until the 20th century the primary sources of blue dye (indigo) were Dyers woad and several other unrelated species.

An interesting invasive pattern is shown by black locust, a tree native to central and southeastern U.S. but not to the northeast. After it was intentionally introduced to the northeast it has become invasive as it has in several other parts of North America. What had limited its spread previously is unknown. Again appreciating that what a weed is is subjective, black locust might be considered a weed in the northeast but not in the areas where it is native.

Another interesting pattern is seen in *Phragmites australis*, 'common reed grass'. Apparently a variety of this species was native to North America and was present when European's arrived. This native variety of the species is not invasive and does not form large monotypic stands. Ecologists noted that the behavior of the plant changed drastically in the 20th century, with the plant becoming much more invasive. What actually happened was that a European variety of the same species had been introduced and this was the plant was exhibiting the invasive behavior. The two varieties (non-invasive North American; invasive European) are very closely related (same species) and very difficult to distinguish. Apparently minor genetic changes can be responsible for invasive behavior.

However, lots of weeds are 'natives' (ragweed, giant ragweed, sunflower, Jerusalem artichoke, milkweed, New England Aster, goldenrod) and most of these have not invaded new habitats but have continued to occur in the disturbed habitats found in any particular region.

Weed control

In most situations weeds cannot be permanently eliminated but their populations may be controlled using three approaches: (1) chemical control, using pesticides (herbicides) to kill the weed (2) biological control, using biological agents (pathogens, herbivores) to reduce weed populations and (3) cultural control, modifying how the land is maintained in order to reduce weed populations.

Fig. 6 Phragmites australis, a grass with both weedy (invasive) and non weedy varieties.

Chemical control

Chemical control is a recent innovation, only becoming a significant control agent in the last eighty years. The basic idea is simple: find some chemical that kills weeds. The difficulty is that most chemicals that kill weeds are non-selective, i.e. they don't just kill weeds, they kill all or most plants, including those whose growth you are trying to promote. A wide variety of herbicides have been developed but the three below are widely used and show a degree of selectivity. Therefore can be used in some situations without damaging the plants/crops one is trying to grow.

> **2,4 D** (2,4, dichlorophenoxyacetic acid) is the oldest widely used herbicide. Its discovery as a useful product, a weed killer, was the result of 'basic' research, i.e. research that was not focused on utility (developing a weed killer) but rather research that simply involved developing an understand of the natural world. In

this case, workers were studying the effects of auxin, the first chemically identified plant hormone, originally studied by Darwin one hundred years earlier. The only naturally occurring auxin is indoleacetic acid, but early in the 1940's workers discovered a number of chemicals, with structures similar to indoleacetic acid, that could produce similar effects on plant growth and development. One of these artificial auxins was 2,4 D. It was up to Dr. Franklin D. Jones to do some 'applied' science, i.e. apply basic research to a practical problem. Dr. Jones was looking for something to kill the poison ivy that was plaguing his children. He tried 2,4 D and found it was very effective in killing poison ivy. Significantly, 2,4 D is selective: it kills most broadleaf plants (dicots) but spares 'narrow-leaved' plants, grasses and similar species. Because this selectivity matches what one might look for eliminating lawn weeds and weeds of cereal grains (e.g. corn, wheat), 2-4 D has proved to be highly useful.

Roundup (glyphosate) was developed in the 1970's and is the most widely used herbicide both in agricultural situations and in home/garden situations. It is not at all selective, basically killing whatever plants to which it is applied. It is also a systemic herbicide, meaning that if it is applied to the leaves it can be transported to the roots and rhizomes and can kill them too. Selectivity has been developed because resistance to Roundup, using genes from bacteria, has been genetically engineered (i.e. gene transfer) into several crop species, first soybeans ('Roundup Ready Soybeans), and later to corn and cotton. Fields with these specific crops can be treated with Roundup to kill all other plants.

Atrazine is the second most used herbicide in the U.S., but mostly in agricultural situations and less in residential situations. It is selective, killing most broadleaf species and many weedy grasses, but being tolerated by several crop species: corn, sorghum, and sugar cane (all are grasses). Additionally, an atrazine resistant (GMO) canola variety has been developed as well.

Concerns about herbicides abound and include: human health concerns, ecological concerns and concerns about the development of herbicide resistant 'superweeds'. Both Roundup and Atrazine have been used extensively enough that there are new varieties of weeds that are unaffected by these chemicals, comparable to the evolution of antibiotic resistant bacteria.

Biological control

Biological control involves the use of other organisms to deter the growth of weeds. In general, this type of control is developed for introduced, invasive species of weeds. A search is made for herbivores or pathogens (see Chapter 30 on disease) that are native to where the introduction came from but are not present in the region that they have invaded. Care must be taken to avoid introducing species that might be harmful to existing native species. This is more likely if the biocontrol agents selected are 'specialists' in their feeding habits. Purple loosestrife is an example of an invasive weed that has been controlled (not eliminated) by introductions of insect herbivores, beetles and weevils that specialize on purple loosestrife. These species are common in purple loosestrife's native habitat (Europe and Asia) but were not introduced to North America when purple loosestrife was.

Cultural control

By definition weeds are **always** a problem, at least a problem for someone. Although weeds can be an 'issue' in native habitats, the vast majority of weed problems involve humans (gardeners, farmers) trying to raise specific plants, i.e. trying to 'culture' plants that are somehow desirable. The cultural practices that are followed can influence the magnitude of the weed problem. The choice of crops, the timing of planting, the seeding density, the distance between rows, the number of sequential seasons that a crop is planted, all are cultural practices that may influence the severity of weed problems. Because most crops are annuals, they need to be planted each year, and planting involves disturbance, thereby encouraging weed growth. Indeed, some early 19th century farmers considered early versions of the plough to be 'poisoning the soil' and promoting weed growth. Appreciating that farmers are in a catch-22 condition, they need disturbance but disturbance promotes weed problems, there are cultural practices that can lessen the problem: such as the timing of the ploughing and how intensive the ploughing is. A modern technique called 'no-till' farming utilizes minimal tilling, thereby giving weeds less area to utilize. Moreover, the area that is available is seeded with a crop that may out-compete the weeds. Perennial non-woody crops such as alfalfa, asparagus, strawberries, raspberries require different cultural practices that might include items like mulching, mowing, tilling or the intentional planting of understory plants that might suppress weedy growth. This is also true for woody perennial crops like grapes and apples. Cultural practices vary widely depending on the crop and its characteristics. For instance flooding is an effective means of weed control but can only be utilized if crops, e.g. rice, tolerate the flooding. Fire can be used for annual crops and for woody (tree) crops if it is a low intensity surface fire.

Fig. 7 No till farming: Instead of ploughing the entire field, a narrow trench is 'drilled' where the seed is planted. Note last year's corn stalks.

Most weed management strategies utilize '**Integrated Pest Management**', an approach that incorporates chemical, biological and cultural approaches to manage not only weeds but also insect pests and pathogens.

Further Reading and Viewing

- "The Discovery and Development of 2,4-D" by Gale E. Peterson.
    - https://www.jstor.org/stable/3740338#metadata_info_tab_contents

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CHAPTER 30: THREATS TO AGRICULTURE: INSECTS AND PATHOGENS

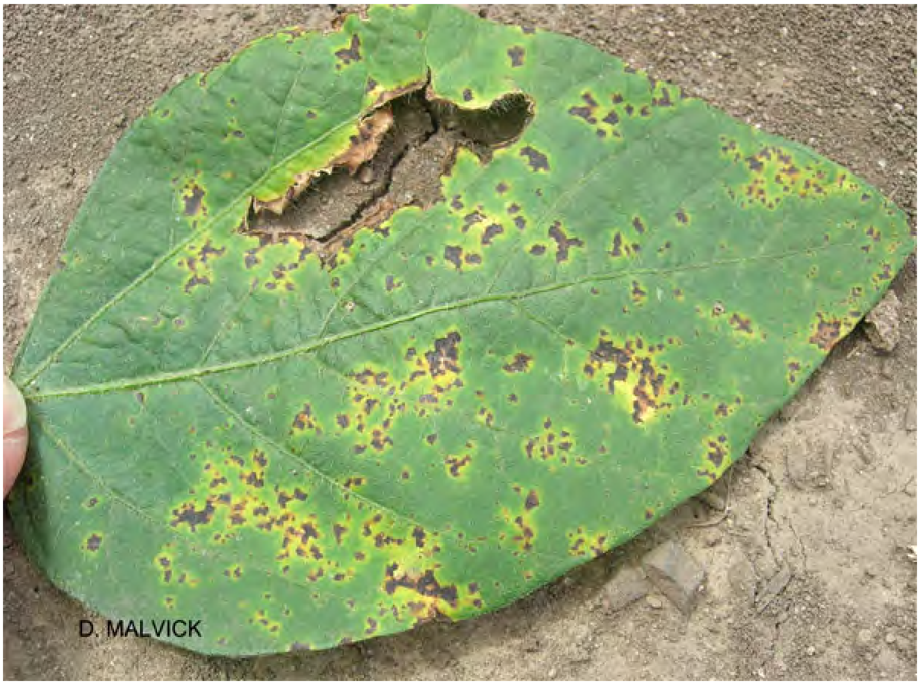

Fig. 1 Bacterial blight on soybean leaf

As any farmer will tell you, there are many threats to growing plants. Some of these have been covered in earlier chapters: extremes in temperature and moisture (Chapter 26); and interactions with other plants, i.e. weeds (Chapter 29). A large number of additional threats come from trophic interactions with a vast diversity of grazers, parasites and and predators. Certainly the most familiar of these are insects but other invertebrates (mites, nematodes, mollusks) and vertebrates can be significant obstacles to growing plants. Moreover, a large number of fungi, bacteria (Fig. 1) , protists and viruses are also be important threats.

TOPICS

- Grazing herbivores
- Absorbing herbivores
- Plant defenses
    - Boundary
    - Chemicals
    - Phenology
- A sampling of plant disease
    - Phytoplasmas and defining disease
    - Late blight of potato—the disease triangle
    - Wheat rust disease—complex pathogen life cycles
    - Corn smut disease—Mexican truffles
    - Dutch elm disease —overreaction can kill you
    - Rice blast disease—changing strategies
    - Fire blight of apple—bacterial phytopathogens
    - Crown gall disease—making a disease a tool
    - Viral diseases—tobacco mosiac virus, cauliflower mosaic virus, ring spot disease of papaya

Grazing herbivores

Most animal herbivores, e.g. woodchucks and adult japanese beetles, are considered grazers, eating parts of the plant and using their mobility to get to other plants. However, a substantial number of insect herbivores have feeding stages (generally larvae, e.g. leaf miners, emerald ash borers, larval potato beetles) that are immobile to the extent of getting to new host plants. These might better be considered parasites because they feed solely on one host plant. Most non-animal herbivores (fungi, bacteria) are basically immobile and are considered parasites although some are capable of grow ing from one host to another and many are transported from one plant to another by wind, rain and insects.

Most grazers on plants are ingesters (see Chapter 27), they remove and consume part of the plant, shred it to some extent and then digest the pieces in an internal tube, and

Fig. 2 Japanese beetles on peach leaves, an example of a grazing insect pest.

ultimately excrete undigestible to their environment. Grazers, although they can severely reduce crop yields, rarely completely kill the plant it is eating both because they tend to specialize on only part of the plant (most commonly leaves) and because the plant is capable of replacing the organs/parts of organs that have been lost.

The plant material acquired by grazers is generally not very nutrient dense but varies substantially depending upon the part of the plant eaten. Nutritional quality is largely influenced by how many living cells are present (dead cells are basically all cell walls and are indigestible for most herbivores). Most herbivores specialize on one of the tissues listed below, but there are some generalists that feed on multiple tissues, e.g. browsers like moose and deer often eat stems, leaves and meristems.

- primary growth of stems and roots — although stems and roots in primary growth have more living cells than those with secondary growth, they still are nutrient poor. Most of those cells that are living are not very metabolically active and consequently they are poorer in nutrients when compared to cells that are more metabolically active (e.g. leaf mesophyll cells).

- woody stems and roots, heartwood: Heartwood has no living cells and has increased levels of secondary chemicals. It generally has the lowest nutritional quality of any plant tissue. Nonetheless, there are heartwood specialists.
- woody stems and roots, sapwood: Sapwood has some living cells (the rays) and these may be 'loaded' with starch and other nutrients, depending on the season. Hence sapwood is considerable more nutritious than heartwood but still is largely composed of cell wall material.
- woody stems and roots, vascular cambium — this meristematic tissue is nutrient rich and has relatively less cell wall material compared to mature cells. Moreover, it is more extensive than apical meristems, i.e. there is more material available to eat.
- the bark tissue of woody stems is nutrient poor with few living cells and an abundance of secondary chemicals. The portion of cells that are living decreases as the stem/root ages and hence bark of younger stems is more nutritious than the bark of older stems.
- stems and roots that have been modified as storage structures — rhizomes, corms, bulbs, stolons. These are composed of living cells that are storing carbohydrates, usually in the form of starch. They are rich in digestible carbohydrates but may be deficient in amino acids (proteins) and other nutrients.
- phloem feeders: These organisms (including aphids, leaf hoppers, mealy bugs and white flies, all significant agriculture pests) are not consuming any cells, but instead tap into the phloem transport system and acquire the materials that are being transported through it. Phloem sap has very high concentrations of sucrose along with much smaller concentrations of amino acids and some minerals. Because the ratio of carbohydrates to amino acids in phloem sap is so high most phloem feeders excrete 'honeydew', essentially phloem sap — still rich in carbohydrates but with most of the amino acids removed. Honeydew is utilized by several other organisms, in particular some ant species and the sooty mold fungus.
- xylem feeders: Xylem sap has very few nutrients, almost no carbohydrates but with some of mineral ions. Also, while phloem feeders acquire sap passively because it is under pressure inside the phloem cells, xylem sap is under tension and requires 'sucking' (developing greater tensions than already present) in order for it to flow into xylem feeders. Nonetheless, there are some insects (larval cicadas, larval spittlebugs) that feed on xylem.

Fig. 3 Emerald Ash borer larvae only eat the ash tree that the adult has chosen to lay an egg in.

Absorbing herbivores

In contrast to grazers, most non-animal plant herbivores are absorbers (see Chapter 27), absorbing nutrients from 'their environment', with 'their environment' being the interior of a plant. Most of these organisms are bacteria and fungi, but some, like water molds, are protists and a few are animals (e.g. nematodes, the larval stages of some insects). Most of these organisms are considered parasites and are generally considered to be plant pathogens. They invade plant tissues and then acquire materials in one of three ways: (1) the parasite feeds on materials that 'leak' from host cells. (2) the parasite kills host cells, causing cellular materials to become available. Organisms that feed this way are described as being necrotrophic (feeding off dead material). (3) the parasite and host form a structure called an haustorium, a fusion of both the host cell membrane and the parasite cell membrane. (Note that the development of the haustorium generally requires breakdown of the cell walls of both the host and parasite). Materials are transferred from host to parasite through the haustorium and both host and parasite stay alive. Organisms that feed this way are described as being biotrophic (i.e. feeding off living material). Some biotrophs are relatively benign herbivores (they benefit from keeping their host alive), and consequently many acquire relatively small amounts of resources from their hosts. But many biotrophs (e.g. rusts, smuts, downy mildew, powdery mildew) can be devastating to farmers as infestations often can reduce plant yields to next to nothing.

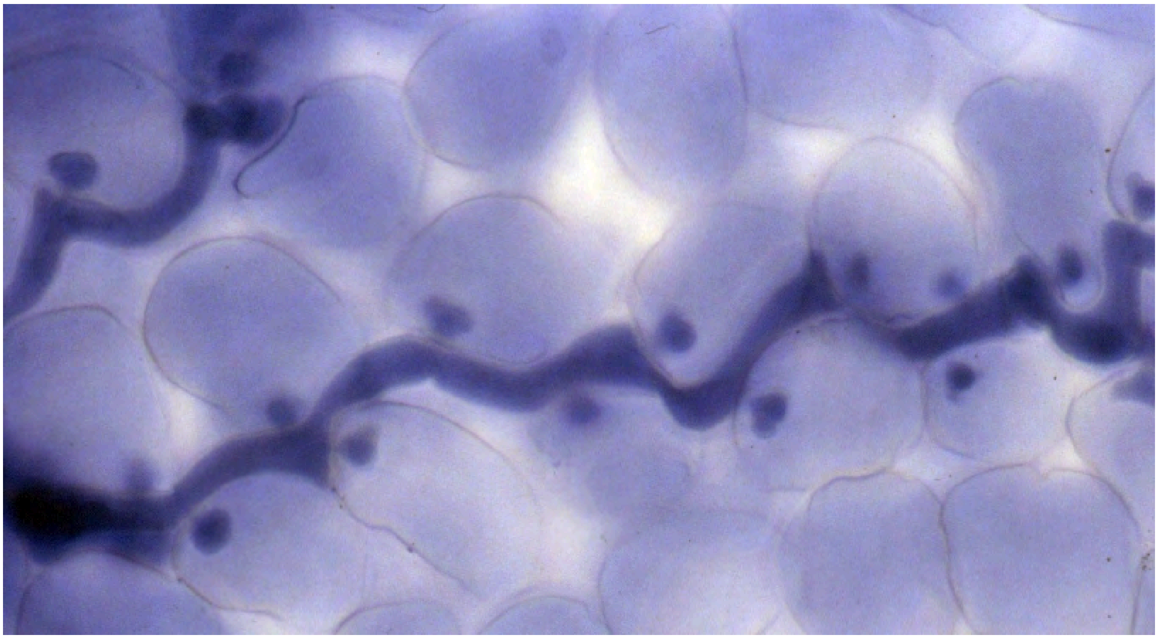

Fig. 4 Downy mildew (oomycete) hyphae winding intercellularly between plant cells with haustoria (circular structures) penetrating intracellularly.

Plant defenses

An effective boundary: Except for large grazing animals, organisms need to get inside plant tissues in order to feed on the plant. The boundary makes this difficult by producing a surface that is hard to penetrate and inhospitable for life (see Chapter 3). For above ground primary growth, the boundary consists of epidermal cells that are tightly bound to each other, making it difficult to penetrate between cells. Additionally, above ground primary growth is coated with a cuticle that is difficult to pierce and hard to live on because it is hydrophobic. Below ground, mature primary roots have an endodermis that serves many of the same functions as the epidermis+cuticle does above ground. However, the youngest parts of roots have not developed an endodermis. This makes water acquisition easier but it also makes it easier for pathogens to enter.

Pathogens/herbivores gain entry both by utilizing stomatal openings and also by having mouthparts that can penetrate the cuticle/epidermis; or having a needle-like or saw – like ovipositer (egg-laying organ); or, in the case of some fungi, producing an appressorium, a specialized cell type that is able to fuse with the epidermis and produce a structure that can penetrate it. Pathogens and herbivores also gain entry through wounds and openings in the epidermis as the result of growth processes, e.g. branch roots and the shedding of leaves and branches.

Chemistry: All plants produce diverse chemicals that influence herbivory and pathogens. Some are feeding deterrent chemicals that are poisonous or may advertise that poisons are present within the plant. At the same time, some chemicals produced by plants clearly attract certain herbivores. The assumption is that these chemicals had once served as feeding deterrents but that the herbivore has developed means to detoxify the poison and is now using the chemical to identify a host that relatively few competitors will be able to utilize. For example most insect herbivores will not eat milkweed but several insects (monarch butterfly larvae, the milkweed beetle and milkweed bugs) choose to feed on milkweed. Some even utilize the plant's poisons as their own, making them less likely to be consumed.

Plants also produce chemicals because they recognize that they are under attack. The production of these 'induced' chemicals imply that the plant has an ability to sense the presence of the pathogen and the chemicals produced may: (1) kill the invader (phytoalexins), (2) trigger defensive responses in neighboring plants and/or attract predators that may control the herbivore, or (3) elicit an 'hypersensitive response', causing the invaded tissue to rapidly die. Note that the hypersensitive response may be effective in deterring biotrophic pathogens but actually benefits necrotrophic pathogens.

Phenology: Plants (and farmers) may be able to avoid herbivores/predators by adjusting the timing of seed germination, growth and flower / fruit production.

A Sampling of plant diseases:

Poinsettias, phytoplamas and the nature of plant disease

Poinsettia's did not always look as most of them do now. The plant in the wild and the plant that was originally propagated as an ornamental plant was much taller plant. It also produced relatively few 'flowers' (the structures that look like a flower are actually a cluster of flowers surrounded by colorful, usually red, bracts). Early in the 20th century a plant with a novel form appeared, one that was much shorter, branched much more frequently, and produced more flowers. This form could be propagated by cuttings and the assumption was that the original smaller plant was a mutant, a 'sport', like the original naval orange (see Chapter 28). Sports generally cannot be perpetuated by seed because the mutations making them distinctive are often recessive. But they often can be perpetuated by cuttings because cuttings are essentially continued growth of the original plant. There are other phenomena besides mutations that might account for an altered growth pattern that can be perpetuated by cuttings. Two possibilities are viruses and phytoplasmas (small bacteria lacking cell walls that live only in plant cells). Note that all three possibilities for the abnormal plant (mutation, viral infection phytoplasma infection) could be described as 'plant disease' but that what is unusual is that in this case the diseased plant is desirable not undesirable. It turns out that almost all the poinsettia produced today are diseased! And the culprit turns out to be a phytoplasma.

So what is plant disease? In the poinsettia discussion it was associated with 'abnormal plants' A difficulty with this definition is that it is 'normal' for biological entities to be 'abnormal'. That is, if you look at a population (group of organisms) they aren't all alike, they vary, some are 'outside the norm'. Additionally, 'normal' is not readily defined. It can be defined statistically as a central tendency, e.g. abnormal is more than one standard deviation from the mean. Although not perfect, the 'abnormal' definition works with plants partly because the most plants under consideration are typically those of economic importance and 'normal' is a type of plant that provides the most economic return. Additionally, most crops have been bred to be uniform.

Thus a diseased plant is recognized by abnormal structure or functioning. Common symptoms of diseased plants include stunted or deformed growth and yellowed

Fig. 5 A diseased plant?? The desirable form of this plant is a consequence of a phytoplasma that has infected the plant.

(chlorotic) or dead (necrotic) leaves. But occasionally one might find a diseased plant that is 'bigger than normal', that branches more than normal, or that has leaves that persist on the plant longer than normal. In an arbitrary manner, plant disease generally excludes conditions due to insect herbivores even though they may result in similar effects as 'true' plant pathogens. Since this book is dealing with inanimate life we will not consider insect herbivores except as introduced in the chapter on biotic interactions and as covered in the next chapter dealing developing new plants.

Late Blight of Potato and the 'disease triangle'

Fig. 6 Late blight of potato, caused by the water mold *Phytophthora*

The causes of abnormal functioning, i.e. diseased plants, are legion, including: weather conditions, nutritional (soil) factors, genetic changes and a wide spectrum of disorders resulting from interactions with a variety of other organisms — bacteria, fungi, water molds, nematodes, insects and with biotic entities like viruses. With respect to these biotic causes of plant disease, plant pathologists describe what is called the 'disease triangle' where disease results from a combination of environmental conditions, host susceptibility, and the virulence of a disease-causing organism. Disease is a consequence of a combination of three factors, hence a triangle: a susceptible plant encountering a competent (i.e. virulent) pathogen under environmental conditions that favor the invasion and spread of the pathogen. A classic example of the disease triangle is late blight of potato, caused by the water mold *Phytophthora*. Potato is native to South America but was brought to Europe in the 17th century as a food crop. The disease organism, which also affects tomatoes, apparently originated in Mexico in the early 1800's. The disease requires cool, moist conditions, a susceptible potato host and a virulent pathogen. The pathogen spread throughout North America in the early 19th century and made it to Europe probably as a result of importation of diseased potatoes to Belgium in 1845. It quickly spread throughout Europe, and in particular to Ireland, where potatoes were the primary food source and were grown extensively in monocultures. The cool moist conditions typical of

Ireland were well-suited to the growth and reproduction of the pathogen. Moreover, the potatoes grown were genetically uniform and also highly susceptible to the blight. The result was devastating, over a million Irish died of starvation and another million emigrated, mostly to the United States. The severity of the blight varied over the next twenty years, primarily due fluctuations in environmental conditions. Note that crop failure not only eliminates food, it also eliminates 'seed potatoes' (potatoes saved to be planted the following year). Thus, even if favorable conditions might yield a relatively high crop (yield per acre), food shortages persist because fewer acres may have been planted. Late blight of potato continues to be a problem, with outbreaks tied to environmental conditions. There are partially resistant varieties but these are only temporary because the pathogen evolves to overcome the plant's resistance.

Fig. 7 Phytopthora infestans on tomato, a close relative of potato.

The pathogen is an obligate biotrophic parasite, meaning it can only survive on a living host (but it does eventually kill substantial parts or all of its host). It survives from year to year on potato tubers or potato plants left in the field. It spreads readily by spores (usually asexual) that require moisture to stay alive and are dispersed by wind and by raindrops. Pathogen growth and spread can be extremely fast if weather conditions are appropriate. The spores germinate quickly and enter susceptible plants through stomata, wounds, and directly through the cuticle. Once inside the leaf they produce hyphae that grow between cells and produce haustoria that penetrate the cell wall and interact with the host cell membrane and allow nutrients to pass to the fungus.

The disease requires a match between the host and the pathogen. *P. infestans* infects potato and also tomato, which is a close relative of potato. But many other close relatives are not suitable hosts. And there are other species of *Phytophthora* that affect other plant species but do not infect potatoes, e.g. *P. quercina* causes sudden oak death syndrome

Wheat rust—complex parasite life cycles

There are many different rust diseases that affect a variety of hosts, and some utilize two different hosts. All are host specific meaning that they can affect only a group of closely related plants: a variety, a species or several species from a single genus. The life cycle for wheat rust was introduced in Chapter 12 and a figure from that chapter is reproduced below. Note that five different types of spores are produced. They differ from each other by their ploidy level (diploid, dikaryon or haploid), what type of plant they are produced on, and what type of plant they can grow on (if any) and how they function. These are described below:

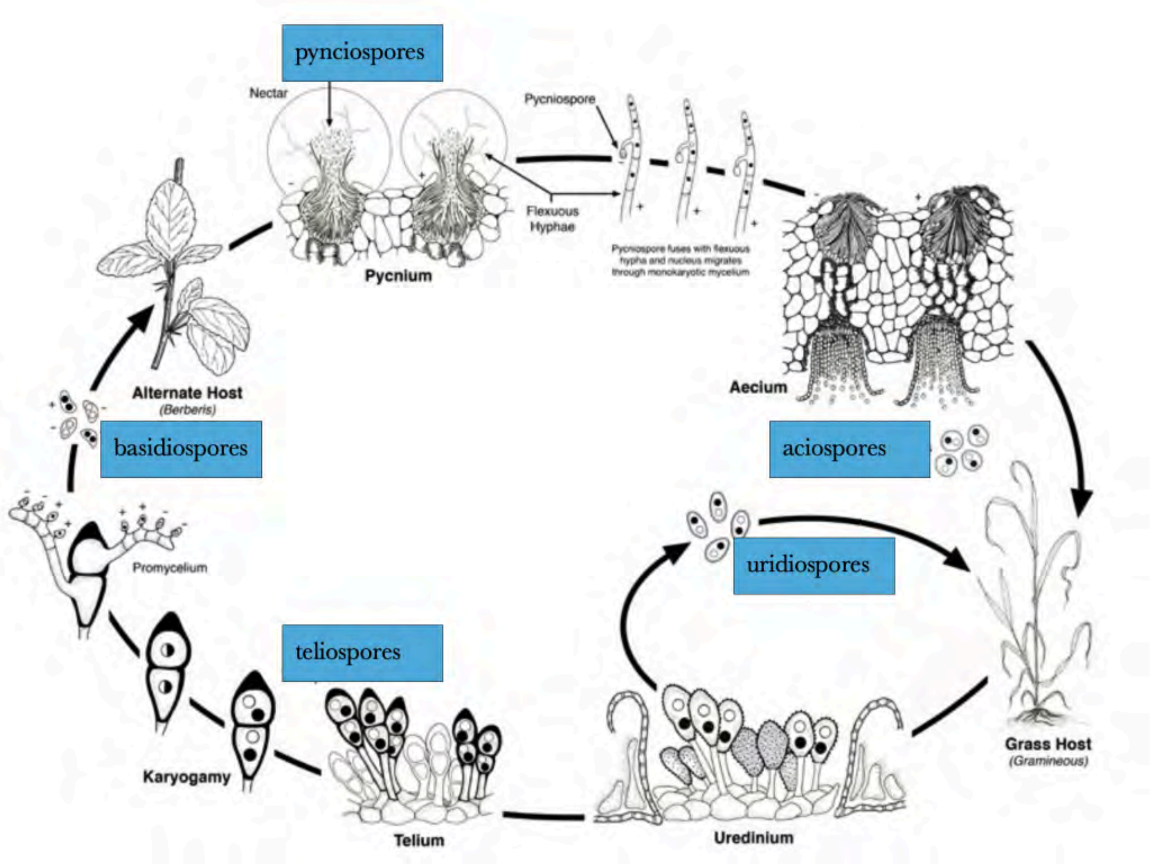

Fig. 8 Life cycle of wheat rust, showing the five types of spores that are produced.

teliospores are dikaryon spores and the only stage of the life cycle that grows, albeit very temporarily, independent of a host. It also is the only stage that can overwinter.

basidiospores are haploid spores produced after the teliospore germinates and undergoes karyogamy to produce a diploid cell. This cell then undergoes meiosis to produce haploid basidiospores. These spores are dispersed in the air and only germinate and grow on barberry plants.

pynciospores are haploid spores produced from hyphae produced in a structure emerging from the upper surface of barberry leaves. Also in this structure are haploid receptive hyphae which can receive pynciospores and fuse with them (plasmogamy) to form dikaryon hyphae. These grow to the lower surface of the leaf and form a structure called an aecium that produces dikaryon **aeciospores** that are dispersed by the wind and infect wheat plants.

Mycelial dikaryotic growth from the aeciospores can cause significant damage to the host wheat plant and also produces **urideospores**, produced in and orange structures called uremia. The uridospores spread *Puccinia graminis* to other wheat plants, facilitating disease spread.

As the wheat plant starts to senesce, both from the pathogen and from its natural, monocarpic cycle, the dikaryotic hyphae in the wheat plant produce **teliospores**, spores that can survive the winter and thus completing the life cycle.

Fig. 9 *Puccinia graminis* on wheat stems—the orange structure are ureidia and produce urediospores that can infect other wheat plants.

Because wheat is an extremely important crop and because the disease spreads rapidly and evolves quickly, wheat rust is probably the most significant agricultural disease. Resistance to the disease involves the genetics of both the fungus and the plant. Resistant plants have an ability to recognize invasion by the fungus and to respond to it. Recognition of the fungus is the result of the plant perceiving a chemical produced by the fungus. An avirulent fungus can become virulent by becoming unrecognizable, typically by not producing a specific chemical that that the avirulent (and thereby recognizable) fungi had been making. Hence virulence in the pathogen is typically recessive (inability to make something that the wild type does make). Plant resistance requires a dominant gene that gives the plant the ability to recognize and respond to the presence of the virus.

Corn smut—Mexican truffles

Fig. 10 Corn smut. Infected plants produce deformed fruits (galls) instead of regular corn kernels.

Corn smut produces large, distinctive galls that are edible and highly desirable in Mexico. In other parts of the world the disease is very unwelcome, substantially reducing crop yields. Like the rusts, smut diseases are basidiomycetes and like the rusts the fungus is generally found in the dikaryon state, with cells possessing two haploid nuclei. Basidiomycetes only produce only a single diploid cell that immediately undergoes meiosis to form haploid spores. These germinate and grow into haploid hyphae that, in smuts, can produce new cells by budding like yeast and like yeast can be grown on an artificial medium, meaning that this stage is NOT biotrophic but acts like a saprophyte. However, when haploid hyphae of two different mating types find each other and fuse and form a dikaryotic hyphae, it is now biotrophic, only able to survive on living cells of spe cific plants, in this case, corn and teosinte (a close relative of corn). Hence, to be a successful pathogen the haploid hyphae need to find each other on living corn (or teosinte) plants. Additionally, the dikaryon hyphae only invade active tissues, most commonly the flowers, where they induce abnormal growth, galls, with greatly enlarged cells surrounded by hyphae. They do not form typical haustoria but do form structures that allow the transfer of materials from the plant to the fungus. As the galls mature they change color from silky white to black and also change textures, becoming softer. Although the galls look 'fungal' (if such a thing is possible!) they are actually mostly plant tissue. Inside the galls some fungal cells undergo karyogamy (fusion of the two haploid nuclei) to form a diploid cell and complete the sexual cycle. Corn smut is the most significant smut disease but there are other smut fungi that infect other agricultural grasses (sugarcane, barley, oats) as well as smuts that attack wild grasses and sedges.

Rice blast disease—changing pathogen strategies

Fig. 11 Rice stems infected with rice blast disease

Rice blast is a devastating fungal disease that affects several cereals but is most significant in affecting rice. It is an ascomycete and the dikaryon stage is brief in time and extent. The pathogen is technically described as a hemibiotroph because initially it behaves like a biotroph, surviving on living plant cells, but eventually becomes a necrotroph, killing cells and obtaining nutrients from them. Haploid spores land on rice leaves, developing fruits, and other plant parts, and are able to penetrate the cuticle by generating substantial pressures hydrostatically within a specialized cell called an appressorium. Once inside the fungus is able to spread by entering individual plant cells through plasmodesmata. After a certain amount of time that depends upon the tissue that has been invaded, the fungus shifts to a necrotrophic lifestyle, killing the host cells.

Fig. 12 Rice leaves infected with rice blast disease.

Dutch elm disease—overreacting can be deadly

Dutch elm disease is caused by an ascomycete fungus that has a symbiotic relationship with a bark beetle, a type of beetle that feeds on the vascular cambium and tissues (secondary xylem and phloem) that the vascular cambium produces. The fungus is transported from infected trees to new trees by the beetle and benefits not only by the transport but also by being placed inside the plant in the tissues that the fungus feeds on. The fungus feeds only on dying cells. but, unfortunately for the tree, its presence triggers the production of gums. Presumably such a response could help stop the spread of the fungus by making it more difficult to move. However, in elm trees the substances that are produced plug the vessels and trachieds of the host, making them unable to transport water up the plant. Like a number of human diseases, the damage of a pathogen stems mostly from the host response and less so from the actual activity of the pathogen. Dutch elm disease is one of many 'wilt diseases' caused by both fungi and bacteria that result in reduced water transport and therefore wilting. In most of these the blocking of xylem tissue is the result of the plant response to the pathogen.

Fig. 13 'Galleries' of bark beetle that spreads the fungal disease that causes elm death. The beetle feeds on the inner bark (phloem) and is able to carry spores from infected trees to uninfected trees.

Fire blight and bacterial phytopathogens

The majority of plant pathogens are fungal, but some, like late blight of potato, are oomycetes and some, like the phytoplasmas of poinsettias are bacteria. While phytoplasmas are unusual because they are obligate intracellular parasites, most bacterial diseases do not enter into the cell but they do produce 'effector' molecules that they are able to transfer into living cells and effect specific results such as hormonal responses that bring about tumors, exudation of materials, or cell death. Most bacterial plant pathogens are not easily classified as biotroph/necrotroph although clearly phytoplasmas are biotrophs, as is the gall-forming *Agrobacterium* (see below). Fire blight is interesting in this respect. It is caused by *Erwinia amylovora* and affects members of the rose family, in particular apples and pears, sometimes with catastrophic results. The bacteria can live as a harmless epiphyte living on sugars exuded by the stigmas of flowers and the nectaries at the base of petals. From these locations *E. amylovora* can be spread by pollinators throughout a plant and throughout an entire orchard. At some point it is triggered to become a much less benign associate and it becomes necrogenic, killing host cells as a consequence of the effector molecules it produces.

Fig. 14 Fire blight, a bacterial disease that kills members of the rose family, including apples and pears.

Crown gall disease—a disease used as a tool against disease

Many plant diseases alter the growth pattern of plants, often producing characteristic structures called galls. The abnormal growth that is manifested in a gall usually is a consequence of changes in the amounts of plant growth regulators, aka hormones. This can be the result of the pathogen producing these chemicals. In fact, one plant hormone,

Fig. 15 A 'crown gall', an abnormal growth on a tree caused by the presence of *Agrobacterium tumifaciens*. Crown gall disease affects a wide variety of plants, not just trees.

gibberellic acid, was first discovered as a result of it production by a fungal disease. But altered levels of plant growth substances can also be a consequence of the pathogen causing its host to produce more or less of a particular substance. The most common way this happens is that the pathogen alters gene expression in its host. *Agrobacterium tumifaciens* does this by actually altering the genes present in host cells via a process called transformation, a type of horizontal gene transfer. Among other genes that are transferred is one that codes for the production of the plant growth substance cytokinin which plays a role in the cell proliferation required for gall formation. The bacterium lives saprophytically in the soil but is able to recognize wounded plants when it contacts them and is transformed into a virulent form that makes its way into the plant. *A. tumifaciens* is a significant pathogen on several crop species, in particular perennial ones like walnut, apricot and plum. *Agrobacterium tumifaciens* is notable for its very broad range of hosts. This is one of the reasons why it has proved useful in the genetic engineering of plants where it is used to transfer specific genes from one organism to another (Chapter 31).

Tobacco mosaic virus, cauliflower mosaic virus, and ring spot disease of papaya

Plants are affected by a large number of viruses that can cause very significant crop losses. Tobacco mosaic virus (TMV) is not one of the most damaging viral pathogens, but it is

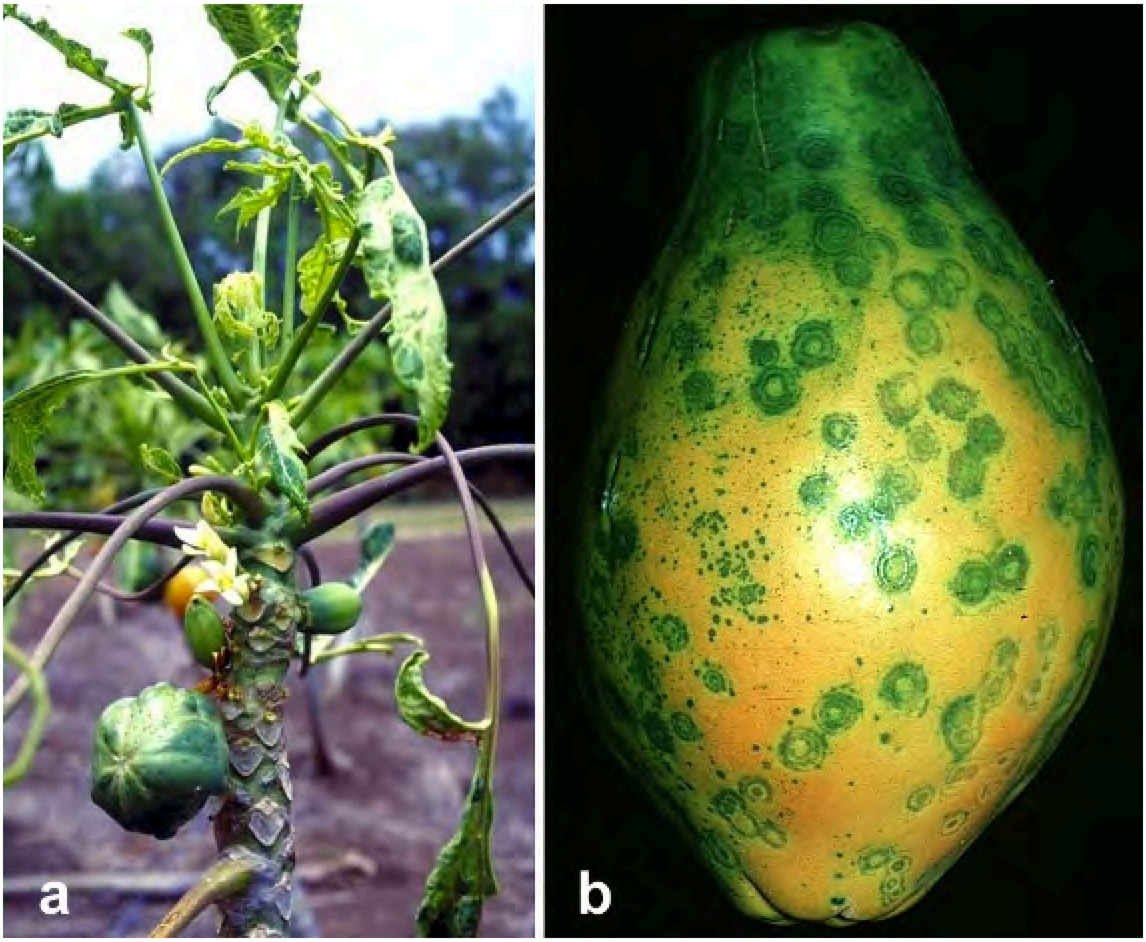

Fig. 16 Ring spot virus on papaya

notable both because of its role in the understanding of viruses and its use in bioengineering. TMV was the first virus to be isolated and purified and this allowed for the recognition that infectious agents need not be cellular in order for them to cause disease. Viruses are composed of both protein and genetic material (either DNA or RNA) and upon entry into a cell they insert genetic material that codes for the production of viral protein and genetic material. A critical part of the inserted viral genome is a region called a promoter that 'promotes' the expression of the genes downstream from it, thereby ensuring their expression. Genetic engineers have utilized this region of the genome of several viruses in order to insert desirable genes from one organism into another organism. In particular the cauliflower mosaic virus (CaMV) has proved to particular useful in producing 'genetically modified' organisms. One crop where the CaMV promoter was very useful was in the development of strains of papaya that are resistant to the ring spot disease of papaya, a disease that is caused by yet another virus that threatened to eliminate the papaya as a commercial crop.

Further Reading and Viewing

- "An Overview of Plant Defenses against Pathogens and Herbivores" by Brian C. Freeman and Gwyn A. Beattie.
    - https://www.apsnet.org/edcenter/disimpactmngmnt/topc/Pages/OverviewOfPlantDiseases.aspx
- "Necrotrophic and biotrophic pathogens of plants" by David Moore, Geoffrey D. Robson, and Anthony P. J. Trinci.
    - http://www.davidmoore.org.uk/21st_Century_Guidebook_to_Fungi_PLATINUM/Ch14_10.htm
- "Obligate biotrophy features unraveled by the genomic analysis of rust fungi" by Sébastien Duplessis et al.
    - https://www.pnas.org/doi/10.1073/pnas.1019315108
- "Plants Rule – Biotrophic Versus Necrotrophic Fungi" by Helga George, Ph.D.
    - https://www.plantsrule.com/biotrophic-versus-nectrotrophic-fungi/

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CHAPTER 31: PROPAGATING PLANTS AND DEVELOPING NEW PLANTS

Fig. 1 Propagating rice. Rice is an annual and must be replanted each year. In the above case, seeds are germinated, allowed to grow to a seedling and then transplanted to flooded fields. In other areas rice is grown on upland sites with seeds directly plant into the soil.

Ancient agriculture required plant propagation, making new plants. Plants don't live forever and many crops are annuals or are harvested less than a year after planting. Although the earliest agricultural efforts may not have involved intentionally propagating plants, fundamental to the development of agriculture was the acknowledgment that making new plants is an essential part of the process. The techniques used to propagate plant crops vary depending upon the crop. For most familiar crops it required storing some seed (i.e. not eating it) and planting it at some point in the future. For crops such as cereal grains and most legumes, where the seed is the part that is harvested and eaten, development of the 'store and plant' technology was relatively straightforward and rapid. However, crops such as tomato, squash and eggplant, where a fleshy fruit is harvested and the seeds are small and inconspicuous, required more technology: a recognition that seeds were present in the fruit and a method for processing of some of the fruit to obtain seeds for planting. Perennial plants do not require propagation each year, they could be maintained without propagation. But eventually they required some means of making new plants, especially if the agriculturalists are moving to a new area. For reasons discussed below, propagation of perennial plants often did not involve seeds but instead asexual means of propagation.

For most of its existence agriculture did not involve attempts to produce novel plants, plants with characteristics that distinguished them from their parents. However, the hope from the earliest onset of agriculture was that one might be able to improve the characteristics of the crop, producing crops that yielded more, tasted better, stored better, were easier to harvest, and were more tolerant of hardships, in particular, more tolerant of disease. Primitive farmers were happy when they found desirable novelties and were able, knowingly or unknowingly, to gradually change the crops they grew. But they did not have the understanding and technology to intentionally create something novel. This has become possible over the last 100 years. Although an understanding of aspects of asexual reproduction was important for some crops, it was the recognition of the sexual process in plants, in particular the functioning of flowers and pollination, that has been critical to the development of the technologies of crop improvement (Fig. 2). All of the major crops have been, and continue to be, intentionally modified. And this is one of the many factors that has changed, and made more complex, the business of agriculture. Where it was once basically controlled by a farmer who served both as a producer and salesman, it is now a vastly more involved system that depends on farmers, seed producers, researchers, fertilizer producers, equipment manufacturers, agricultural scientists, the government, and vast array of 'middle-men'.

TOPICS

- Asexual reproduction—propagation by cuttings
- Sexual reproduction by seeds and the importance of breeding system
- Hybrid seeds
- The green revolution
- Creating novel plants

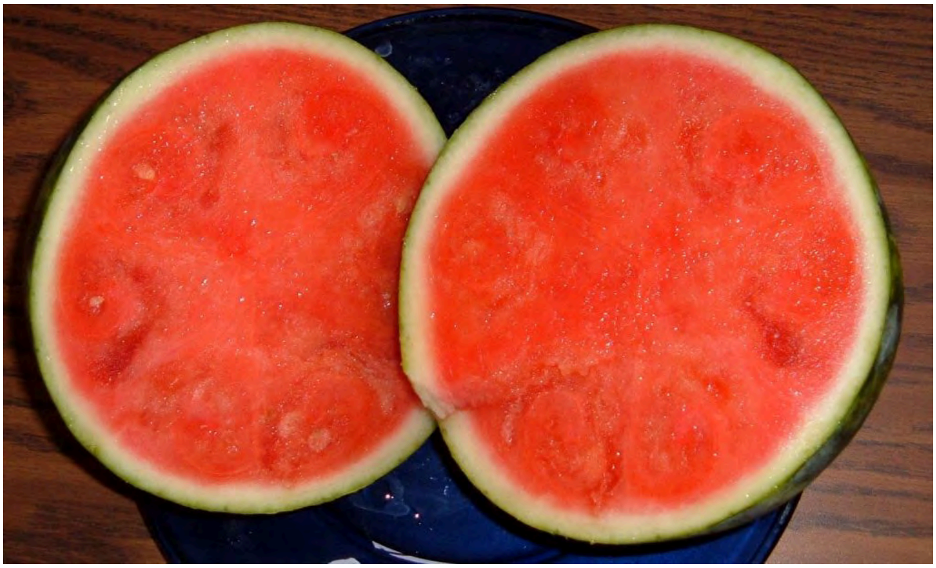


Fig. 2 Seedless watermelon, a novel type of fruit developed recently that has the desirable feature of not producing seed. Although it produces no seed the plant that grew to produce this watermelon did come from a seed. It is a sterile hybrid, comparable to a mule.

- grafting
- generating variability
- genetic engineering

Asexual reproduction

Most woody plants do not 'breed true', meaning that if you plant a seed from your favorite apple tree, or from a 'wild' tree growing in the woods, it is highly unlikely that the seed will grow into a tree comparable to the parent. In fact, the apples that you might harvest will probably be less than desirable. Similar patterns would be found for grapes and olives, two ancient crops. In order to perpetuate desirable plants of such species these crops have been propagated not from seed but instead asexually. The easiest technique is 'rooting', cutting a stem and placing it in moist soil in hopes that it will sprout roots (see the discussion adventitious roots in Chapter 8). A similar procedure can be done with roots, inducing them to produce new shoots. Since the middle of the 20th century an artificial plant hormone has been used to promote adventitious growth in shoots/roots that might not do so otherwise.

Obviously, asexual propagation does not produce novel material, it only perpetuates existing ones. It is important in a large number of vegetable crops including banana, pineapple, potato, sweet potatoes, cassava and many more. It also is the most common means of propagating many ornamental flowering plants (e.g. geranium, begonia). For some of these plants (e.g. banana and some hybrid flowers) asexual reproduction is essential because the plant is a sterile hybrid and cannot produce viable seeds. For other species, e.g. potato (Fig. 3), pineapple (Fig. 4) and many others, asexual reproduction is simply an easier and quicker means of propagation, eliminating the seedling stage that is sometimes more sensitive to conditions than cuttings are. A disadvantage of asexual propagation is that the clones are genetically uniform and thus crops are more susceptible to widespread failure (e.g. in late blight of potato). Another problem is that viral diseases are transmitted in cuttings but not through seeds.

Fig. 3 Sprouts on a potato, these are branches growing from a modified stem (the potato). These will grow into new plants and is the primary means of propagating potato.

Fig. 4 Pineapple is a monocarpic plant that dies after flowering. It is propagated by planting the 'top' of the fruit or by planting 'sprouts' that may appear at the base of the plant.

Sexual propagation—seeds and the significance of breeding system

Fig. 5 Early 20th century seed catalog, showing several varieties of green beans.

Propagation by seeds is probably the most familiar process to most of us. For annual species grown as crops, propagation only requires the discipline to store seeds for the next season. Unlike asexual reproduction, sexual reproduction can result in variation. Variation has positive and negative effects on farming. On the one hand it allows for crop improvement and the production of novel plants (see below). On the other hand crop uniformity is generally helpful to agriculture because it makes cultural practices (e.g. planting and harvesting) more easily handled. Significant to crop variability is the breeding system of the crop. If the crop has a closed breeding system (Chapter 17) as the result of being apomictic or from having a bisexual flower and being self fertile, then offspring are likely to be the same as their parents and a crop may show little variation. Additionally, if a novel plant does appear, a closed breeding system makes it easier for a farmer to perpetuate plants with that specific feature. For instance, an important characteristic for cereal grains is to have 'non-shattering' heads, meaning inflorescences that do not shed their seeds, holding them on the plant and making harvesting easier. With a closed breeding system, seeds from non-shattering heads are likely to pass that feature on to their offspring since they may have no sexual process at all (apomixis) or are most likely to breed with themselves. In contrast, plants with a more open breeding system are more likely to be variable, with offspring that don't all look alike and don't necessarily look like their parent. And when a plant with favorable characteristics is found, it is more difficult to perpetuate these features through time. In fact, it is likely that these features will disappear quickly, from being 'washed out' by breeding with individuals that do not possess the feature. It is also significant that population size and reproductive isolation influence variability. A population of plants with an open breeding system may be very uniform if the population is small and reproductively isolated from other populations of the same plant, as can be the case for crop species.

Hybrid seed

Even before an understanding of the basis of genetics was developed the phenomenon of 'inbreeding depression', had been noted: the decline in vigor in populations that are continually inbreeding. The degree to which this happens varies among species. It is probably not surprising that inbreeding depression is not a generally a problem for species with closed breeding systems. But for plants with open breeding systems, inbreeding can cause substantial reductions in crop yield. This was recognized by farmers and was part of the reason that seed companies, who took steps to avoid this problem, developed a clientele. Early in the 20th century plant breeders realized that although inbreed lines show reduced vigor, a 'hybrid cross' between two inbreed lines, produced plants that were more vigorous than either of the parental lines before they had been inbreed. Central to the production of hybrid seed is the need to control who breeds with whom. The technique requires that multiple generations bred only with close relatives, something that is easily accomplished by having populations isolated from each other. The next step is more difficult: ensuring that the inbreed lines NOT breed within the population but instead breed with individuals of another inbreed line. This was first done with corn, a plant with separate male and female flowers that are located in different parts of the plant. Crossing of inbreed lines can be accomplished by removing the male flowers (detasseling) from one inbreed line, thereby making these plants solely female and ensuring that any seed produced had a male parent from a separate plant, usually from a second inbreed line that was planted nearby. Hybrid corn was first developed in the 1930's and became the dominant seed source by 1950, with yields increasing dramatically.

Large scale production of pure hybrid seed is nearly impossible in plants with perfect flowers (both male and female structures in the same flower). However, botanists discovered that it is possible to make plants with perfect flowers become unisexual. In the late 18th century workers noticed that not all pollen was viable and the ability to produce viable pollen sometimes often showed maternal inheritance. Later work indicated that there were cytoplasmic (i.e. non-nuclear) factors, inherited maternally (in plastids), that influence the production of viable pollen. Thus, geneticists were able to produce plants that were 'male sterile', not able to produce viable pollen. Having plants that were unisexual (female) made the crosses that were needed to produce hybrid seed much more feasible. Hybrid seed production was further enhanced when 'restorer genes' were found that would restore the ability to make viable pollen. This allowed breeders to two cross two lines, one of which was unisexual, yet have the resulting hybrid produce flowers that are fully functional. Because of cytoplasmic male sterility the number of plants for which hybrid seed could be produced increased dramatically. Another means to the same end is the use of 'chemical hybridizing agents', chemicals that make plants male (usually) sterile.

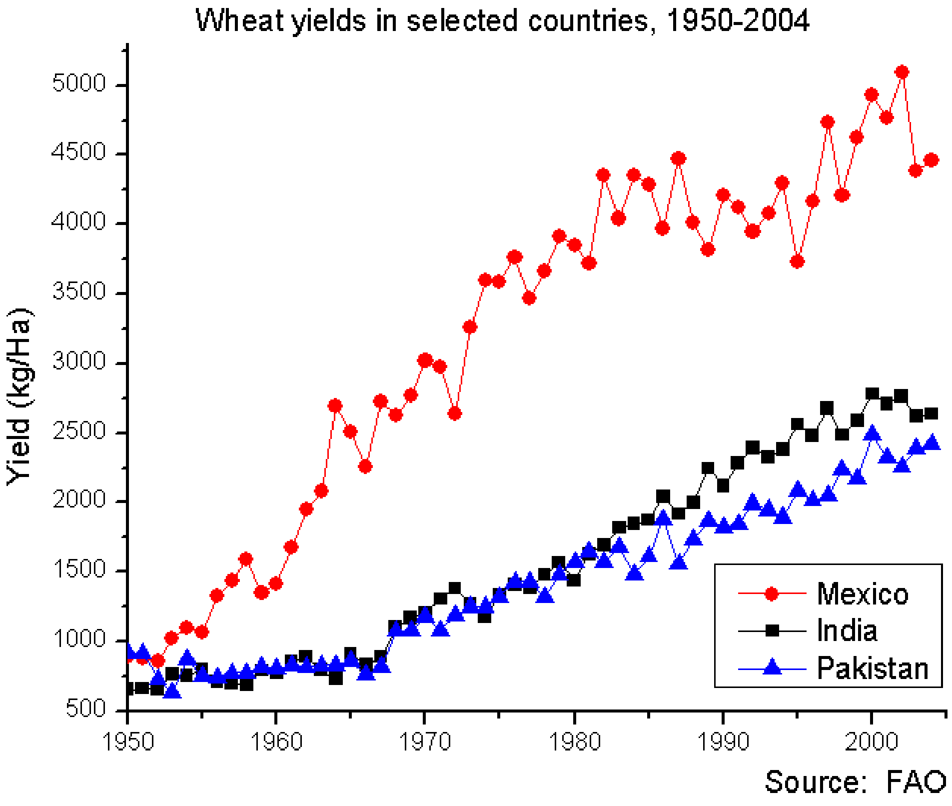
Hybrid seed has several favorable features in addition to producing vigorous plants. The plants in a hybrid crop are more uniform than those produced from open pollinated seeds. Uniformity in size and time of maturation may greatly enhance harvesting. Hybrid crops also allow favorable traits developed in parental lines to be combined.

A negative consequence of planting hybrid seed is that seed cannot be stored year to year. Although the hybrid plant is vigorous, offspring of the hybrid plants are much less vigorous and also more variable. Growers utilizing hybrid seed need to purchase seed each year or switch to using open pollinated seeds instead of hybrid seed.

Another negative consequence of hybrid seed was highlighted by the southern leaf blight that had a significant impact on corn production in the U.S. in 1970 and 1971. The blight was a problem because of crop uniformity, a uniformity caused by the fact that although there were multiple strains of corn that were grown, they all were hybrid seed that had been developed using the same cytoplasmic male sterility factor which, along with affecting male sterility, also made them susceptible to a novel strain of fungal pathogen that appeared in the 1960's. In subsequent years corn breeders reverted to the older strategy of detasseling corn.

The Green Revolution

In the late 1960's several scientists warned of an inevitable global famine, based in part on the assumption population increases would vastly outpace increases in agricultural production based on the assumption that crop yields could not be significantly improved. Fortunately agricultural research, with a series of innovations that became known as the 'green revolution' was able to drastically increase yield (Fig. 6) and the global famine did not occur, although local famines continue to be a problem, usually the result of politics and war. Central to the green revolution were the efforts of Norman Borlaug, both as an agricultural researcher who developed high yielding varieties and as administrator who worked extensively to have new agricultural practices accepted by countries including Mexico, India and Pakistan. Central to the green revolution was hybrid seed and the development of new high yielding varieties of wheat and rice. Surprisingly, these varieties were actually dwarf plants. This had one direct effect: the problem of 'lodging' (plants being knocked over, usually as the result of wind) was lessened because the plants were shorter. But the new varieties also had a number of other features that helped to increase yield: increased seed production per plant, enhanced disease resistance (especially against rusts) and greater tolerance of drought or excessive rain. Also significant was the ability of new varieties to respond with increased yield to increased levels of fertilization. As a result of the new varieties and the new agricultural practices, crop yields increased dramatically throughout the end of the 20th century.



Source: FAO

Fig. 6 Changes in wheat yield in three countries during the 'Green Revolution'

How can crops be improved? And who does the work of crop development?

Crop development requires careful observations and recognition of individuals with favorable traits. By the end of the 19th century the importance of generating variability was increasingly recognized as being significant to crop development. However, in general, farmers desire crop uniformity because it makes growing and harvesting easier and their focus is on growing crops not developing crops. During the 19th century, seeds were increasingly provided by the sources other than the farmer storing seeds or exchanging seeds with neighbors, and crop improvement was increasingly out of farmers' hands. During the latter half of the 19th century the federal government provided seed to anyone who asked for it. And, at the end of the century, land grant universities were charged with improving agriculture and this included developing improved varieties of crops. During this time period, private commercial seed companies became increasingly important as both a source of seeds and as a venue for improving crop quality.

Creating new plants using asexual methods of propagation

Although asexual reproduction is cloning, simply perpetuating what already exists, it has often been important in crop innovation. Novel plants are sometimes produced spontaneously by mutations in the seed or in branches of existing plants, and asexual reproduction of these mutants allows them to become new crops. This is what happened with navel oranges (Chapter 28), McIntosh apples (and many other apple varieties), poinsettia (Chapter 30), and a large number of ornamental plants. Cloning is also important as a means of perpetuating plants (generally hybrids) that have been created naturally (without human intervention) or artificially (with human intervention) that are unable to reproduce sexually.

Related to asexual reproduction is grafting, cutting a branch or bud off one plant and attaching it to a different plant, producing a novel organism, a chimera. There are a variety of reasons why this practice might be desirable, but one obvious one is in order to combine the favorable traits of two individuals into one individual, e.g. a good root system with a good shoot system. This is well represented by wine grape propagation. Stems from a European species are grafted on to root stocks from a North American species. The

Fig. 7 Grafting two grapes together, the stem on the right comes from a North American rootstock. The stem on the left comes from a European variety that is valued for wine production. Successful grafting depends on the vascular cambium or the two plants fusing and then functioning normally as a lateral meristem.

North American species produces inferior grapes for making wine but its root system can withstand attack from the insect pest *Phylloxera.* The root system of the European species is highly susceptible to *Phylloxera* but produces grapes of superior quality for wine. *Phylloxera* was mistakenly introduced from North America to Europe in the early 1800's and devastated European wine production. It was revived when workers were able to plant grapes composed of European shoots grafted on to North American rootstocks. Most fruit trees (apple, peach, plum) are similarly constructed with rootstocks that are vigorous and disease resistant grafted to shoots that produce desirable fruits.

Creating novel plants using the sexual process

Recall that the sexual process generates variability and evolutionists would argue that while this may not be the reason for its origin, it probably is the reason for its widespread occurrence. As discussed above, crops can be modified utilizing variation developed through the sexual process. But below are listed techniques that are capable of more variation more rapidly:

Crossing with relatives

The relatives might be ancestral varieties that the crop originated from or species closely related to the crop. Technically, a crop species should should not hybridize with other species (i.e. it is an isolated gene pool, see Chapter 17) but sporadic seed production does occur when plants are crossed with close relatives. Although successful crosses may be infrequent, as long as there are some viable offspring, these can be back-crossed to the original crop (i.e. cross the hybrid plants with plants from the parental population) with significant introduction of novel traits (i.e. variability) that may include desirable features. Occasionally, workers are successful crossing with more distant relatives (different genera, even different families). Part of this surprising possibility may be poor taxonomy (i.e. they actually are more closely related than depicted in the taxonomy) but apparently sometimes crosses can happen between plants that are not that closely related.

Polyploidy

For a cross to be successful the parents need to have the same chromosome number and the chromosomes of the two parents need to be similar enough that they can pair during meiosis. When hybrids between different species are produced they are generally sterile because of the inability to pair chromosomes during meiosis. Although the hybrid is sterile it is often possible to propagate it asexually, i.e. to clone the hybrid, . A number of ornamental plants are perpetuated this way. It also is what has occurred with banana, the plant that is cultivated is a sterile hybrid, unable to produce seed but this one of the features that make the commercial banana desirable! Another 'solution' to the problem of hybrid sterility is polyploidy, increasing the chromosome number. This sometimes happens without human involvement (see discussion of the evolution of wheat in Chapter 28) but in the last 100 years workers have developed techniques to promote polyploidy following hybridization, thereby creating a new species with characteristics of both parental lines.

Treatment with mutagens

A common means of generating variability, and perhaps producing favorable traits that can be selected for, is to treat the seeds with a chemical mutagen or radiation. Although most of the treated seeds do not survive or have unfavorable features, usually some seeds survive and some of these may have desirable features. These plants can be crossed with existing varieties in hopes of introducing favorable features to the crop. The technique is also used with asexual propagation. The original ruby red grapefruit appeared as a sport on a normal grapefruit tree. Irradiation of branches of the original ruby red has produced the even redder varieties: Rio Red and Star Ruby.

Genetically modified organisms

A much more focused technique of combining traits from different organisms is the production of 'GMO's, genetically modified organisms; the phrase should be non-sensical to any trained biologist because all organisms are genetically modified, that is what evolution is about. But if we focus only on agricultural organisms the term has come to distinguish 'normal' agricultural organisms, all of which have a long and substantial history of genetic modification by humans from 'abnormal' agricultural organisms, ones produced using the relatively recent techniques of molecular biology that allow for much more focused genetic modification, with genes manipulated in various ways including: turned on, turned off, duplicated, removed and, in particular, moved from one organism to another. One famous example is 'golden rice', rice to which additional genes, genes that cause the rice produce beta-carotene, a vitamin D precursor, have been introduced into the endosperm of the seed. A second example is 'Bt' corn, which has a gene derived from the bacterium *Bacillus thuringiensis,* that produces a protein that is toxic to some insects, in particular the corn borer moth. Consequently 'Bt-corn' can avoid predation by corn borers. Interestingly, these bacterial toxins had been used by organic farmers, after being mass produced by culturing *B. thuringiensis,* extracting the toxins and then spraying them on corn plants. A final example is 'Roundup ready' soybeans. Roundup is a commonly used herbicide that is effective because it blocks an important bio-synthetic pathway. Plant molecular biologists were able to introduce genes into several crops, including soybean and cotton, that greatly reduced the the toxicity of roundup to these crops, making them 'roundup ready'. The advantage of modern molecular techniques is specificity: plants are modified in very specific ways. In contrast, developing new crops by hybridization or by chemical or radiational means will have multiple effects — yet the breeder is only paying attention to a small number of characters they are hoping to modify.

GMO's have been vigorously opposed by a variety of groups for a variety of reasons. This opposition has decreased substantially in the last five years, partly because many of the problems that were cited have not appeared even though GMO plants have been in wide use over the last fifteen years. Any large-scale production of crops with novel characteristics will have possible risks, but the GMO's are probably one of the more benign techniques to generate variability. Consequently the production and use of GMOs is likely to increase in the coming years.

Further Reading and Viewing

- "The genome of cultivated sweet potato contains Agrobacterium T-DNAs with expressed genes: An example of a naturally transgenic food crop" by Tina Kyndt et al. A fascinating tale of a natural occurrence of gene modification in traditionally developed sweet potato.
    - https://www.pnas.org/doi/10.1073/pnas.1419685112
- "Southern Corn Leaf Blight: A Story Worth Retelling" by H. Arnold Bruns. Corn blight associated with cytoplasmic male sterility.
    - https://www.ars.usda.gov/ARSUserFiles/60663500/Publications/Bruns/2017/Bruns_2017_Corn%20Leaf%20Blight.pdf

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ORGANISMS

A SAMPLING OF INANIMATE LIFE

The following 'Organisms' section of the book considers more than 50 groups of organisms as examples of the diversity of inanimate life. How might these fifty-plus groups be organized? The simplest method is an alphabetical list; this is done in the Table of Contents of the book and is also present as a list at the end of this section. Another, and a more 'biological', way to organize (i.e. classify) these groups would be in a taxonomic scheme, utilizing four of the five kingdoms sometimes used to group organisms: Monerans, Protists, Fungi and Plants. But, as discussed in the introduction, the five-kingdom classification has largely been replaced with more phylogenetic approaches. Unfortunately, such classifications are still in flux and are also unwieldy, as a visit to most general biology textbooks will attest.

Instead, and since this book emphasizes the structure and nutrition of different groups, the following classification of organisms is presented based on

- their mode of energy acquisition
  - heterotroph, autotroph (photosynthetic and chemosynthetic)
- their structural features
  - prokaryote vs. eukaryote,
  - composition (cellular nature, see Chapter 3)
    - unicellular, multinucleate, colonial or multicellular

Table 1 presents such a classification and Table 2 repeats it with links to the groups covered. Note that the groups identified vary considerably in taxonomic level, with some at the level of species (e.g. corn, potato), some at the level of genera (e.g. pines, *Chlamydomonas*), some at the level of orders (e.g. rusts, coccolithophores) and some groups that do not represent a recognized taxonomic entity (e.g. molds, bracket fungi and lungwort lichen).

For each group there is information relating to the coverage in the text, outlining the group's:

- phylogeny and classification,
- structure,
- reproduction
- matter and energy considerations
- interactions with physical and biotic factors, including humans.

In many instances a genus has been chosen to represent a larger group (e.g. *Rhizopus* to represent the bread molds (Zygomycota); late blight of potato (*Phytopthora)* to represent the water molds (Oomycota)). As discussed in Chapter 2, one has to be aware that variation is 'hidden' in any name (i.e. grouping)—not all bread molds are the same, and any entity that might be selected to represent a group is certainly not a 'perfect' representative of the group. Also note that much of the information for any of these groups may not come into focus until reading the 'textbook' part of the book (chapters 1-31).

TABLE 1: A classification of inanimate life

Heterotrophs

Prokaryotes (lacking a nucleus and cellular organelles

- unicellular
    - most Bacteria
    - most Archaea
- filamentous (colonial)
    - some Bacteria
    - some Archaea

Eukaryotes (possessing a nucleus and other organelles)

- Unicellular with a single nucleus
    - some chytrids (Chytridiomycota, a fungal group with some colonial members)
    - yeasts (these are atypical members of generally multicellular or colonial fungal groups; most are cup fungi = Ascomycota
    - cellular slime molds (these are multicellular during parts of their life)
    - some dinoflagellates (but most are photosynthetic)

- Unicellular and multinucleate organisms
    - Plasmodial slime molds
    - Bread molds (a fungal group)
    - Glomeromycota (a fungal group, most associate with plants)
    - 'Water molds' (not a fungal group)
- colonial organisms
    - Club fungi (Basidiomycota)
    - Cup fungi (Ascomycota)
- multicellular organisms
    - Club fungi (Basidiomycota)
    - Cup fungi (Ascomycota)
    - (gametophytes of club mosses)
    - (a few seed plants)

Autotrophs

Chemosynthetic autotrophs (all are prokaryotic)

- a few Bacteria (e.g. nitrifying bacteria)
- a few Archaea, including some methanogens

Photosynthetic organisms

- Prokaryotes
    - some Bacteria (the Cyanobacteria and also several other groups)
- Eukaryotes that are unicellular
    - Euglenophytes
    - Crypto-monads
    - Dinoflagellates
    - Haptophytes (including cocolithophores)
    - Chlorophyta—Green algae (but many are multinucleate, colonial and some are multicellular)
    - Bacillariophyta — diatoms (mostly unicellular, some colonial)
    - Rhodophyta—Red algae (a few unicellular but most are colonial or multicellular)

- Eukaryotes that are unicellular and multinucleate
    - some Chlorophyta—Green algae
- Eukaryotes that are colonial
    - some diatoms
    - some Chlorophyta—Green algae
    - some Phaeophyta—Brown algae
    - some Rhodophyta—Red algae (a few are unicellular)
- Eukaryotes that are multicellular organisms
    - aquatic
        - some Chlorophyta (Green algae)
        - some Phaeophyta (Brown algae)
        - some Rhodophyta (Red algae)
    - terrestrial
        - lacking seeds and lignin ('non-vascular plants')
            - Bryophyta—mosses
            - Hepatophyta—liverworts
            - Anthocerophyta—hornworts
        - lacking seeds, possessing lignin ('vascular plants without seeds')
            - Pterophyta—ferns
            - Lycopodiophyta—club mosses
            - Equisetophyta—horsetails
        - with seeds, without flowers ('gymnosperms')
            - Coniferophyta—conifers
            - Cycadophyta—cycads
            - Ginkgophyta—ginkgo
            - Gnetophyta—gnetophytes
        - with seeds and flowers
            - Anthophyta = angiosperms = flowering plants
                - monocots, including grass family and orchid family
                - 'dicots', including pea family and sunflower family

Autotrophs that need organic carbon

(groups with both autotrophic and heterotrophic members), and groups with members that can shift between autotrophic and heterotrophic; all are unicellular.

- Prokaryotes
  - some Bacteria (some of the nitrifying bacteria)
  - one genus of Archaea (*Halobacterium*)

Mixotrophic organisms

(groups with both autotrophic and heterotrophic members), and groups with members that can shift between autotrophic and heterotrophic; all are unicellular.

- Prokaryotes
  - some Bacteria
  - some Archaea
- Eukaryotes (all are in groups considered 'algae ')
  - Euglenophytes
  - Cryptomonads
  - Dinoflagellates

TABLE 2: Groups covered in the organism section of the book

Heterotrophs

Prokaryotes (lacking a nucleus and cellular organelles

- unicellular
  - most Bacteria *Rhizobium*, *Thermus aquaticus*
  - most Archaea
- filamentous (colonial)
  - some Bacteria
  - some Archaea

Eukaryotes (possessing a nucleus and other organelles)

- Unicellular with a single nucleus

    - some chytrids (Chytridiomycota),
    - yeasts
    - cellular slime molds
    - some dinoflagellates
- Unicellular and multinucleate organisms
    - Plasmodial slime molds
    - Bread molds
    - Glomeromycota (a fungal group, most associate with plants)
    - Water molds (not a fungal group)
- colonial organisms
    - Club fungi (Basidiomycota)
    - Cup fungi (Ascomycota), tar spot disease, molds
- multicellular organisms
    - Club fungi (Basidiomycota), *Agaricus*, bracket fungi, rusts
    - Cup fungi (Ascomycota)
    - (parasitic flowering plants *Corralorhiza)*
    - the gametophyte stage of clubmosses *Lycopodium*

Autotrophs

Chemosynthetic organisms (all are prokaryotic)

- a few Bacteria nitrifying bacteria, some methanogens
- a few Archaea, including some methanogens

Photosynthetic organisms

- Prokaryotes
    - some Bacteria (the Cyanobacteria — *Nostoc*
    - one genus of Archaea *Halobacterium*
- Eukaryotes that are unicellular
    - Euglenophytes–*Euglena*
    - Cryptomonads
    - Dinoflagellates *Gonyaulax*
    - Haptophytes (including cocolithophores)

    - Chlorophyta—Green algae- *Chlamydomonas*, *Acetabularia*, *Caulerpa*, *Chara, Oedogonium*
    - Bacillariophyta — diatoms
    - Rhodophyta—Red algae (a few unicellular but most are colonial or multicellular)
- Eukaryotes that are unicellular and multinucleate
    - some Chlorophyta—Green algae *Caulerpa*
- Eukaryotes that are colonial
    - some diatoms
    - Chlorophyta—Green algae *Oedogonium*,
    - Phaeophyta—Brown algae
    - Rhodophyta—Red algae — *Porphyra*
- Eukaryotes that are multicellular organisms
        - aquatic
            - some Chlorophyta (Green algae)
            - some Phaeophyta (Brown algae)–*Fucus*, *Laminaria*
        - terrestrial
            - lacking seeds and lignin ('non-vascular plants')
                - Bryophyta—mosses *Polytrichium*, *Sphagnum*
                - Hepatophyta—liverworts–*Marchantia*
                - Anthocerophyta—hornworts
            - lacking seeds, possessing lignin ('vascular plants without seeds')
                - Pterophyta—ferns sensitive fern, wood fern, *Marsilea*
                - Lycopodiophyta—club mosses
                - Equisetophyta—horsetails
            - with seeds, without flowers ('gymnosperms')
                - Coniferophyta— hemlock, redwoods, juniper, pine
                - Cycadophyta—cycads
                - Ginkgophyta—ginkgo
                - Gnetophyta—gnetophytes *Ephedra*
            - with seeds and flowers
                - Anthophyta = angiospersms = flowering plants
                    - monocots, corn, wheat, rice,
                    - 'dicots' aspens, dandelion, alfalfa, soybean, sagebrush, sunflower, coltsfoot, pitcher plant

Autotrophs that need organic carbon

(groups with both autotrophic and heterotrophic members), and groups with members that can shift between autotrophic and heterotrophic; all are unicellular.

- Prokaryotes
    - some Bacteria (some of the nitrifying bacteria)
    - one genus of Archaea (*Halobacterium*)

Mixotrophic organisms

- Prokaryotes
    - some Bacteria
    - some Archaea–*Halobacterium*
- Eukaryotes (all are unicellular, aquatic and include members that are considered 'algae')
    - Euglenophytes–Euglena
    - Cryptomonads
    - Dinoflagellates

Alphabetic listing of groups

Acetabularia, an unusual unicellular green algae

Agaricus bisporus, the commercial mushroom

Alfalfa

Bracket Fungi

Calupera, a large coenocytic green algae.

Chara, the stoneworts

Chlamydomonas, a small unicellular green alga

Chytrids, tiny fungi

Clubmosses: Lycopodium

Coccolithophores, photosynthetic unicellular algae

Coltsoot: Tussilago farfara

Corn

Corralorhiza, a plant that eats fungi

Cryptomonads, unicellular photosynthetic algae

Dandelion

Diatoms, unicellular photosynthetic algae

Dictyostelium: a cellular slime mold

Ephedra: jointfir

Euglena: a unicellular algae

Ginkgo

Glomeromycota: important mycorrhizal fungi

Gonyaulax: a dinoflagellate

Halobacterium

Hemlock

Horsetails, the genus Equisetum

Juniper

Kelp: Laminaria, a brown algae

Lungwort lichen (Lobaria pumonaria)

Marchantia: thalloid liverwort

Sensitive fern

Soybeans (and other beans)

Sphagnum-peat moss

Sunflower: Helianthus annuus

Tar Spot Fungus

Thermus aquaticus

Wheat

Wood ferns

Yeast

ACETABULARIA, AN UNUSUAL UNICELLULAR GREEN ALGAE

Acetabularia is a member of a very diverse group, the green algae. Other members of the same group that we will consider are *Oedogonium*, *Chlamydomonas* and *Cladophora*, all of which are quite different in form and structure.

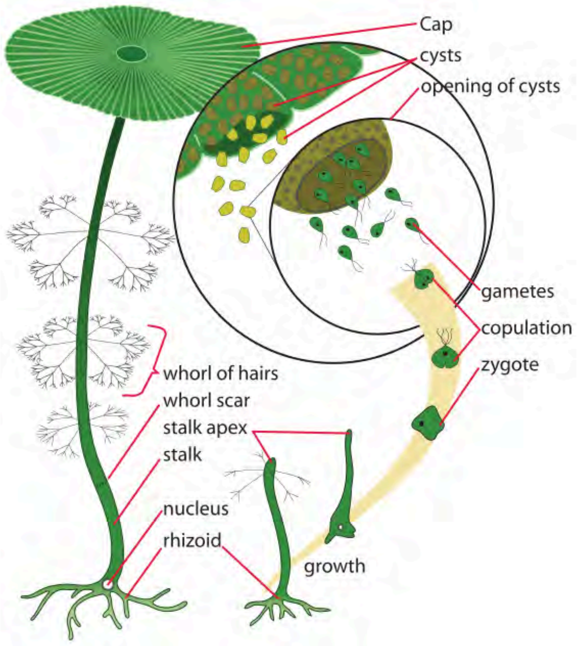
Taxonomy and Phylogeny

The green algae are generally put in their own phylum, Chlorophyta, but this phylum is placed variously depending upon the perceptions of the observer. Some workers still consider them to be one of the protist phyla. Workers who reject the protist kingdom often put green algae in the 'Archaeplastid supergroup'. However, since some of the green algae are closely linked to plants, some workers combine plants and some or all of the green algae into a 'Viriplantae' group. (See the reading on *Chlamydomonas* for more details on green algal classification.)

Structure

Acetabularia has an unusual structure by being large, unicellular and possessing features that might be considered organs —' roots, stems and leaves'. The single cell is attached to the substrate by root-like cellular extensions. These extensions connect to an elongate stalk that ends in an umbrella-like cap which is often 1 cm or more across. The single nucleus of this remarkable organism is found at the base of the stem. If the stalk is cut it can regenerate a new top and the top can generate a new base, although it is short-lived, presumably because it lacks a nucleus.

Reproduction



Sexual reproduction in *Acetabularia* is initiated when the single (diploid) nucleus goes through multiple mitotic divisions; these nuclei subsequently undergo meiosis and migrate to the cap where they are released in cysts that break open to release mobile gametes. If these gametes find gametes from another alga they fuse to form a zygote that attaches to a substrate and grows into the mature form. Asexual reproduction is also possible if mobile (diploid) zoospores are released and behave like zygotes, attaching to a substrate and developing into the mature form.

Matter and energy

Acetabularia is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and as building materials to synthesize a variety of biomolecules. In some species the chloroplasts show an endogenous circadian movement from the cap to the rhizoids at dusk and back at dawn. Since the organism is capable of regenerating caps if they are removed (even though it is a single cell), this movement may be adaptive by preserving resources. In addition to acquiring the minerals elements required for life (Chapter 22) *Acetabularia* is unusual in being able to take up and sequester mercury.

Interactions

Acetabularia is generally found in warm, marine waters. Since it attaches to substrates and requires light for photosynthesis it is generally found in shallow waters, to depths that depend on water clarity. *Acetabularia* is eaten by sea urchins and fish.

Media Attributions

- Acetabularia mediterranea life © LadyofHats is licensed under a Public Domain license

AGARICUS BISPORUS, THE COMMERCIAL MUSHROOM

Agaricus bisporus, is the most familiar mushroom for most of us — it is the commercial mushroom sold in grocery stores and put on pizza. It comes in various forms: button versions, brown versions and large portobello versions — all of which are varieties of the same species. Its popularity is not so much a consequence of flavor as it is a consequence of its suitability for commercial production. *Agaricus* does grow wild, typically in fields or lawns but all of the *Agaricus* mushrooms sold in stores are grown on a controlled medium and in a controlled environment, often in caves or underground structures, not so much for the darkness but because of constant temperatures and high humidities.

Phylogeny

Agaricus, and nearly all of the fungi that would be described as mushrooms, i.e. that produce stalked structures with a cap, are club fungi = basidiomycete fungi (Phylum Basidiomycota). Most mushrooms have ‘gills’ on the underside of the cap where spores are produced, and *Agaricus* shows this feature. Historically all mushrooms with gills were put in a taxonomic entity (usually an order, the Agaricales) but recent molecular analysis has demonstrated that gills are not a sound feature on which to base a phylogenetic classification. Although there still is an order Agaricales, named for *Agaricus,* it does not contain all gilled mushrooms and it does include a number of fungi that do not possess gills.

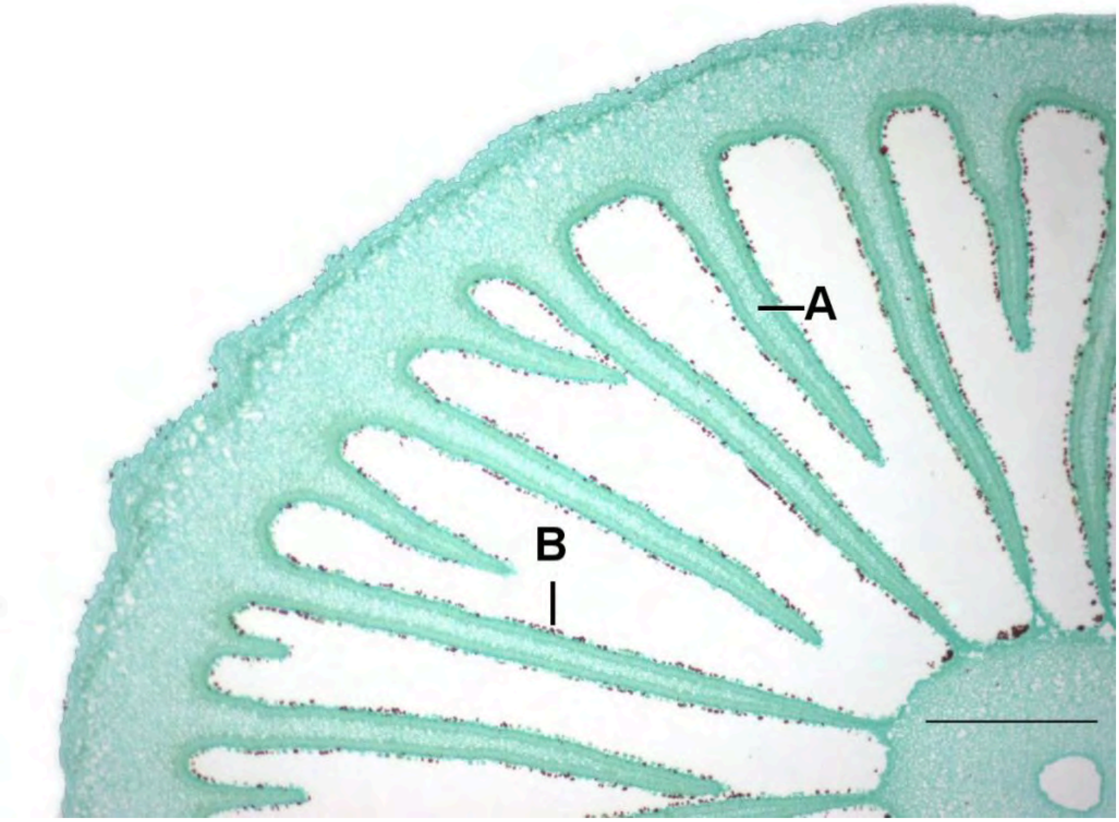
Structure

Like nearly all fungi and nearly all club fungi, the bulk of a mushroom's structure is a network of branching filaments, one cell thick (hypae), that permeate a substrate. In the case of wild *Agaricus,* the substrate is the soil; for cultured *Agaricus* the substrate is a prepared compost, typically manure with other material added to it. In club fungi the filaments are cellular, meaning that there are individual cells delineated by the presence of cross-walls (septa). The septa are not complete but usually have a pore in the middle that allows cytoplasm to move from one cell to another. The fruiting body of *Agaricus* is a consequence of drastic change in the behavior of hyphae. Instead of growing in a diffuse manner and spreading throughout their environment, they grow close to each other and intertwine, forming a solid structure that emerges from the substrate it is growing in and produces the familiar mushroom structure

The underside of a mushroom cap, showing the gills, the location of spore production.

Sex and reproduction

Agaricus completes its sexual cycle by producing basidiospores on the margins of the gills of the mushroom. Like almost all fungi in the Basidiomycete group, the organism exists primarily in a 'dikaryon' state where each cell has two nuclei, one from each parent produced after two haploid hyphae fuse. Only in certain parts of the fruiting body do the two nuclei fuse to form a diploid cell that then undergoes meiosis to produce haploid, 'sexual' spores. However, for a mushroom farmer, reproduction of *Agaricus is* totally asexual. They do not sow spores, instead they use pieces of mycelium (the name given to cluster of hyphae), induce it to grow, and then stimulate it to produce fruiting bodies. Some of the mycelium remains and can be used to continue the process. The mycelium is probably capable of living thousands of years.

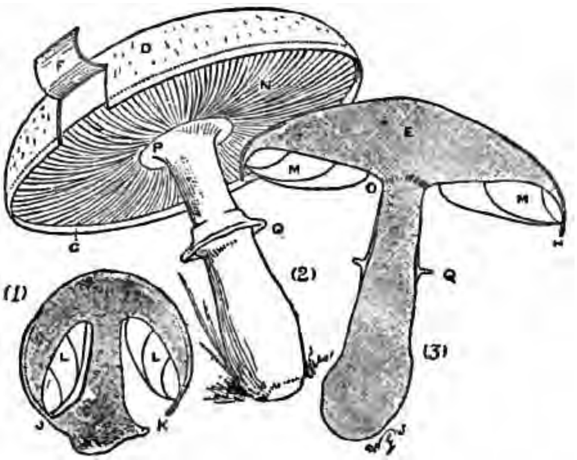


Light microscopy of gill mushroom showing a sectional view of the mushroom where the gills can be seen with basidiospores lining the gills. A=Gill, B=Basiospore. Scale bar = 0.3mm

Light microscopy of gill mushroom sowing the edge of the gills where basidium can be seen with basidiospores. A=Sterigma, B=Basidium, C=Basidiospore, D=Immature basidia. Scale bar = 0.01mm.

Matter and energy

Agaricus is a typical heterotroph that feeds upon biomass produced by other living organisms. They secrete enzymes into their environment that break down organic matter into simple forms that can be absorbed into the hyphae and then they re-assemble these materials to make new fungal biomass. Fungi are considered 'decomposers', but what is not often appreciated is that their nutrition is the same as predators, herbivores and omnivores (including humans). All are heterotrophs and obtain nutrition by breaking down (decomposing) organic material produced by other organisms. As a result of their activities they make more of themselves (i.e. they could be considered a 'producer') but because they break down much more material than they produce they are **net** 'decomposers'.



In commercial operations, the mycelia are feed 'conditioned' compost. You may have heard that mushrooms eat horse droppings — this isn't exactly true. To feed commercial mushrooms farmers take compost containing horse droppings and other materials (e.g. straw) and allow it to ferment for a week or two. During this time the compost is 'eaten' by bacteria, other fungi and microscopic animals. These organisms break down the compost, putting it in a form more acceptable to the commercial fungus. They also build up their populations, and the commercial fungus feeds on these 'primary decomposer' populations. So the commercial fungus doesn't eat horse droppings, it eats things that themselves eat horse droppings, along with the remnants of horse droppings left behind after the 'first' eating.

Interactions

Like most organisms, interactions between *Agaricus* and other organisms and the physical environment are extremely important to its success. This is reflected in the links below that describe how mushrooms are commercially grown. As described above, *Agaricus* is known as a 'secondary decomposer '— it feeds on material after it has been eaten by 'primary decomposers'; this is similar to the interaction of cows with the microorganisms in their stomachs. Cows cannot digest grass, they need the microbes to act on the grass (in one of their stomachs) and produce something that they can utilize. *Agaricus* is also very strongly affected by (i.e. interacts with) physical conditions, in particular temperature, humidity and the concentration of carbon dioxide. These conditions both control the mycelium to growth rate and also the initiation of fruiting bodies.

Further Reading and Viewing

- "Agaricus bisporus" by Michael Kuo.
    - http://www.mushroomexpert.com/agaricus_bisporus.html

- “Agaricus bisporus, the white button mushroom or pizza mushroom, also known as Portabella and Crimini” by Tom Volk and Kelly Ivors.
    - http://botit.botany.wisc.edu/toms_fungi/apr2001.html
- “Fungiculture” on Wikipedia.
    - https://en.wikipedia.org/wiki/Fungiculture

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ALFALFA

Alfalfa (*Medicago sativa),* is an important perennial herbaceous crop. Most people are familiar with annual crops (planted in the spring and harvested in the fall), and with woody perennial crops (grapes, apples, cherries) but there also are perennial crops that are non-woody. While a few produce food for humans (sugar cane, asparagus, rhubarb, groundnuts) most herbaceous perennial crops are 'forage' crops producing food (usually called 'hay') for domesticated animals, especially horses and cattle. While many think of hay as being annual and perennial grasses, there are a number of dicot flowering plants, including alfalfa and clover, both perennials, that are very important sources of 'hay'. Humans do eat alfalfa plants, but only in the form of alfalfa 'sprouts', young germinated seeds.

Phylogeny

Alfalfa is in the pea family. It is a flowering plant (angiosperm) and is a dicot (eudicot) in one of the largest and most important plant family, the pea family, which includes numerous important crops and many ecologically important species.

Structure

Alfalfa growth produces a typical stem with alternate, trifoliate leaves and branches that originate in the axils of these leaves. However, this growth only lasts a year in most of the (temperate) habitats where the plant grows, habitats where winter cold kills most of the above ground plant. Alfalfa's existence as a perennial depends upon what is known as a 'crown', which is a section of the stem close to the ground surface. This structure produces adventitious buds that provide for growth after most of the above ground portion of the plant dies in the winter. Under agricultural conditions the crown also allows the plant to re-sprout after nearly all of the above ground portion of the plant has been harvested. Harvesting often occurs up to six times over the growing season.

Sex and reproduction

Alfalfa flower from several perspectives: top, side and bottom are on the left and directly in front is on the far right.

Alfalfa is a typical flowering plant that has bisexual flowers that require pollination in order to set seed. Flowers are 'irregular', meaning that they are not radial symmetrical like a rose or buttercup. Irregular flowers are typical of the pea family. The anthers and pistil are under tension between a pair of petals that form the 'keel' of the flower. To effect pollination an insect must land on the keel in such a way to trigger a rapid movement of the stamens to 'slap' the underside of the visitor. (see the "Alfalfa Pollen Explosion" video). Honeybees are poor pollinators of alfalfa, they visit to obtain nectar but don't trigger the movement of the stamens, perhaps because they don't like being slapped by the anthers. If successfully pollinated, corkscrew fruits develop with small seeds.

Seed pods of alfalfa.

Matter and energy

Alfalfa is a photosynthetic autotroph which uses the C 3 photosynthetic pathway. Like many of the pea family alfalfa houses *Rhizobium* bacteria in nodules on its roots. The *Rhizobium* bacteria provide a source of nitrogen to the plant, but also represent a sizable drain on photosynthate because substantial amounts are needed to 'feed' the bacteria.

Interactions

Alfalfa originated in the Middle East, probably Iran, and has been cultivated by humans for over 2500 years to provide food for livestock. Because of human introductions it is now found world-wide, primarily in temperate habitats. It is slightly invasive and can be found on roadsides and other disturbed habitats in addition to habitats that are under cultivation. It is drought tolerant and does well on sites that are quite dry. Consequently alfalfa is grown extensively in the western US. Its root system commonly goes down three meters into the soil to acquire water and occasionally goes down 15 m (over 50 feet!!!!). Interestingly, it produces chemicals that deter the germination of its own seeds, necessitating that fields alternate from alfalfa to another crop before being reseeded in alfalfa.

Because honeybees are poor pollinators, farmers growing alfalfa for seed (as opposed to growing it for hay in which case pollination doesn't matter) rely on other pollinators. These other pollinators need to be managed to produce generate the high pollinator population densities needed to effect pollination.

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- Hay bales © Gary D Robson is licensed under a CC BY-SA (Attribution ShareAlike) license

BRACKET FUNGI

Two examples of bracket fungi: *Fomes* and *Ganoderma*

Bracket fungi

If you are observant and spend much time hiking in the woods you are sure to encounter a bracket (shelf) fungus, fruiting bodies of wood decay fungi that are found both on standing and fallen trees and form a hard outgrowth with a spore producing surface facing downward. Unlike most mushrooms (gill fungi) that produce spores on linear rows (gills) (see Agaricus), these fungi produce spores in a tissue perforated with numerous cylindric pores, generally from 0.2 to 2 mm in diameter, through which the spores are shed. Fungi producing such structures are called polypore ('many pores') fungi, and while there are a few polypore fungi that do produce a ' mushroom' shaped fruiting body, the majority of polypore fungi are bracket fungi, growing off trees trunks and branches like a shelf or a 'bracket'.

Phylogeny

Pores on the underside of Ganoderma, measuring 0.2 mm = 200 um across

Both of the genera discussed here (*Fomes* and *Ganoderma*), and all fungi considered bracket fungi, are Basidiomycetes (club fungi) in the Kingdom Fungi. When fungal taxonomy was based on morphology (form) , all woody polypore fungi were lumped together, i.e. there was a taxonomic entity that included all woody polypore fungi. M ore recent analysis has revealed that woody polypores come from multiple lines, i.e. that a grouping of bracket fungi or of 'polypore fungi' is artificial, not phylogenetic.

Structure

Both of these fungi are typical fungi, producing colonial filaments of cells (hyphae) that branch and fuse to form a feeding structure called a mycelium. This branched dendritic form penetrates the heartwood of trees to obtain nutrition. As a result of certain stimuli the hyphae will grow in a very different way (highly condensed and intertwined) and in a different place (outside the tree stem) to produce a fruiting body, where special cells associated with sexual reproduction, are produced. The fruiting body of both these genera is described as being 'trimictic', meaning that it is composed of three different types of hyphae: generative hyphae, the ones that produce spores; skeletal hyphae, with very thick-walled hyphae and little branching; and binding hyphae, hyphae with extensive branching.

Sex and reproduction

Both of these fungi undergo the normal sexual process shown by basidiomycete fungi ('club-fungi'). Haploid spores of two different mating types need to germinate on a tree and find each other to form a dikaryotic mycelium that feeds on the tree and grows. At some point a fruiting body is produced in which special cells undergo karyogamy to produce a diploid cell that immediately undergoes meiosis to form haploid basidiospores that are dispersed through the air to other trees.

Matter and energy

These fungi are typical heterotrophs that feed upon biomass produced by other living organisms. They are called 'heart rot fungi', feeding on the heartwood, the central cylinder of tree trunks that contains no living cells. Sapwood, the outer part of a wood, does contain some living cells, although a majority of the cells are dead at maturity. The living cells of the sapwood provide the tissue with greater resistance to fungal invasion, hence most wood eating fungi are able to infect heartwood but not sapwood.

Both of these fungi are described as 'white-rot' fungi, a name that describes the feeding preferences of the fungus. Wood has three main components: cellulose, hemicellulose (both polysaccharides) and lignin (a complex polymer of phenolic subunits). Wood rot fungi often specialize, i.e. they have dietary preferences, for either carbohydrates or lignin. These species leave behind the material that they don't 'choose' to eat, either lignin, which is generally brown in color, or cellulose, which is white. Brown-rot fungi leave behind the lignin, white-rot fungi leave behind the cellulose. Since using wood for paper or to make ethanol requires removing lignin, there is an interest in developing technologies that utilize white-rot fungi to do this.

Interactions

Since they kill no living tissues, these fungi will not directly kill trees but they may decrease the mechanical strength of trunks and cause them to break more easily (however, some argue that hollow cylinders are stronger under some circumstances than solid cylinders, in which case the action of these fungi might be considered to improve strength). The fungi need some sort of damage to the tree to allow them to enter the heartwood, this damage can come from a variety of agents: shedding of branches; damage from abrasion by the falling of neighboring trees or branches; feeding by wood eating herbivores such as beaver and porcupine; abrasion by deer and moose 'rubbing' the tree with their antlers or by bears stretching their claws; boys playing with hatchets.

The fungal hyphae are sometimes food for insects (larvae) that may in turn be food for other insects or for woodpeckers.

Both these fungi have interesting interactions with humans–read more about these below.

Further Reading and Viewing

- "Ganoderma applanatum, the artist's conk" by Thomas J. Volk.
    - http://botit.botany.wisc.edu/toms_fungi/march99.html
- "Fomes fomentarius, the tinder polypore" by Thomas J. Volk.
    - http://botit.botany.wisc.edu/toms_fungi/dec2001.html

Media Attributions

- Fungi in Borneo © Cayce is licensed under a CC BY (Attribution) license

Birch polypore (Piptoporus betulinus) on the trunk of a birch, a common parasite that primarily feeds on birch. Unlike the species mentioned above, this species often kills its host.

- Ganoderma applanatum © George Chernilevsky
- Fomes fomentarius © Algirdas is licensed under a Public Domain license
- Berkenzwam © Dominicus Johannes Bergsma is licensed under a CC BY-SA (Attribution ShareAlike) license

CAULERPA, A LARGE COENOCYTIC GREEN ALGAE

Caulerpa, another example of green algal diversity

Caulerpa prolifera

Caulerpa is a large green algae that appears to be multicellular because it is organized into different parts, seemingly leaves, stems and roots. But it is actually just a single large cell. And since an individual organism might be two meters in extent, Caulerpa produces the largest cells on earth, except for maybe some plasmodial slime molds. They are mostly found in shallow waters in warmer oceans but a few occur in fresh water.

Phylogeny and Taxonomy

Caulerpa is in the green algal phylum (Chlorophyta), in a group generally considered to be a class labelled the Ulvophyceae, a group not considered to be closely related to land plants although other green algae are. There is more discussion of green algae in the *Chlamydomonas* page.

Structure

Caulerpa is siphonaceous (coenocytic) meaning that the cells are multinucleate and specifically in this case there is only a single cell per organism. They typically have a horizontally running structure off of which come extensions to attach it to the substrate ('roots') and extensions to increase photosynthetic area. Depending on species, these may be blade-like, feather-like or spherical.

Sex and Reproduction

Caulerpa sertularioides

Most commonly *Caulerpa* reproduces asexually by fragmentation but it is also capable of sexual reproduction, although the details are not completely known. The algae sometimes concentrate their protoplasm in the tips of blades/leaves where it becomes cellular and is released as uninucleate gametes while the rest of the plant senesces and dies. The released gametes are capable of fusing with each other. At this point the knowledge of the life cycle falters. Meiosis must occur at some point but it is not known if it occurs right after syngamy, right before the production of gametes or perhaps that there are both haploid and diploid plants that look alike (cf. *Ulva*, see Chapter 11).

Matter and Energy

Caulerpa is a typical photosynthetic autotroph, acquiring carbon as bicarbonate ion (HCO_3^-) which is produced when carbon dioxide reacts with water to form carbonic acid which then ionizes. The carbon is used to produce hexose sugars that are then used both for material needs (to make cell walls, cell membranes, amino acids, etc) and also for energetic needs when the hexose are oxidized in oxidative phosphorylation. *Caulerpa* acquires 14 other elements obtained by absorbing small ions from the water.

Interactions

Caulerpa oxygenates the environment it is in and serves as a food source for a number of animals. However, it does produce toxins. Like the toxins associated with red tides and produced both by dinoflagellates and cyanobacteria, some toxins affect certain herbivores while others herbivores are unaffected but may accumulate the toxin, thereby allowing it to affect consumers of the herbivore. *Caulerpa* is native to warm waters around New Zealand and Australia but is invasive in parts of the Mediterranean and off southern California, where it is sometimes causes a variety of problems. It's spread to new areas may be partially due to its use in aquaria and their disposal in nearby waters.

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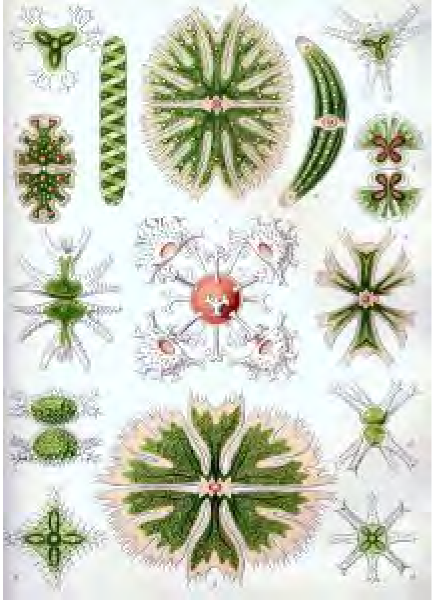
- Feather algae, Caulerpa sertularioides at 11 meters depth on ridge © U.S. Government work is licensed under a Public Domain license

CHARA, THE STONEWORTS

Stoneworts are a distinctive green algae that look quite 'plant-like'. As is often the case, especially in taxonomy, looks can be deceiving (think convergent evolution). And, although *Chara* are among the green algae most closely related to plants, the visual similarity doesn't actually attest to this. Instead the connection is justified because of biochemical features (sporopollenin and precursors of lignin), plasmodesmata, the presence of a cell plate during mitosis, the presence and structure of flagellated sperm and, of course, a multitude of molecular data

Stoneworts get their name because they usually have calcium carbonate deposits in their cell walls, a consequence of the hard water (high calcium) habitat that they often grow in, perhaps coupled with their own activities increasing the pH, which can cause calcium carbonate precipitation out of the aqueous solution. Stoneworts are large algae that can dominate some habitats.

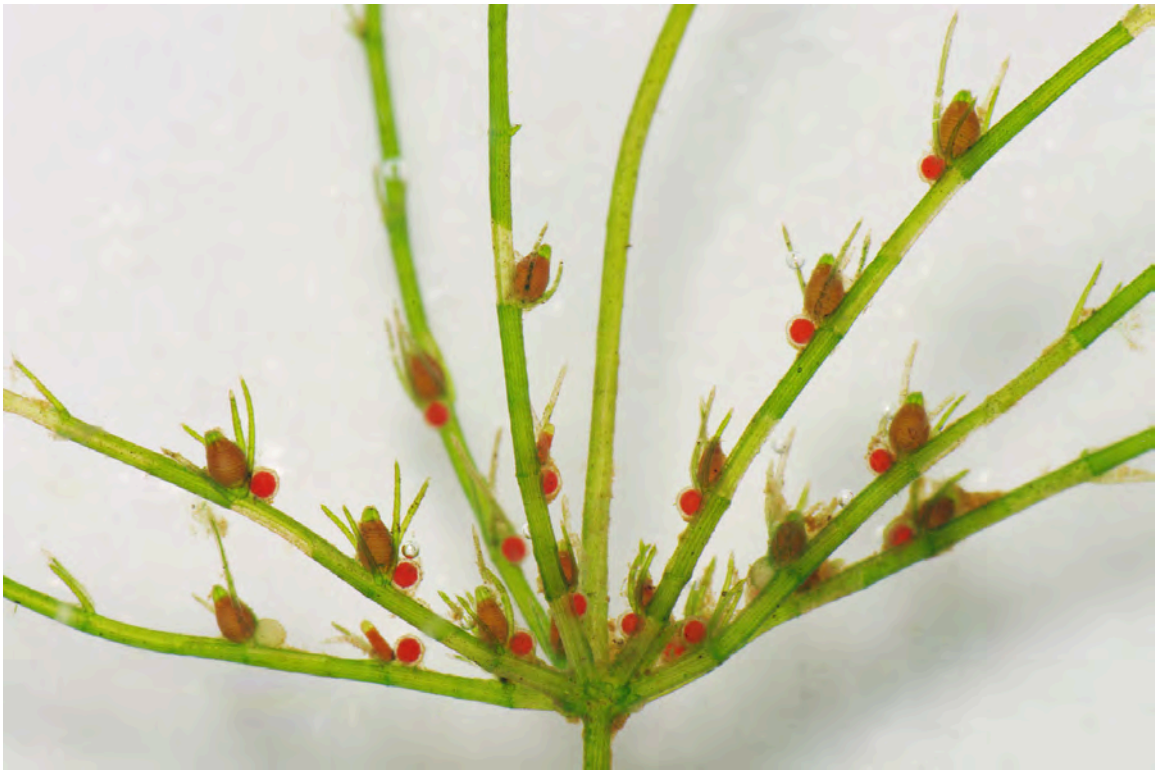
Taxonomy and Phylogeny



The Green Algae group is in flux. The group has clear connections with plants but if plants are put in a separate kingdom (Kingdom Planta, of the five kingdom classification), this affiliation is hidden unless the green algae are also placed in the plant kingdom. Some workers do this. Others split the green algae in two, putting algae with the closest affiliation to land plants in a streptophyte group, and putting all other green algae (the majority of species) in a chlorophyta group (this would include the other green algae covered in the 'Organism' section of this book: *Chlamydomonas, Oedogonium, Acetabularia, Calurpa*). Stoneworts would be in the Streptophyte group and although they look 'plant-like', other streptophytes do not, e.g. the filamentous algae *Spirogyra,* or the unicellular desmids. Stoneworts are usually put in the Characeae family with a group of five other genera besides *Chara*.

Structure

Stoneworts are large algae easily visible with the naked eye and possessing a distinctive whorled form, with a cluster of branches at nodes and elongate internodes separating the nodes. The internode consists of a single elongate cell up to 10 cm in length which in some species is surrounded by a ring (cortex) of smaller cells. Particularly significant evolutionarily is that the cells possess plasmodesmata and this is associated with the formation of a cell plate during cell division. *Chara* has filamentous rhizoids that attach it to a substrate. Sexual structures occur as short branches at the nodes and are of two types, both multicellular: egg producing structures and sperm producing structures.



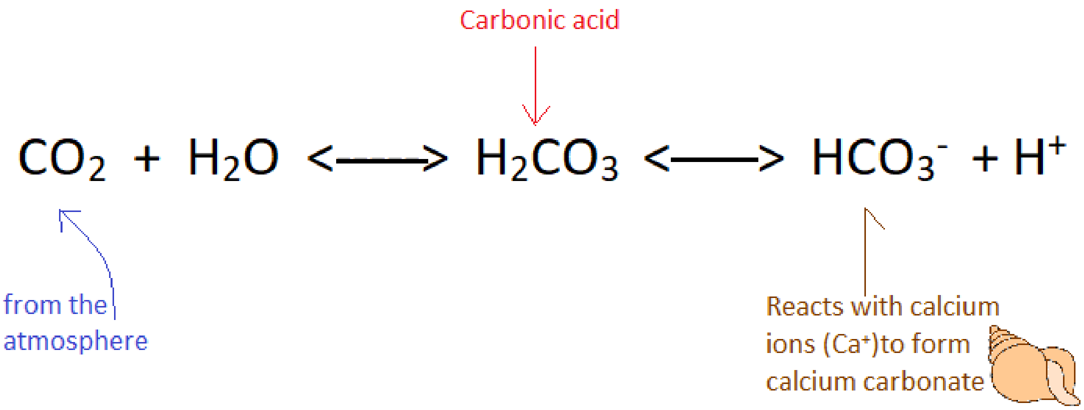
Detail of a stoneworts alga showing the typical reproductive organs: male antheridia (red) and female archegonia (brown).

Reproduction

Chara reproduces asexually by producing several different types of structures that can be detached, dispersed and then develop into new plants. They also reproduce sexually, producing eggs that are retained and mobile, flagellated sperm. After a zygote is formed (the only diploid cell in the *Chara* life cycle) it develops into an oospore that is tolerant of adverse conditions and is capable of dispersal. When conditions are favorable the oospore germinates and undergoes meiosis; three of the four haploid nuclei degenerate with the other one dividing to produce a new haploid plant.

Matter and energy

Chara is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide. It is significant that it often grows in areas with pH values of 7 and above, where bicarbonate is a significant source of carbon dioxide. Bicarbonate and protons can combine to form carbonic acid and this can be converted to carbon dioxide and water. This latter reaction is catalyzed by carbonic anhydrase enzymes found in the cell walls of *Chara* and the reaction also raises the pH and causes the precipitation of calcium carbonate in the cell walls. In addition to the accumulation of carbon, hydrogen and oxygen in carbohydrates *Chara* accumulates 14 mineral elements obtained from the solution that it grows in.



Interactions

Chara is commonly found in hard water (high calcium ion concentrations) environments and sites with brackish waters. They often form extensive beds and are found in slow moving streams and shallow lakes, especially if the water is clear. *Chara* may contribute to that clarity by absorbing and immobilizing nutrients, making them less available for other algae. While some species of epiphytes (algae that grow on other plants) avoid *Chara*, perhaps because of allelochemics, some nitrogen fixing cyaanobacteria associate with *Chara* and may provide nitrogen. Some species of Chara are considered weeds and may be invasive. The extremely large cells of *Chara* and closely related *Nitella* have been used to study membrane electrophysiology and the behavior of the membrane.

Media Attributions

- Chara fragilis © Christian Fische
- Haeckel desmidiea © haeckel

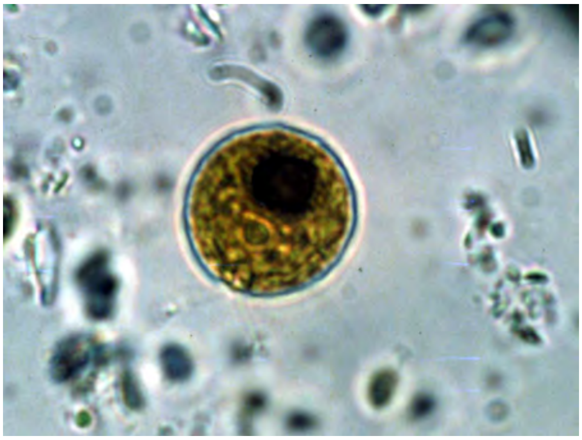
Further Reading and Viewing

- "Chara: Occurrence, Features and Reproduction" by Neelesh T. A good presentation of *Chara* structure.
  - https://www.biologydiscussion.com/algae/chara-occurrence-features-and-reproduction/46890
- "The Ecology of the Charophyte Algae" by Maximiliano Barbosa et al.
  - https://edis.ifas.ufl.edu/publication/AG448

- Chara © Christian Fischer is licensed under a CC BY-SA (Attribution ShareAlike) license
- Equilibrium of carbonic acid in the oceans © OLEsem2 is licensed under a CC BY-SA (Attribution ShareAlike) license

CHLAMYDOMONAS, A SMALL UNICELLULAR GREEN ALGA

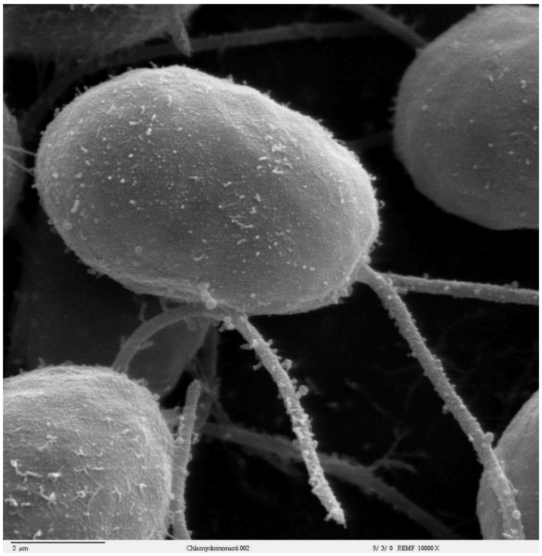
Chlamydomonas, a unicellular green algae



Chlamydomonas

Chlamydomonas is a unicellular organism in the Chlorophyta group (the green algae). It is included here not because one is likely to encounter it (except in laboratories and botany classes) but because it represents one of the many forms found in the green algae and also because it is a 'model organism', one that has proven to be useful in the study of biology. *Chlamydomonas* is certainly not a typical green algae but one could say that about any member of the group that includes filamentous forms (*Oedogonium),* sheet forming forms (*Ulva*), siphonaceous forms (*Caulerpa* and *Cladophora*), and multicellular forms (*Chara*) and even unicellular forms that are 1000 times bigger (*Acetabularia*) than *Chlamydomonas.*

Taxonomy and Phylogeny

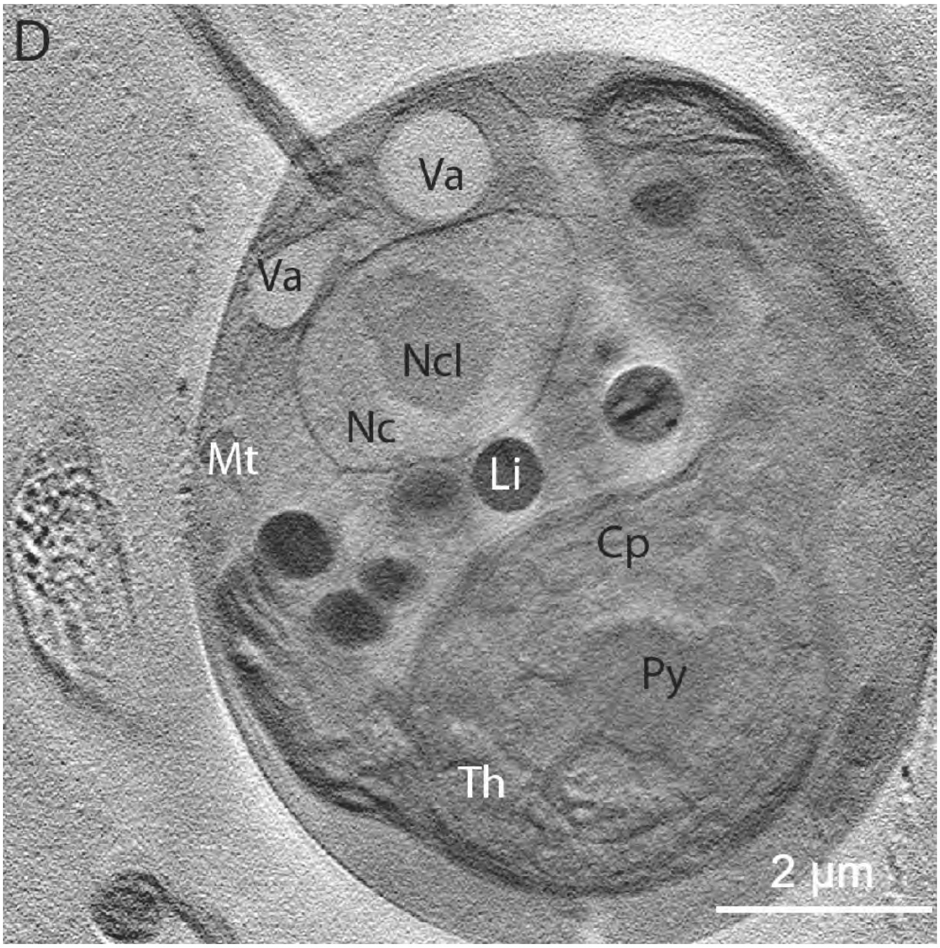


Chlamydomonas, showing the two flagella

The green algae (= Chlorophyta) are a group of eukaryotes that have some characteristics in common with plants (they are photosynthetic, possess both chlorophyll a and b, generally store carbohydrate as starch and have cellulose cell walls. But they also differ from plants in several ways: most are not multicellular, being either unicellular, siphonaceous or filamentous; they do not retain embryos inside the previous generation as all plants do; few grow on land as almost all plants do. Because land plants are thought to have originated from ancestral 'green-algal like organisms' putting green algae and plants in separate kingdoms, as done in the 'five-Kingdom' classification, with a Protist Kingdom that includes green algae and a separate Plant Kingdom, is very artificial. One remedy is to put green algae in the plant kingdom and some observers do this. Another alternative is to simply throw out the Kingdom level of taxonomy and this is what many modern treatments do. If this were done then one might split the green algae into two phyla, one that includes land plants (Streptophyta) and one that doesn't (Chlorophyta).

Structure

Chlamydomonas is a small (<10 um) unicellular, mobile organism. It is roughly spherical in shape with two anterior flagellae that it uses to 'swim' in a breast-stroke-like manner. Unlike many green algae, the cell wall is not made of cellulose (as it is in land plants) but instead of a glycoprotein.



Electron micrograph of Chlamydomonas, showing: vacuole (Va), nucleus (Nc), nucleolus (Ncl), mitochondria (Mt), chloroplast (Cp), and pyranoid (Py).

Reproduction

Chlamydomonas reproduces asexually when haploid cells divide (often multiple times) and form 2, 4, 8 or more daughter cells, that are then released. Sexual reproduction occurs when special cells (gametes) are produced that are capable of attaching to one another, first by their flagellae, and later by their anterior ends, thereby achieving protoplast fusion and forming a zygote. This develops into a zygospore (dormant, resistant cell) in which meiosis occurs. Eventually zygospore germination occurs, releasing haploid mobile cells (see discussion in Chapter 11).

Matter and energy

Chlamydomonas is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide/bicarbonate ion and water and then using the carbohydrates as a both an energy source in cellular respiration and also as building materials to synthesize a variety of biomolecules. However, it can live in the dark if supplied with acetate — (why this is significant is considered in Chapter 19). In addition to the accumulation of carbon, oxygen and hydrogen in carbohydrates, *Chlamydomonas* accumulates 14 mineral elements which are present in dilute levels in its aquatic habitat.

Interactions

A species of Chlamydomonas containing a red pigment and creating reddish 'watermelon snow'.

Although the genus *Chlamydomonas* is found primarily in fresh and salt water habitats, it also can be found in soil (in the upper regions that get enough sunlight) and in snow (specifically *C. nivalis*, the organisms that causes 'watermelon snow', producing a red pigment that is thought to protect it from high light intensities. Significant to the alga's success is the fact that the organism is mobile and phototactic, using a pigment similar to the rhodopsin of human eyes to direct its movement. As phytoplankton, *Chlamydomonas* is eaten by small heterotrophs, e.g. *Daphnia.*

Further Reading and Viewing

- "Chlamydomonas" by M.D. Guiry
    - http://www.seaweed.ie/algae/chlamydomonas.php
- "Reasons to Rejoice in Green Algae: Essay" by Lynne Quarmby, discusses reasons to study different organisms
    - http://numerocinqmagazine.com/2011/05/19/reasons-to-rejoice-in-green-algae/
- "Watermelon Snow: A Strange Phenomenon Caused by Algal Cells of The Chlorophyta" by W.P. Armstrong
    - http://waynesword.palomar.edu/plaug98.htm

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- Chlamydomonas reinhardtii
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CHYTRIDS, TINY FUNGI

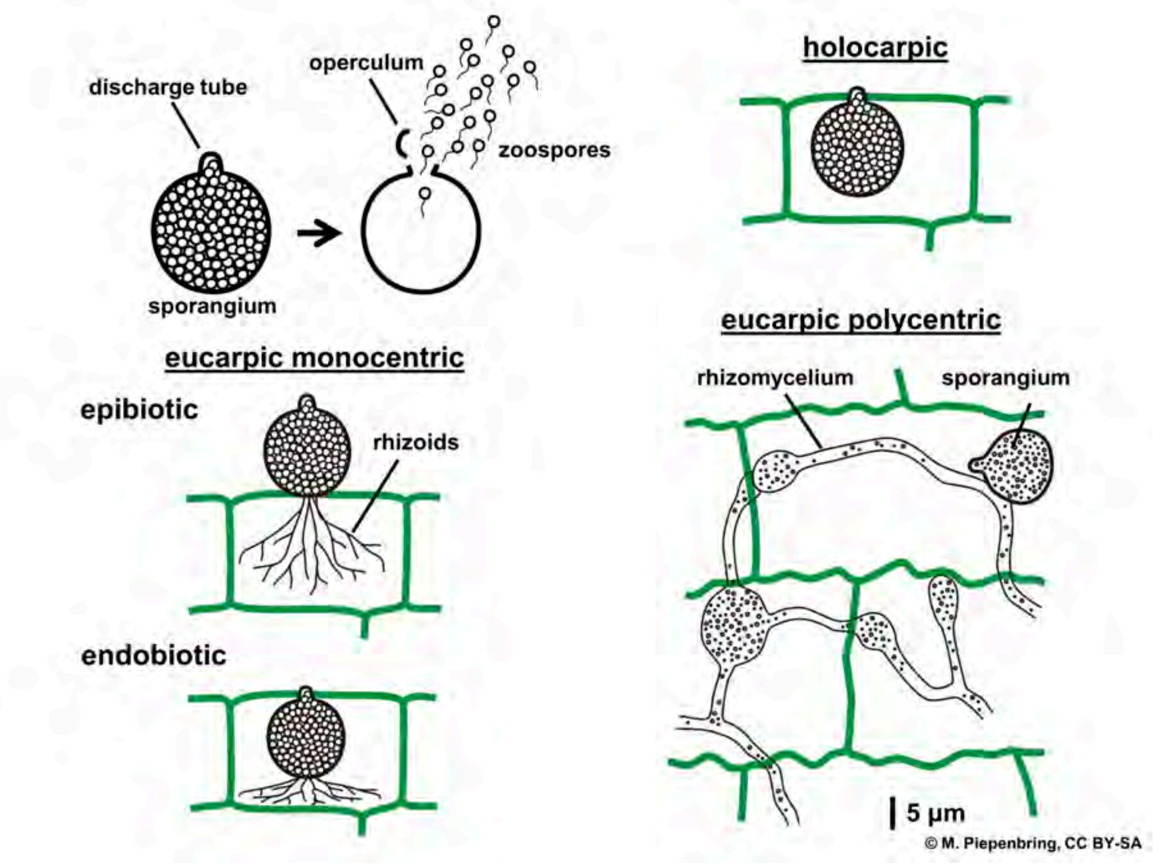
Chytrids (Chytridomycota) are a group of fungi that are rarely directly encountered, primarily because they are small and they generally eat things that are small.

Taxonomy and Phylogeny

Chytrids are a distinct group within the fungi and like all fungi they possess a cell wall made of chitin and store carbohydrates in the cytosol in the form of glycogen. The chytrid group is distinguished from other fungi by the fact that they produce flagellated zoospores; flagellated cells are not present in any other fungal groups (an exception is a very small group that has only recently been separated from the chytrids). Chytrids are sometimes described as the most primitive group of fungi, but a more appropriate description might be that they are the group that diverged first along the line that produced four other fungal groups: bread molds (Zygomycota), endomycorhizal fungi (Glomeromycota), club fungi (Basidiomycota) and cup fungi (Ascomycota).

Structure

Many chytrids are unicellular: a single cell grows from a zoospore and eventually develops into a single celled sporangium that produces more zoospores (see the ‘holocarpic’ example in the image above). In some species the sporangium develops entirely within a host cell, sometimes producing root-like rhizoids (see the ‘endobiotic’ example). Other species penetrate the host cell and develop rhizoids inside it but produce a sporangium that is attached and outside of the host cell (‘epibiotic’ in the image above). Some chytrids are coenocytic, producing cells with multiple nuclei and sometimes producing short coenocytic hyphae, cylindrical structures with multiple nuclei (‘eucarpic polycentric’ in the image above).



Sex and reproduction

Some chytrids reproduces solely by asexual means via zoospores. Other species do reproduce sexually, producing gametes capable of fusing (syngamy) and cells capable of undergoing meiosis. A few species exhibit an alternation between a haploid and a diploid generation, as found in plants (Chapter 11).

Matter and energy

Chytrids are heterotrophs, like all fungi and like humans. Like humans they sometimes consume dead materials (i.e. are saprophytes) but also may consume living materials, in which case the chytrids may act as a parasite or predator. An interesting aspect of chytrids is that many consume small things: spores, pollen, unicellular algae and protozoans or single cells of multicellular organisms.

Interactions

Chytrid ability to consume pollen is significant because of the copious amounts of pollen, especially conifer pollen, that is produced in some habitats.

They are an interesting group because, although aquatic, their small size allows them to be successful in the soil in the films of water that surround soil particles.

Some chytrids are significant because of diseases that they cause, most notably chytridiomycosis, a skin disease of amphibians that is thought to have been significant in causing global declines in frog and toad populations, including some extinctions.

Chytrids also cause diseases in plants.

Further Reading and Viewing

- "The ecology of chytrids in aquatic ecosystems: roles in food web dynamics Author links open overlay panel" by Frank H. Gleason et al. Chytrid ecology in aquatic systems.
    - https://www.sciencedirect.com/science/article/abs/pii/S174946130800002X
- "The Chytridiomycota" by David Malloch, New Brunswick Museum.
    - http://website.nbm-mnb.ca/mycologywebpages/NaturalHistoryOfFungi/Chytridiomycota.html

Media Attributions

- 10 types of thalli, Chytridiomycota © M. Piepenbring is licensed under a CC BY-SA (Attribution ShareAlike) license

CLUBMOSSES: LYCOPODIUM

A common clubmoss of the Adirondacks: ground pine, Dendrolycopodium obscurum (= Lycopodium obscurum)

Clubmosses are representatives of the Lycopodiophyta, plants that are very important in the fossil record and in the history of plant life but are not particularly diverse or common now. World-wide there are around 1000 species in the group. As is the case with many of the ferns, the common names for clubmosses have been much more stable than the scientific names, several of which have been changed in the last thirty years. Several species are frequently encountered in the understory forests of the Adirondacks of New York and in forests in New England. All members of the group that exist today are small plants, typically less than 10 cm in height. But in the past members of the group were much larger and formed forests. The group originated over 400 million years ago in the Paleozoic and the phylum is the oldest group of vascular plants that still has members today. Tree forms up to 35 m in height were common at the end of the Paleozoic, roughly 300 million years ago, and were important in forming deposits that are sources of coal and oil. All the tree forms disappeared at the end of the Paleozoic.

Taxonomy and Phylogeny

The clubmosses form a distinct group that is generally recognized at the phylum level (Lycopodiophyta). They are one of the groups of 'fern allies', groups unified by having vascu lar tissue but lacking seeds. The other groups are the ferns, horsetails and wisk ferns (some people lump these three groups together into one phylum). Although ferns and clubmosses can be linked by what they do not have (seeds) this is not a good criterion for forming a group and for this reason, and many others, ferns and clubmosses are NOT thought to be phylogenetically close, so the 'fern allies' are not grouped together. The Lycopodiophyta includes three groups, clubmosses, spikemosses and quillworts.

Structure

As the name implies, clubmoss sporophytes (the spore producing form) look like mosses but they are generally bigger, reflecting the fact that they have vascular tissue, and they often have 'clubs' or strobili, structures where spores are produced. The plants have the typical plant structure of an elongating axis that bears flaps of tissue, 'leaves' that possess on a single strand of vascular tissue. Clubmoss leaves are called 'microphylls' to distinguish them from true leaves ('megaphylls') that have more extensive venation. On some clubmoss and spikemoss species the leaves are overlapping and resemble those of cedar, which gives some species a common name of ground cedar. Most species produce above and/or below ground stems that run horizontally and send up vertically oriented branches. The gamete producing plant is often small, often only a few mm in size, rarely over a cm in size, and has an amorphous structure that produces small egg-producing archegonia and sperm producing antheridia.

Reproduction

Like all plants, clubmosses exhibit alternation of generations. The group has a relatively large sporophyte and hard-to-find gametophyte that is small, uncommon and subterranean. The gametophyte depends upon an association with fungi to obtain carbohydrates. Gametophytes are bisexual and the flagellated sperm swims to the to the structures, the arechegonia, that produce eggs, Other groups within the Lycopodiophyta (*Selaginella* = spikemosses, *Isoetes* = quillworts) are heterosporous and some members, both

A common clubmoss of the Adirondacks: bristly clubmoss, *Lycopodium annotinum*. Note the terminal spore producing strobili and the stems with little branching.

living and fossil, produce structures approaching seeds, having megaspores are retained on the sporophyte and also a female gametophyte that develops endosporically (see Chapter 13).

Matter and energy

The clubmoss sporophyte is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and as building materials to synthesize a variety of biomolecules. The gametophyte is a heterotroph, a parasite on fungi (mycotroph), that obtains matter and energy from a fungus that it associates with.

Interactions

Although clubmosses a re common in northern hardwood forests, they are not particularly important. They are not obviously eaten by common herbivores, perhaps because of their chemistry, which contains alkaloids. Historically, the spores were used as an early form of photography 'flash powder' as they can ignite explosively. The spores were also used as a type of lubricating body powder.

Further Reading and Viewing

- "Clubmosses: An Ancient and Interesting Group of 'Fern Allies'" by Marion Lobstein
    - https://vnps.org/princewilliamwildflowersociety/botanizing-with-marion/clubmosses-an-ancient-and-interesting-group-of-fern-allies/

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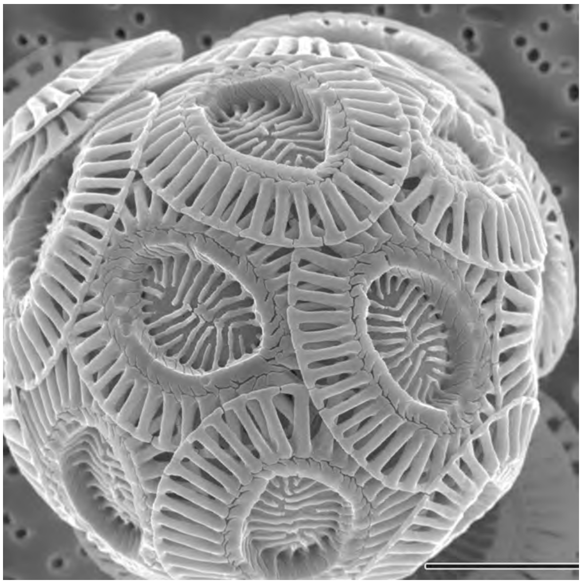
COCCOLITHOPHORES, PHOTOSYNTHETIC UNICELLULAR ALGAE



Coccolithophores are some of the most important organisms that you have never heard of!! They are very small marine organisms who have a very significant impact on earth's geology and ecology. They are distinctive because they have a coating that consists of a number of ornate calcium carbonate plates.

Phylogeny and taxonomy

Coccolithophores are closely related to a group of organisms (Haptophytes) that lack the plates. These two groups, together with some other organisms, have been classified a number of different ways. In a five-kingdom classification they are considered to be in the phylum Haptophyta in the kingdom Protista. The coccolithophores are sometimes considered members of the 'golden algae' group and some treatments lump 'golden algae' (haptophytes including coccolithophores and other groups), brown algae and diatoms together in a group called 'Stramenopiles', largely on the basis of pigments. Other workers feel that the pigmentation similarity is an artifact of two independent secondary symbiotic events.

Structure

The distinguishing feature of haptophytes is a flagellum-like structure called a haptonema that is distinct from a flagellum due to a different microtubule structure. Most members of this group also have two flagella. Within the Haptophyta, the coccolithophores are distinguished by having an outside boundary of overlapping calcium carbonate plates / shields, called coccoliths. Because they are made of calcium carbonate, coccoliths represent a 'sink' for carbon dioxide: the carbon to form them is derived from dissolved carbonate ions, which are (generally) derived from dissolved carbon dioxide, which (generally) is derived from respiring organisms, either aquatic or terrestrial. What happens to the coccoliths when the organism dies depends on conditions. Under certain conditions they dissolve back into solution, under other conditions they sink to the ocean floor and can form deposits hundreds of meters thick. Such deposits form the dramatic 'white cliffs of Dover' and the Alabaster Coast of Normandy.

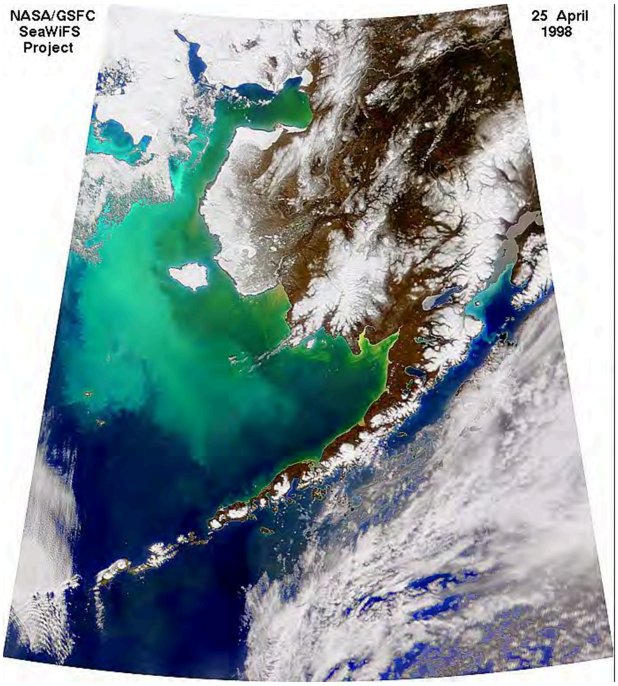
White cliffs of Dover, formed by deposits of coccolithophores.

Reproduction

The primary means of reproduction is asexual cell division. Since both haploid and diploid forms are found, the assumption is that they can undergo the sexual cycle but neither syngamy nor meiosis has been observed. It is believed that some members show a heteromorphic alternation of generations with a diploid, planktonic flagellate stage and a haploid, filamentous stage.

Matter and Energy

Most members of the group are photosynthetic and autotrophic but some members lack pigments and are heterotrophs; and many of the photosynthetic forms appear capable of absorbing organic material as well as synthesizing it. They are significant in being tolerant of low nutrient conditions and are found in the open oceans where nutrient supplies are very low.



Satellite photo showing the impact of a bloom of coccoliths in the Bearing Sea off the west coast of Alaska. This is the actual color of the ocean.

Interactions

Coccoliths are tremendously important in a number of ways:

- they are the main photosynthetic forms of the open ocean and make a significant contribution to the oxygen production that most forms of life require
- they can remove carbon from ocean waters by forming coccoliths that can sink to the ocean floor and form geological deposits

- their optical properties can change water albedo and thereby ocean temperatures
- they produce sulfur compounds that are metabolized by bacteria to dimethylsulfide, DMS, that can influence cloud formation and acid rain (see also dinoflagellates, who also produce the same chemical)
- they serve as a food source for a number of other organisms
- they can form toxic algal blooms

Further Reading and Viewing

- "Emiliania huxleyi" by Tobey Tyrrell
    - http://www.soes.soton.ac.uk/staff/tt/
- "Emiliana" on *Microbe Wiki*
    - http://microbewiki.kenyon.edu/index.php/Emiliana

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COLTSOOT: TUSSILAGO FARFARA

Tussilago farafara is a common herbaceous plant throughout much of North America, occurring in disturbed habitats, usually in relatively moist sites. It is one of the first flowers to be found in the spring, often on roadsides. Like many familiar plants (e.g. milkweed, goldenrod, tulips, dahlias) it is an herbaceous perennial but its phenology is unusual, flowering before leaves are produced.

Taxonomy and phylogeny

Colts foot is a flowering seed plant (an angiosperm) in the Aster family (Asteraceae) , one of the largest families of flowering plants. The group is usually easy to recognize when flowering because the 'flower' is actually an inflorescence, a cluster of flowers. The flowers are often of two types: flowers with elongate petals radiating outward and flowers with short petals that are vertical. Coltsfoot and many familiar members of the family (sunflowers, asters, daisy) have both types of flowers but other members of the family (dandelion, chicory) may only have one of the two types of flowers.

Erect, mature flowers (inflorescences) with mature seeds that have a form similar to dandelions, with each fruit having an white hairs that aids in wind dispersal

'Nodding' flower (inflorescence) after pollination.

Structure

Coltsfoot is a perennial that spreads extensively by underground stems (rhizomes) that produce shoots that live for two years. The first year the shoots are vegetative and produce a cluster of large leaves with grayish hairs, especially on the lower side. In the fall, flower buds develop at the base of the leaves while the leaves senesce and fall off. The following spring the flower buds (which are actually branch shoots) develop. These branches bear no true leaves, only rudimentary scales, but produce a dandelion-like inflorescence ('flower'). The flowering shoots emerge very early in the spring and elongate to produce a gray stem roughly 10 cm long with a yellow 'flower' at its end that is the same size and color as dandelion but unlike a dandelion it has both flower types, like an aster. The 'flower' develops into a head of fruits, looking again very similar to a dandelion and, like dandelions, the tip of the flowering stalk arches over as the fruit develops and then returns to an erect position after the fruits are mature and ready to be dispersed.

Sex and reproduction

As a typical angiosperm, Coltsfoot reproduces sexually and produces seeds in the ovaries of flowers. The seed contains an embryo that develops from a zygote formed by the union of a male gamete derived from pollen and a female gamete produced in the female gametophytes (embryo sacs) that are present in the ovules of the flower. The center flowers of a head do not have ovules while the outer flowers possess both male and female parts. The plants are self-incompatible and need pollen from another plant in order to set seed. Pollen transfer is accomplished by bees and beetles attracted to the flowers by nectar rewards and scent.

Matter and energy

Coltsfoot is a typical photosynthetic autotroph. Carbohydrates, synthesized in the summer are stored in the rhizomes to provide both matter and energy in the spring when there are no leaves and no photosynthesis. This is an excellent example of plant growth that is accompanied by no increase (actually a decrease) in plant weight. The rhizomes are depleted of carbohydrates, and therefore lose weight, in order to power the growth of the developing flowers.

Interactions

Native to Europe, coltsfoot has established itself in North America. While it generally is found in disturbed ('weedy') habitats, it occasionally invades 'natural' habitats as well.

A flowering head of coltsfoot, showing mature fruits (brown) crowned by a group of hairs that aid in dispersal.

Coltsoot leaf.

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- Leaf of coltsfoot © R.A. Nonenmacher is licensed under a CC BY-SA (Attribution ShareAlike) license

CORN

Corn (*Zea mays),* or maize, is an annual grass crop species that survives only because of its cultivation by humans. Its ancestry tells some interesting tales. For most crop species a wild 'relative' is readily apparent. This is not the case for maize but the answer may actually depend on what one means by 'apparent'. There is no plant that bears strong resemblance to corn, especially in terms of its 'ear', a cluster of female flowers and later fruits. Its closest relative, called teosinte, differs in several ways from corn. Significantly, it differs in ways that make it an unlikely 'proto-crop', one that humans might manipulate by selective harvesting and planting in order to make it more desirable. However the genetic differences between teosinte and corn turn out to be quite small, differences in developmental genes that can greatly alter the 'looks' of a plant and, significantly, alter features that make it a desirable crop. Thus there IS an ancestor of corn, a species of teosinte that grows wild in Mexico. But it doesn't look much like corn and has features, in particular a small number of fruits that are encased in very rigid structures, that don't make it a likely candidate for domestication.

Whether teosinte was actually utilized agriculturally and favorable characteristics (more fruits that are easier to open) were selected for, or a more suitable version appeared 'on its own', without human intervention, is not known. Regardless, once a version of corn appeared, probably 9000 years ago, it was rapidly transformed by early farmers selecting for favorable traits, in particular larger ears. Less than 2000 years ago modern versions of the crop appeared in the area that is now part of Mexico and rapidly spread throughout most of the Americas. It is an unusual grass in a number of ways: there are separate male and female flowers (most plants and most grasses have bisexual flowers) and it produces seeds that do not fall off the plant as those of most grasses do.

Female flowers

Tassels, clusters of male flowers

Male flowers with stamens exerted.

Unisexual flowers of corn: female flowers (above) are clustered on a branch called an ear. There are typically 1 to 3 ears per corn plant, occurring (as they always do!) in the axils of leaves, male flowers are also clustered on special stems, these occur at the top of the plant in structures called tassels.

Phylogeny

Corn is a flowering plant in the monocot group, a phylogenetic entity that includes orchids, palms, lilies and grasses. The grasses are put together in the Poaceae family, a large family that includes staple crops (wheat, rice) and is also extremely important ecologically, often dominating regions.

Structure

To people who think grasses always look like those in their lawns, corn looks quite different: it is large, both in terms of height and in the width of leaves. Initially the 'stem' is actually just the round basal parts (the sheaths) of individual leaves, with the oldest leaves on the outside and newer leaves being produced inside. As is the pattern in grasses and many other monocots (see the discussion of banana 'stems' in Chapter 8), the shoot apical meristem stays at the very base of the plant, near the ground. The 'stem' is produced by the sheaths of multiple leaves. Eventually a true stem emerges from the interior as the shoot apical meristem is elevated, 'telescoping' up the space formed by the sheaths of several leaves. The stem elongation ends when the shoot apical meristem transforms into a flowering meristem, producing a clusters of male flowers (the tassel) at the top of the stem. As is typical of all plants, branches form in the axils of leaves; what is unusual is that these branches produce very little stem, only a short axis with multiple female flowers. The base of this flowering branch produces multiple leaves that grow over the flowers to form the ear of corn. Emerging from the tip of the ear are the strands of 'silk': the stigma and style of each individual flower enclosed in the ear.

Corn produces prop roots, a type of adventitious root (Chapter 7) that functions to support the stem. Adventitious roots are roots that originate in an abnormal place, usually from the stem, the result of a meristem developing in the stem that produces a structure that grows at a roughly 45 degree angle rather than straight down. Prop roots do not function to absorb water and nutrients, instead they attach the stem more firmly to the soil.

Sex and reproduction

Corn reproduces sexually and is difficult to propagate vegetatively. Because it has separate male and female flowers it is very easy to control breeding and corn was the first crop for which hybrid seed was produced. Hybrid seed is produced by crossing two different inbreed lines and results in F1 plants that are particularly vigorous (see Chapter 28 and Chapter 31).

Matter and energy

Corn is a photosynthetic autotroph that uses the C4 photosynthetic pathway. Like most C4 plants, it has a particularly high rate of photosynthesis, has a high water use efficiency (carbon dioxide fixed compared to water loss) and will benefit less from rising carbon dioxide levels than C3 plants (Chapter 20).

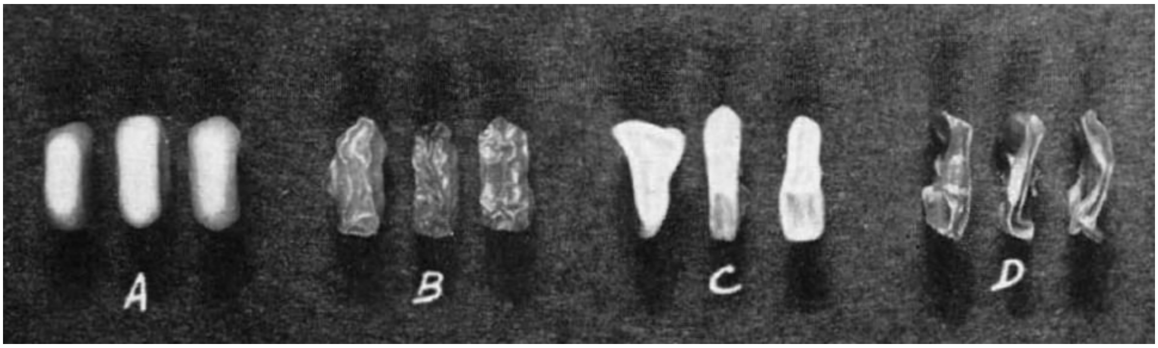
Interactions

Corn is obligately tied to human agriculture and could not survive were it not for our efforts. It has been developed for a wide number of uses including animal feed (fodder, silage), fuel (ethanol), home heating (corn/pellet stoves), and a wide variety of food products. It is now grown world wide and is second only to rice in terms of world-wide production. It is affected by many pests/diseases including smut and rust fungi, army worms (moth larvae), aphids and viruses.

Corn carbohydrate chemistry

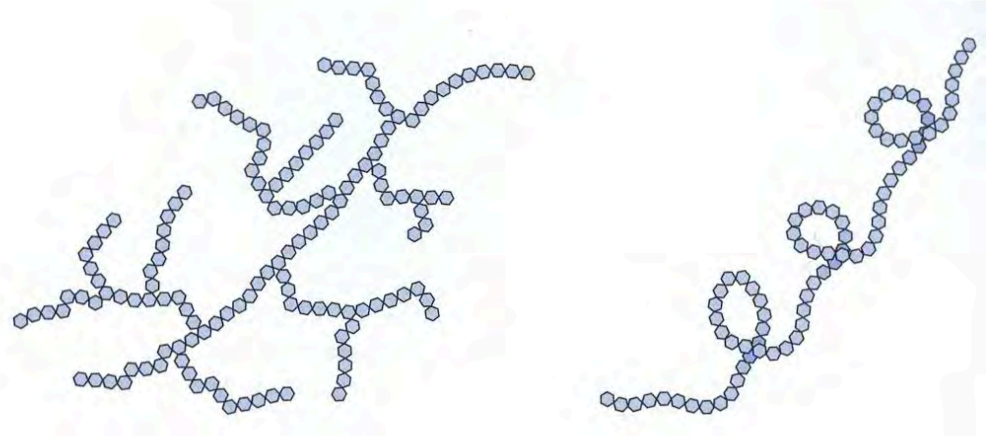
The bulk of a corn kernel (which is technically the fruit of the plant) is amylose starch, a carbohydrate with a very simple structure, consisting of a string of 6-carbon glucose molecules attached end to end, i.e. at two points. Some forms of starch (amylopectin starch) are not solely linear chains but are branched by because some glucose molecules are attached to three other glucose molecules rather than two.

The starch in corn kernels is formed from sucrose that is synthesized in photosynthesizing leaves and transported to the developing fruit thru the phloem tissue. Sucrose is a disaccharide formed by combining one glucose with fructose, another 6-carbon sugar. After the sucrose is transported to the developing corn kernels the sucrose is broken down to a glucose and a fructose. The glucose is used to make starch directly; the fructose is converted into glucose and then is also used to make starch.

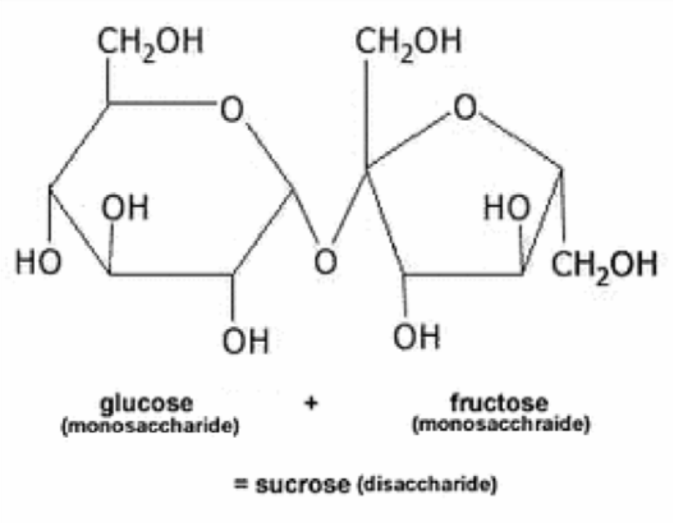


A) 'normal' (wild type) corn kernels B) homozygous recessive mutant which has lessened ability to synthesize starch C) a different homozygous recessive mutant which also has lessened ability to synthesize starch D) double mutant combining (B) and (C), this is the most shrunken 'super-sweet' variety of corn

Corn kernels are sweeter earlier in their development, before the kernel is mature, because more sugar (sucrose, glucose and fructose) is present. As the fruit matures most of the sugars are converted into starch and mature kernels are usually not at all sweet. However, corn plants exhibit variation in the amount of starch produced, thereby producing variation in the degree of sweetness in mature kernels. Native Americans were aware of this when they introduced corn to Europeans. By the early 20th century agricultural research had developed substantially sweeter varieties of corn and isolated the cause of the sweetness, which is a lack of (or lesser amounts of) one or several enzymes that are responsible for synthesizing starch from sucrose. Mature corn kernels of sweet varieties of sweet corn are 'shrunken' because they lack the starch that normally makes them plump.



Two forms of starch, amylopectin on the left and amylose on the right.



Structure of sucrose, a disaccharide made up of two hexoses, glucose and fructose, linked together.

Further Reading and Viewing

- "What Are the Different Types of Corn" by Kansas Farm Food Collection
    - https://kansasfarmfoodconnection.org/spotlights/what-are-the-dif-

    - ferent-types-of-corn
- “Popping Under Pressure: the Physics of Popcorn” by Aleksandr Arkhipov et al.
    - https://depts.drew.edu/govschl/NJGSS2005/Journal/TeamPapers/T3.Popcorn.pdf
- “Time Warp – Popping Popcorn” by FunnyButRandomStuff. Popcorn in slow motion.
    - https://www.youtube.com/watch?v=DWr1kfu9edI

Media Attributions

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CORALLORHIZA, A PLANT THAT EATS FUNGI

Corallorhiza is a representative of the orchid family. The orchids are one of the largest families of flowering plants, a group with over 25,000 species. Although the genus *Corallorhiza* is restricted to North America, with roughly a dozen species, most members of the family are found in the tropics. Probably the most commonly seen orchid in the northeastern US is the pink lady slipper but there are another 10-15 species of orchids that relatively easy to find, although they never are abundant and many occur in restricted habitats, e.g. bogs. *Corralorhiza* is an unusual angiosperm because it is non-photosynthetic, a characteristic that is very rare within plants in general but does occur occasionally in several plant groups.

Taxonomy and Phylogeny

The orchid family is distinctive in a number of ways and its members are generally quite easy to recognize when in flower. They are in the monocot group, which is usually considered a class (remember that families are grouped into orders, orders into classes, and classes into phyla). Monocots are a monophyletic group that is thought to have diverged early (perhaps 130 million years ago) from the rest of the angiosperms. The remaining angiosperms (i.e. all flowering plants except monocots) do NOT form a phylogenic entity and hence modern treatments do not divide angiosperms into two groups (monocots and dicots) but into several groups, the two largest being monocots and 'eudicots', a group that includes most, but not all, of the old dicot members. Monocots have a number of features that distinguish them from other flowering plants: a single cotyledon in the seed, lack of secondary growth, flower parts typically in 3' s, and stems with scattered vascular bundles.

Structure

Orchids are herbaceous perennial plants that have several distinct growth forms. Many orchids are epiphytes, plants growing on the trunks of other plants, and may have features including 'aerial roots' and 'pseudobulbs' which allow them to be successful under these conditions. *Corallorhiza* orchids do not have a typical orchid structure because they are non-photosynthetic and have very reduced/no leaves while most orchids have very visible leaves that may be stiff, oval and overlapping or sometimes may be grass-like. Many orchids produce rhizomes (horizontal stems running below ground), corms (short, fattened vertical stems) or tubers (enlarged stems that are not oriented vertically).

Reproduction

Most orchids exhibit sexual reproduction that is possible because of elaborate pollination mechanisms that most commonly involve bees or wasps. The flowers of orchids are unusual because pollen is not dispersed as individual grains but rather in large packets ('pollinia') that represent the the entire anther of an individual stamen and contain thousands of pollen grains. Seeds of orchids are extremely small, often less than 0.5 mm, sometimes less than 0.1 mm (less than 100 microns). This small size is possible because there is no endosperm, the embryo is much smaller than in most seeds and the seed coat is very thin. Because of the lack of endosperm, the germinating seeds of most orchids must quickly associate with a fungus in order for the fungus to provide the seed with the nourishment needed in order for the orchid to become established. Note that although plant/fungus associations are very common (e.g. in mycorrhizae), the relationship found in in the germinating orchid seeds reverses the normal flow of carbohydrates: in a typical plant/fungus association plants transfer carbohydrates to fungi, but in germinating orchid seeds the flow of carbohydrates is from the fungus to the plant. Once the orchid produces a photosynthetic structure the flow of carbohydrates is reversed; however, this never happens in *Corallorhiza* because it never produces a photosynthetic structure.

Matter and energy

Corallorhiza is a very unusual angiosperm because it is a heterotroph, a parasitic heterotroph, surviving on biomolecules that it does not produce but instead are acquired from a host organism (a fungus) that it associates with. Unlike most orchids that rely on 'mycotrophy' (fungus-eating) just during the seedling establishment phase (see above), *Corallorhiza* plants never become photosynthetic and never produce their own carbohydrates. Their mineral nutrition is also supplied by their host because they produce no roots to explore the soil to acquire nutrients. There are several other unrelated flowering plants with a similar lifestyle, including Indian pipes (*Monotropa uniflora*) and Snow flower (*Sarcodes spp.*). There also are flowering plants that parasitize the roots of other flowering plants: beech drops *(Epifagus virginiana*), witch flower (*Striga spp.),* and also those that parasitize the stems of other flowering plants: dodder (*Cuscuta),* mistletoe (*Phoradendron, Viscum*).

Interactions

Corallorhiza, and orchids as a group, have two interactions that have already been noted: with fungi during seed germination and with bees and wasps in many elaborate pollination mechanisms. In spite of the fact that there are lots of species, the group is not particularly significant ecologically (i.e. it does not dictate the activities of communities/ecosystems). Orchids have limited economic importance, being rarely used as food, although the spice vanilla comes from an orchids. Orchids have become important to the florist industry (e.g. as corsages) and also as house plants.

Further Reading and Viewing

- "Orchids of New York" by Chuck Sheviak and Steve Young
    - https://www.dec.ny.gov/docs/administration_pdf/orchidsofny.pdf
- "Myco-heterotrophy: when fungi host plants" by Vincent Merckx, Martin I. Bidartondo, and Nicole A. Hynson
    - https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2778383/

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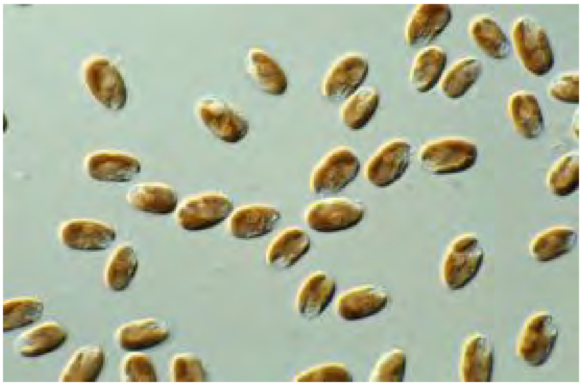
- Corallorhiza maculata, spotted coralroot © Walter Siegmund is licensed under a CC BY-SA (Attribution Share-Alike) license

CRYPTOMONADS, UNICELLULAR PHOTOSYNTHETIC ALGAE

As the name implies, cryptophytes (crypto = hidden) are unicellular algae that are often hidden. This is a consequence of their relatively small size (10-30 um), the fact that they often occur in deeper waters, and the fact that they are often difficult to collect in an intact condition. However, they are significant contributors to aquatic food chains, both marine and fresh water, and have interesting features that relate to their evolution.



Microalgal cultures

Taxonomy and phylogeny

While consistent structural features unify the cryptomonad group, their placement relative to other living things is problematical. Although they have similar pigmentation (chlorophylls a and c and phycobillins) with the dinoflagellates, this may be the result of ancestral forms of both groups separately ingesting the same eukaryotic algae (a red algae) in a secondary endosymbiosis manner.

Structure

Cryptomonads have a distinctive structure. They are unicellular and have two flagella with an anterior groove. Their chloroplasts have four membranes, reflecting secondary endosymbiosis, i.e., that a eukaryote ingested another eukaryote, in this case one with a chloroplast (see Diatoms). Because of pigmentation, the second endosymbiotic event is thought to have involved a red algae being ingested by a unicellular heterotroph. This pattern is also thought to be the case for dinoflagellates and diatoms. Cryptomonads possess unusual structures called ejectisomes that can be discharged when the alga is disturbed, triggering movement that may deter a herbivore. Reflecting their secondary endosymbiotic origin, they have DNA in four locations: a nucleus, the mitochondrion, the chloroplast and in a structure called a nucleomorph, thought to be a remnant of the nucleus present in the cell of the second endosymbiotic event. They have no cell wall but do have a proteinaceous layer just inside the plasma membrane similar to the pellicle found in dinoflagellates. As might be expected for an organism lacking a cell wall, they possess contractile vacuoles to maintain water levels.

Sex and reproduction

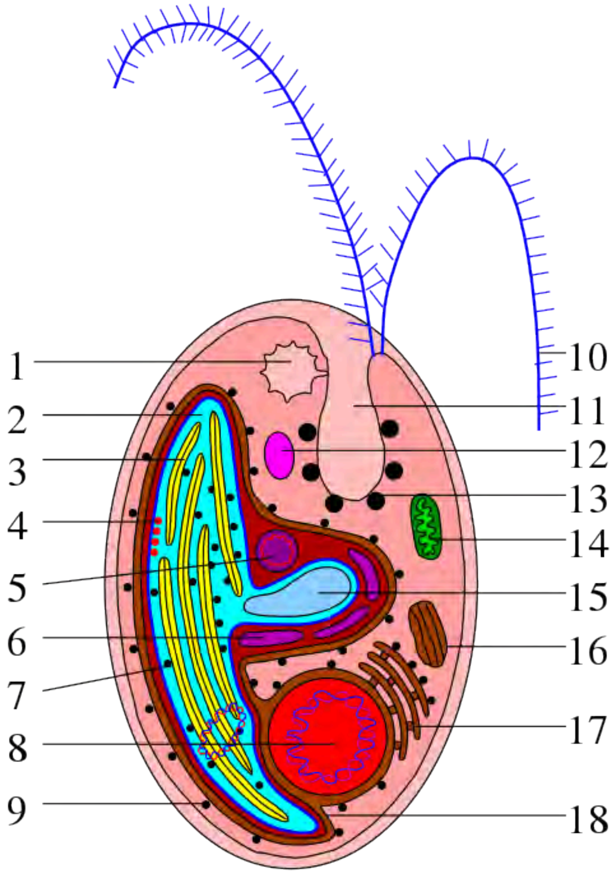
There is some evidence for sexual reproduction in at least one species but primarily they reproduce asexually by mitosis.

Matter and energy

Almost all cryptomonads possess photosynthetic pigments and are photosynthetic autotrophs, acquiring carbon and 16 other elements in inorganic form from their environment. However, cryptomonads do require B vitamins, reflecting their heterotrophic ancestry. And a few species lack photosynthetic pigments and are heterotrophs, obtaining food by phagocytosis (invagination of the cell membrane to engulf a food particle). Some photosynthetic forms are also capable of phagocytosis, indicating mixotrophy (being both an autotroph and heterotroph).

Interactions

Because red light penetrates deeper in the water column and because cryptomonads possess phycobiliproteins pigments that can utilize red light, cryptomonads can photosynthesize at greater depths than other algae, and cryptomonads are often found at greater depths than other algae. Although they are not a particularly diverse group, they appear to be quite important in several habitats, typically cooler ones, both marine and fresh water, serving as the base of food chains.



Cryptophyta cell scheme: 1-contratile vacuola, 2-plastid, 3-thylakoid, 4-stigma, 5-nucleomorph, 6-starch granule, 7-70S ribosome, 8-nucleus, 9-80S ribosome, 10-flagella, 11-invagination, 12-lipid globules, 13-ejectosomes, 14-mitochondrion, 15-pyrenoid, 16-Golgi apparatus, 17-endplasmic reticulum, 18-chloroplast-endplasmic reticulum

Further Reading and Viewing

- "Cryptophyta" by Rocky Mountain Lake Algae. Nice article with good pictures, but note that when they state "(cryptophytes) have pigments found in no other group of algae (phycoerythrin and phycocyanin)," they are forgetting about red algae which have these pigments; it is because of this and other features cryptomonads are thought to have resulted from a secondary endosymbiosis event with the red algae. Also note that *blue-green algae* (which some don't consider to be algae!) also have these pigments.

  - http://culter.colorado.edu/taxa/phylum.php-q-phylum_ID=4.html

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- Cryptophyta cell scheme © Franciscosp2 is licensed under a CC BY-SA (Attribution ShareAlike) license

DANDELION

Dandelion (*Taraxacum officinale*) is an extremely common plant through temperate North America and Europe. Its common name, dandelion, comes from the French 'dent de lion' (tooth of a lion) referring to the shape of the leaves. It is widely recognized as a weed, a word that generally means that it is an undesirable plant (more details in Chapter 29), undesirable because it grows in places where people are trying to grow something else (e.g. in lawns or in crop fields), and, at least to some people, undesirable because of its looks — perhaps not so much the bright yellow flowers, but more likely because of the fruit heads and the rosettes of leaves in an otherwise uniform carpet of grass. In an ecological sense dandelions are weeds because of their ability to disperse and their association with 'disturbed' habitats. In order to persist in a habitat that continually gets disturbed, a plant needs to be 'tough': able to survive, grow and reproduce even when disturbances that might kill other plants occur. Weeds typically disperse readily, grow quickly and are able to reproduce in spite of a variety of adversities. At the same time, most ecological weeds are poor competitors and, if disturbances do not occur, weeds will be replaced by species that are better competitors. Consider the distribution of dandelions in the Adirondack Park: they are rarely found in 'undisturbed' situations but are found where human activity 'disturbs' the area — next to campsites and along the margins of trails, places where competitors of dandelions aren't able to become established because of the trampling by people. In a comparable situation, dandelion can thrive in agricultural fields because it can tolerate the (often) annual tilling the soil because of the ability of roots to regenerate whole plants.

Phylogeny and taxonomy

Dandelion is an angiosperm, the group whose members produce flowers and seeds (Kingdom Planta, Phylum Magnoliophyta or Anthophyta). Dandelions are in one of the largest families within the angiosperms, the aster / sunflower family (Asteraceae), a group that is usually easy to recognize because the flowers occur in dense clusters (inflorescences) that themselves look like a single flower. The genus Taraxacum is a large and complex group, owing to the complications of apomixis and polyploidy (see discussion below).

Structure

Dandelion has a typical plant structure: a root-shoot axis with leaves produced on the shoot. It is an herbaceous perennial plant that forms rosettes, very short stems with leaves occurring in a circular pattern. As is true in all flowering plants, in the axils of each leaf is an axillary bud. In many plants these axillary buds develop into branches but in dandelion these branch shoots only develop into inflorescences, which, after developing fruits will fall off the plant. Dandelion produces an enlarged storage root (little material can be stored in the very short stem). This root is very capable of producing adventitious shoots; consequently, if one attempts to pull the plant up but fails to obtain all of the root, parenchyma cells in the remaining root develop into shoot apical meristems. These grow to the soil surface and again produce a rosette of leaves. One sometimes sees clusters of dandelion rosettes, resulting from a broken root that has produced multiple new shoots.

Sex and reproduction

Dandelions (*Taraxacum officinale*) reproduce by producing seeds, but the seeds are produced by apomixis, i.e. without the sexual process. Dandelion does produce flowers and

these appear normal and develop ovules. However normal meiosis does not occur (because the cells are triploid) in these ovules and no haploid cells are produced; consequently haploid female gametophytes (= embryo sacs) are not produced and no egg is produced. Hence, there is no possibility of syngamy. However, seeds do develop — the embryo found in the seed is not derived from a fertilized egg. Because there is no sex in *Taraxacum officinale* it is not a 'real' species, i.e. an 'interbreeding group '— there are multiple clones that collectively are considered a species. There also are closely related species that are sexual and the multiple entities within the *Taraxacum* genus are difficult to delineate.

Dandelion seeds are actually one-seeded fruits with the fruit and seed wall fused to each other (as it is in sunflower and in all members of the sunflower family). The top of the fruit develops into a parachute-like structure that helps disperse the seed. It has a stalk 1-2 cm long extending from the top of the fruit. The stalk ends with arms that radiate outwards. The arms have feathery branches emerging from them. Although the structure acts like a parachute by keeping the seed aloft for a longer time than would be the case otherwise, the mechanism of action is very different because the structure does not ‘capture air’ as a parachute does but it allows air to flow through it in such a way that that a vortex of low pressure forms above the dandelion fruit and this is what retards the rate of descent (see link below).

Matter and energy

Dandelion is a typical photosynthetic autotroph. It acquires carbon dioxide from the air and 14 mineral elements from the soil in order to grow. Energy from the growth process comes from cellular respiration where the plant oxidizes the carbohydrates formed in photosynthesis in order to acquire energy as ATP.

Interactions

As mentioned above, dandelion interferes with certain human endeavors: gardening, farming, manicured lawns. But dandelion does have some positive interactions with humans — its greens are edible, delicious in fact, if eaten when young. The flowers are not only pretty but are also edible and can also be used to color foods, e.g. dandelion pancakes.

Dandelions can be used to make wine, however the dandelions are only being used as coloring/flavoring agent — the sugars that the yeast ferment must be provided from cane sugar, honey, grape juice, etc.

Dandelions flowers do produce nectar and pollen and these are resources for a number of insects, including honeybees. This would seem to be surprising since the plant does not need pollen or a pollinator bringing pollen, in oder to produce embryos. However, at least some populations of dandelion apparently need the physical stimulation of flower visitors in order to trigger the apomictic process that results in seed production.

Further Reading and Viewing

- “Sexy males and sexless females: the origin of triploid apomicts” by P. Muralidhar and D. Haig. A report with details on diploid and triploid populations.
    - https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5520530/
- “The Flight of the Dandelion” by Awkward Botany. Details on dandelion “flight” on a site with a variety of interesting botanical subjects.
    - https://awkwardbotany.com/2019/06/
- “Taraxacum” on Wikipedia. A good entry for the genus.
    - https://en.wikipedia.org/wiki/Taraxacum

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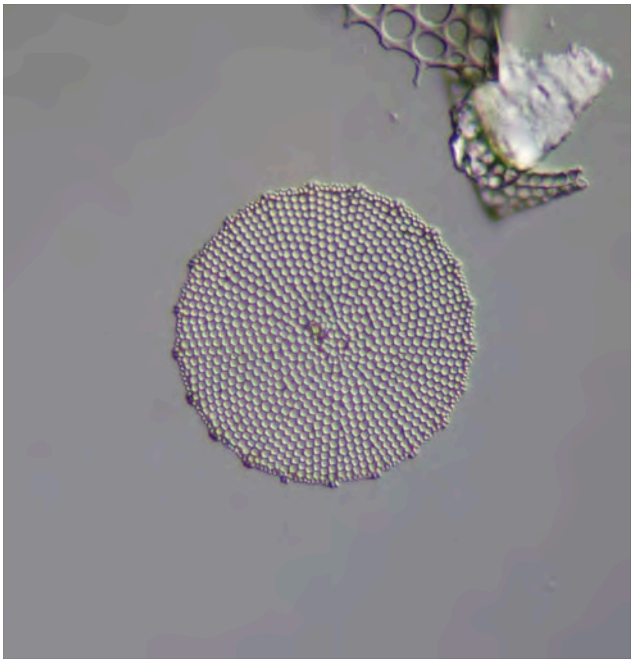
- Dandelion seed © Jmdesfilhes is licensed under a CC BY-SA (Attribution ShareAlike) license
- Dandelion seed in flight © PiccoloNamek is licensed under a CC BY-SA (Attribution ShareAlike) license
- Dandelion seed dispersal © Alex Valavanis is licensed under a CC BY-SA (Attribution ShareAlike) license

DIATOMS, UNICELLULAR PHOTOSYNTHETIC ALGAE



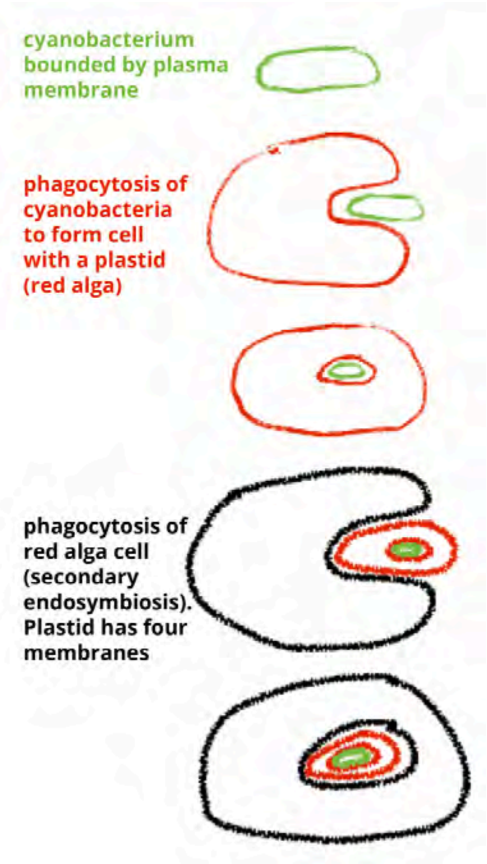
Diatom fossil

Diatoms

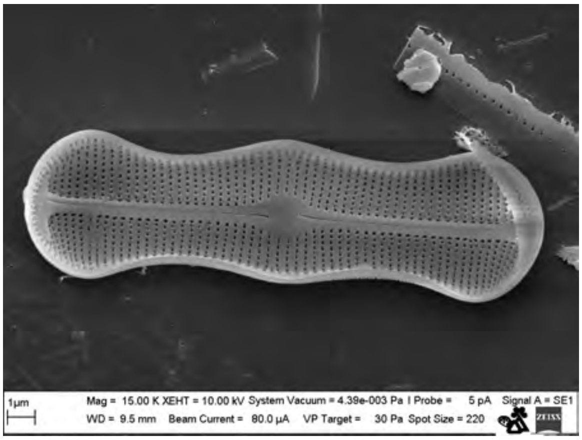
The diatoms are a phylum of unicellular photosynthetic algae and are a group significant for their unique structure and ecology.

Taxonomy and phylogeny

The diatoms represent a distinct group but the placement of the diatom group is problematic both in terms of level (phylum or class) and in terms of phylogeny (i.e. who are they grouped with). They may be placed in the 'miscellaneous' kingdom, the Protist Kingdom, which is practical but not phylogenetically accurate. They have affinities to several other groups, in particular the brown algae. In a number of taxonomic schemes they are placed in a group called 'heterokonts', sometimes in a 'Chromista' kingdom and sometimes in a Ochrophyta phylum. The groups that are sometimes associated with them include the 'golden-brown' algae, the brown algae, and some non-photosynthetic forms, in particular the water molds (Oomycota). It is now thought that the group originated from an endosymbiotic association of a red algae (a eukaryote) with another eukaryote and that the chloroplasts of diatoms and related groups represent derivatives of the red algae. Since the red algae themselves (like all eukaryotes) are thought to have originated from an endosymbiotic event (this is considered to be the primary endiosymbiotic event), the endosymbiosis that that produced diatoms is considered to be a 'secondary endosymbiosis'. Evidence for this can be found in the membrane system of the chloroplasts. The chloroplasts of red algae, green algae and plants have two membranes, one thought to be derived from a prokaryotic symbiont, a cyanobacterium (= blue-green algae), and one derived from the host that engulfed it (the phagosomal membrane (the membrane that surrounds the particle being engulfed). The chloroplasts of diatoms (and groups thought to be related to them) have four membranes. The two 'extra' membranes represent the outer membrane of the engulfed red algae plus the phagosomal membrane of the second endosymbiotic event. Diatoms, and the heterokont/chromista/ochrophyte group as a whole, are thought to be of relatively recent origin, obviously after the origin of red algae and also well after the origin of plants. The coloration of the diatoms, and of the photosynthetic members of the heterokont/chromista/ochrophyte group as a whole, is brown or yellow-brown (ocher is a yellow/brown color) and comes from the presence of a different pigment, chlorophyll c, in addition to chlorophyll a.



Structure



Diatoms are unicellular, and like most (but not all!) unicellular organisms, they are small, generally 20-100 um in size, and only visible to the naked eye as dust. They have a cell wall with a unique (in biological terms) composition, being composed of silica dioxide. Although silica dioxide is a rare component of organisms it is a very common mineral. Quartz is silica dioxide, thus glass, sand and diatom cell walls all have the same composition). The cell walls of most organisms are usually polysaccharide in nature (i.e., carbon based). Thus most cell walls would be considered 'organic' if one defines organic on the basis of carbon (as most chemists do); but if one considers 'organic' to mean relating to living things then silica dioxide sometimes **is** organic, but only rarely, as only a few other groups of organisms utilize the material in their structure (see horsetails). Another distinctive feature of the cell wall of diatoms is that it is composed of two distinct parts ('frustules'), a 'top' half that is slightly larger and whose sides overlap the 'bottom' half, much as the top of a shoe box fits over the bottom. The frustule is 'sculptured' with minute pores that give it a very decorative look. Diatoms come in two basic forms: radially symmetrical forms (image at top of first page) and bilaterally symmetrical forms, like the image at the start of this section. When the diatom dies the two halves separate and the top and bottom, being composed of a very stable material resistant to decomposition, settle to the bottom of the body of water that the diatom was living in and become part of the sediment. Most diatoms exist as separate individual cells but a few are colonial, resulting from the failure of newly produced cells to separate from their parent cell.

Reproduction

Diatoms generally reproduce asexually by mitosis. The two frustules separate, each with a nucleus and cytoplasm. Each daughter constructs a new frustule. The newly constructed frustule is always the bottom (smaller one). This means that one daughter cell (the one coming from the 'top') is the same size as the original, and the other new cell is slightly smaller. Thus, through time, the average size of a population of diatoms gets smaller. For most diatoms, when they shrink to 1/3rd of the maximal size, sexual reproduction is triggered and, in the process, the maximum size is once again produced.

Sexual reproduction requires the normally diploid nucleus to undergo meiosis. The details of the sexual process vary considerably and show variations found in other sexual organisms. For most pennate diatoms, sexual reproduction does not involve distinct gametes (i.e. egg and sperm) and while meiosis produces four haploid nuclei, not all of these persist. Two cells fuse to one another, both undergo meiosis and the movement of haploid nuclei and their subsequent fusion allows one or two auxospores to be produced per pair of cells. In centric diatoms two different types of gametes are produced. Some cells undergoes meiosis and produce one or two immobile eggs (again, two or three of the four haploid nuclei produced by meiosis degenerate). Other cells undergo meiosis. In some species each of the four haploid cells develop into sperm In other species the products of meiosis are not sperm but are sperm mother cells that will subsequently divide to produce up to 128 flagellated cells (sperm). Sperm swim to fertilize eggs which may or may not be released from their parent cell. Upon syngamy a structure called an auxospore is produced that expands to produce the maximum sized cell.

Matter and energy

Diatoms are photosynthetic and are typical autotrophs, using the sun's energy to reduce carbon and accumulate carbohydrates, and using the energy obtained from the oxidation of carbohydrates (i.e. respiration) to carry out a variety of life functions including the acquisition and accumulation of other elements necessary for life. Although, like all life, they require N, P, S, K, Ca, Mg, Fe, Mn, Cu, Zn, Mo, Ni, B, Cl, they also require at least two other elements, silica and selenium, that many organisms (in particular, most plants) do not require.

- A few diatoms are heterotrophic and obtain reduced carbon and other materials by eating other organisms.
- Diatoms generally store reduced carbon, at least for long-term storage, as lipids rather than carbohydrates as plants do. This is significant to their distribution because lipids provide buoyancy and may allow the organisms to stay in the upper

levels of a body of water that receives more sunlight.
- It is maybe significant that the silica cell walls of diatoms require considerably less energy to construct than the carbohydrate based cell walls of most other organisms with walls, in particular other unicellular algae. Some have argued that this is the reason that diatoms sometimes dominate the phytoplankton community.

Interactions

Here are a select few of the many interactions involving diatoms:

- global ecology —It is estimated that diatoms account for over 40% of the ocean's production of oxygen and reduced carbon. Therefore the group has a very substantial influence on important biogeochemical cycles, in particular for oxygen and carbon, but also for mineral nutrients and for silica.
- base of aquatic food chains—diatoms are a key component of phytoplankton communities which serve as 'food' for heterotrophs in these environments. When you are eating salmon, trout or tuna you are consuming at least some organic material that was formed by diatoms and transferred through a number of trophic levels before becoming part of the fish that was your meal.
- competition with other phytoplankton—diatoms interact with a number of other unicellular algae in a competitive way (i.e. diatoms negatively affect the population sizes and growth rates of other algae). In at least some instances silicon plays an important role in this interaction, if silica is abundant diatoms are able to outcompete other algae, if silica is scarce diatoms are outcompeted.
- developing communities—colonial diatoms commonly form a film on both biotic (other algae, snail shells) or abiotic (rocks, boat hulls) surfaces. Mucilage secreted by the diatoms holds the colony together, and a variety of other organisms, bacteria, other algae, nematodes, etc. live in the film.
- economic interactions with humans—diatoms are important to human endeavors in a number of ways, besides their importance to global ecology:
    - diatoms occasionally cause toxic blooms http://www.mbari.org/staff/conn/botany/diatoms/jennifer/toxin.htm
    - the frustules of diatoms, preserved in sediments and rocks derived from sediments, is called 'diatomaceous earth' and has a number of industrial applications: as a porous filter (e.g. in aquaria), as an abrasive (e.g. in toothpaste), as a

mechanical insecticide, as an absorbent, as a stabilizer mixed with nitroglycerin forming dynamite.

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DICTYOSTELIUM: A CELLULAR SLIME MOLD

Different stages of Dictyostelium: A 'slug' (out of focus in the background) and multiple developing sporocarps.

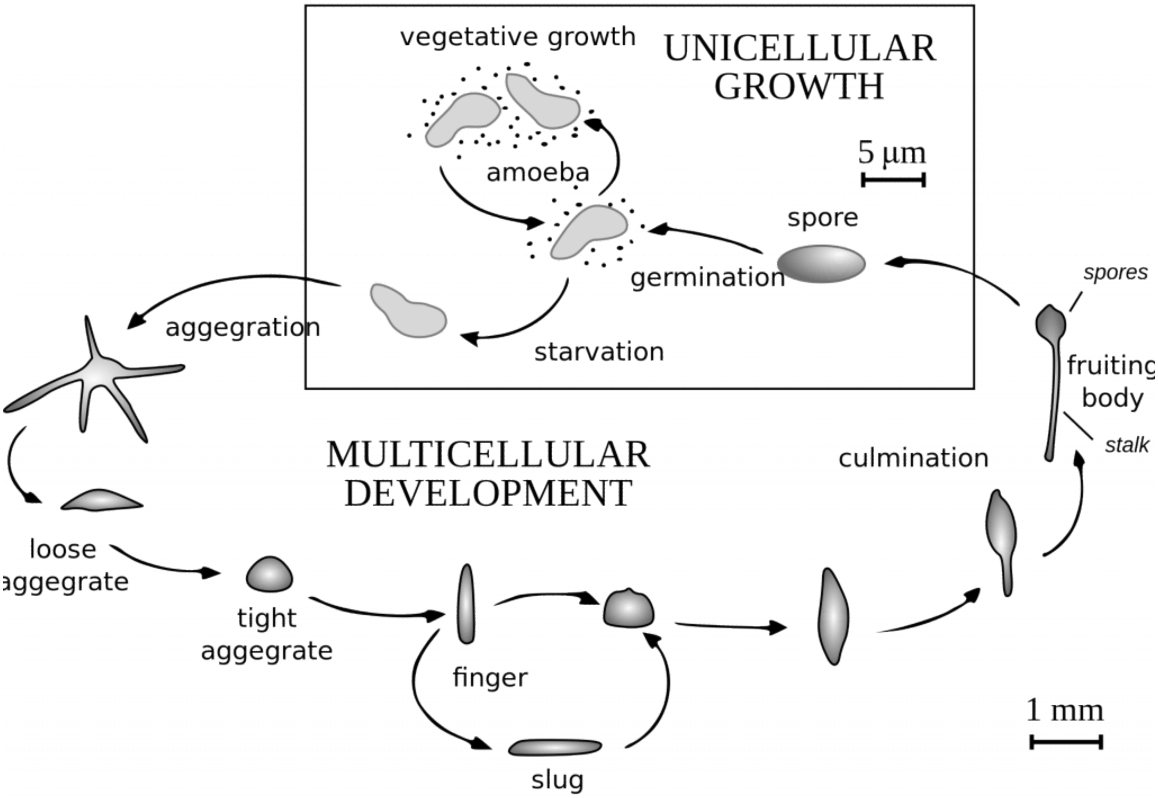
Dictyostelium is a 'cellular slime mold', (to most) a very unfamiliar organism but one that has proved to be useful as a 'model organism' to study significant biological processes, in particular, development. It has a multicellular stage that develops not as a result of a cell dividing repeatedly, producing daughter cells all stuck together. Instead multicellularity is the result of the aggregation of many individual cells. In addition to its use as a model organism, studying *Dictyostelium* offers an excellent opportunity to see life from a different perspective, appreciating that although all life is fundamentally the same it sometimes operates in very different manners.

Phylogeny and taxonomy

Since they are heterotrophic, mobile and (generally) unicellular cellular slime molds used to be considered 'protozoa'. Other early treatments put them with fungi because they produce fruiting bodies and spores. Like a number of other 'misfit' groups, the cellular slime molds have been placed in the Protist kingdom, a heterogenous assemblage of eukaryotes that do not readily group with animals, plants or fungi. While certain aspects of their life-cycle are unique, their amoeboid-like stages aligns them with amoebae, that look similar but are always single celled and never coalescing into a multicellular entity. Another relatively close group are the plasmodial slime molds (see *Physarum*) and some put these three groups (amoebae, cellular slime molds, plasmodial slime molds) together in a group called the Amoebozoa, and the Amoebozoa, along with Choanoflagellates, Fungi and Animals can be united in a group called the Unikonts.

Structure

Dictyostelium is eukaryotic and typically exists as 'amoeboid' cells that are small (typically ~ 5 um in length) , without a cell wall, and capable of ingesting material by phagocytosis. Their normal food is bacteria. Peculiar to the group is the developmental ability of individual cells to come together to form a multicellular entity. Consequently *Dictyostelium* also exists as a multicellular form produced when cells aggregate into a 'slug' ~ 1 mm long. The slug is briefly mobile and then trans forms into an immobile vertical structure up to one cm tall with a round spore producing capsule at its top.



Reproduction

The individual amoeboid cells reproduce asexually by mitosis, but this is only part of the life cycle. The multicellular entity also reproduces asexually: slug — >fruiting body — >spores —— >more amoebae — > more slugs. *Dictyostelium* is capable of a sexual process but does so only rarely, when two amoeboid cells fuse to form a single diploid cell, form ing a structure called a macrocyst. Inside the macrocyst meiosis occurs, followed by mitosis and eventually haploid amoeboid cells are released.

The aggregation stage of Dictyostelium. In response to a chemical signal individual cells stream to a gathering point. The 'dots' are individual cells, the 'arms' are where the the cells have aggregated. They continue their movement to the central structure that develops into an slug.

Matter and Energy

Dictyostelium is a predatory heterotroph, capturing (by phagocytosis) other living organisms (primarily bacteria) and using their biomolecules both as a source of energy (oxidizing them in cellular respiration) and also reconfiguring them into biomolecules of *Dictyostelium*.

Interactions

One of the interesting interactions involving *Dictyostelium* is its 'farming' behavior, an ability to produce spores that contain the bacteria that it feeds upon. The dispersal of such spores makes it more likely that *Dictyostelium* will have something to eat after dispersal (see link below).

Watch

One or more interactive elements has been excluded from this version of the text. You can view them online here: https://milnepublishing.geneseo.edu/botany/?p=75#oembed-1

Further Reading

- The odd life of slime molds.
    - https://blogs.scientificamerican.com/compound-eye/starving-to-be-social-the-odd-life-of-dictyostelium-slime-molds/
- "Starving to be Social: The Odd Life of Dictyostelium Slime Molds" by Alex Wild
    - https://blogs.scientificamerican.com/compound-eye/starving-to-be-social-the-odd-life-of-dictyostelium-slime-molds/
- "Dictyostelium discoideum" by Mary E. Sunderland
    - https://embryo.asu.edu/pages/dictyostelium-discoideum
- "Dictiostelida" in *Microbe Wiki*
    - http://microbewiki.kenyon.edu/index.php/Dictiostelida

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EPHEDRA: JOINTFIR

Ephedra (the common name is also ephedra, and it is also called jointfir) is a representative of a small, diverse group of seed plants that unfortunately has no common name. They are simply called 'the gnetophytes' after the name for the phylum, Gnetophyta. There are three genera in the group, *Ephedra* and *Gnetum*, both with less than 100 species, and *Welwitchia,* which only has a single species. *Welwitchia* has a very limited distribution (the Nambib desert of South Africa) while *Gnetum* is found world-wide in tropical areas and *Ephedra* is found world-wide in shrublands (generally hot and dry habitats).

Taxonomy and Phylogeny

The gnetophytes are generally put in their own phylum, one of four phyla of seed plants without flowers (the others being conifers, cycads and ginkgo). Collectively, these four groups are grouped as 'gymnosperms' a group that some workers consider a phylogenetic entity while others do not, primarily because of difficulties relating their relationships with extinct seed plants and with flowering plants. While gnetophytes have some features (see below) in common with angiosperms (and distinct from other gymnosperms), most feel that there is not enough evidence to group gnetophytes and angiosperms together in a phylogenetic entity. The Angiosperm Phylogeny Group has the pine group as the gnetophytes closest relative.

Structure

Ephedra is a leafless shrub with multiple stems and branches that are typically 2 to 5 mm thick and green. The leaves are small, scale-like and often quickly fall off the plant. Plants produce male cones that produce microspores which develop into pollen, and female cones that produce megaspores which are retained inside the cones and develop into female gametophytes inside structures called ovules. Unlike other gymnosperms, *Ephedra* plants possess vessels in their xylem tissue, a feature that is found in many, but not all, angiosperms.

Reproduction

Like all seed plants, *Ephedra* produces female gametophytes inside ovules. The zygote is formed when the egg, produced by the female gametophyte, is fertilized by a sperm nucleus produced by the male gametophyte (pollen). This zygote develops into a new sporophyte embryo that is packaged inside a seed, a mature (fully developed) ovule. Double fertilization, where there are two sperm nuclei, one fusing with the egg and a second fusing with a second nucleus of the female gametophyte, is a feature once thought to be found only in flowering plants. But it also occurs in at least some members of the genus *Ephedra*, although the details, in particular the lack of development of an endosperm, distinguish what happens in *Ephedra* from what happens in angiosperms. The female cones of some species become ‘fruits’ when the integuments thicken and become colorful. Technically fruits (if defined as ‘ripened’ ovaries, a part of the flower) are only present in flowering plants (angiosperms), but if defined as ‘structures to promote the dispersal of seeds, fruits evolved independently in: angiosperms, some conifers (e.g. juniper, yew), some gnetophytes (*Ephedra*) and ginkgo.

Matter and energy

Ephedra is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and also as building materials to synthesize a variety of biomolecules.

Interactions

Male cones of Ephedra, showing the pollen producing 'microsporangiophores' analogous with anthers.

Ephedra can be a dominant species over a fairly large area, e.g. parts of southern Utah and Nevada. It is eaten by both vertebrate and invertebrate herbivores. At least some species of *Ephedra* are pollinated by insects, another connection with angiosperms. However insect pollination may be an ancestral feature and therefore is probably not a good feature to associate angiosperms with gnetophytes. Female cones of *Ephedra* produce a 'pollination drop' at their tip that serves both to capture wind blown pollen and to attract insects that may happen to be dispersing pollen. Some interpret these observations to point to an evolution of nectar from a fluid that encouraged the capture of wind-blown pollen. But other workers cite evidence that insect pollination is the ancestral condition in the group and that the pollination drops that capture wind-blown pollen are derived rather than ancestral.

'Fruits' (ripened female cones) of Ephedra.

Ephedra is a source of both ephedrine and pseudoephedrine (a steroisomer of ephedrine), alkaloids that have been used in diet pills, as a coffee-substitute, and as a cold medicine. It has the effect of decreasing nasal and bronchial congestion. These alkaloids can also be converted into methamphetamines, which is why a number of common cold medications are no longer sold over the counter.

Further Reading

- "Gnetophytes" on *Plant Life*
    - http://lifeofplant.blogspot.com/2011/03/gnetophytes.html

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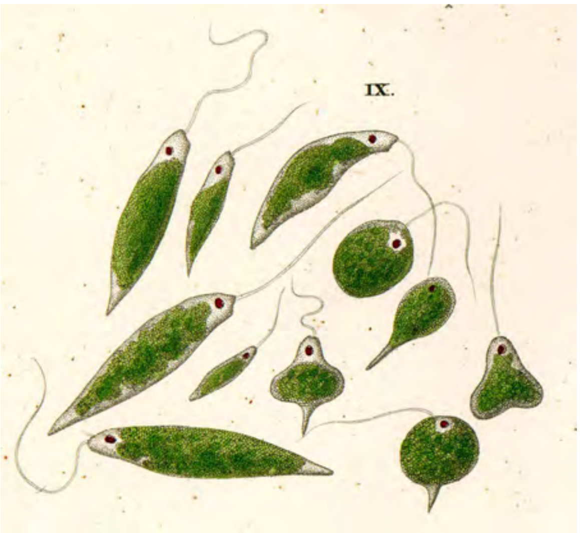
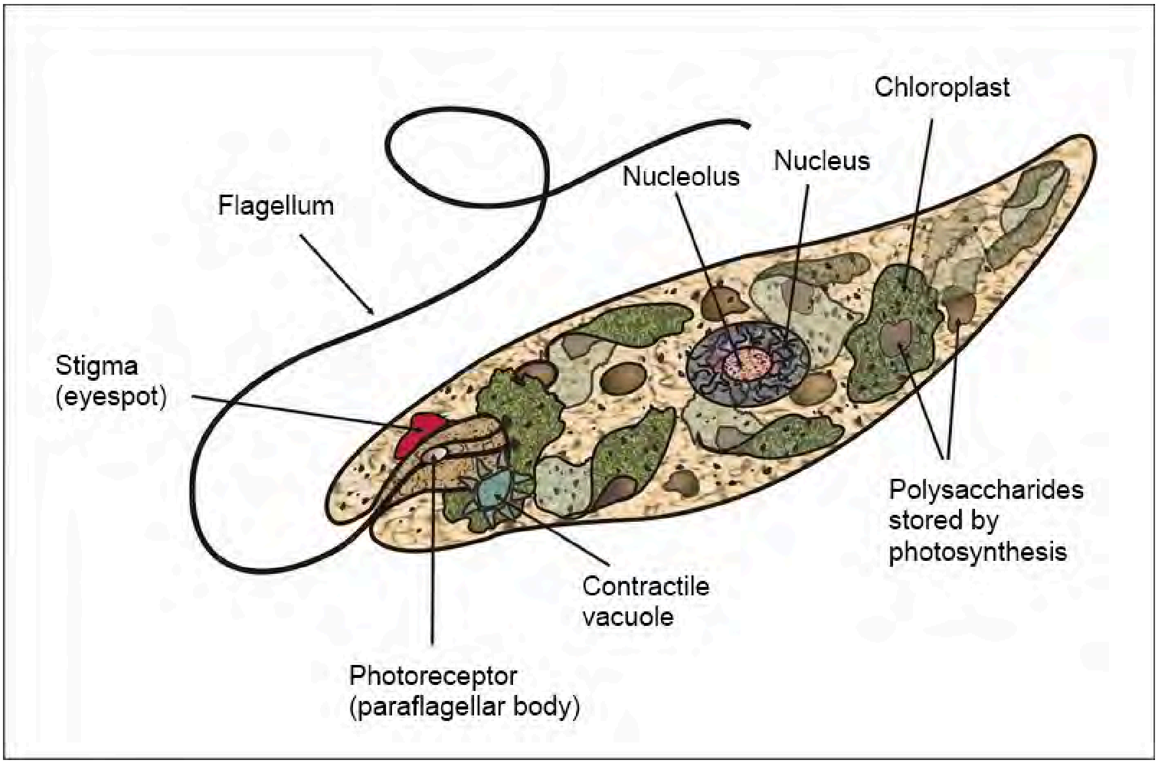
EUGLENA: A UNICELLULAR ALGAE

Euglena is a genus of unicellular, freshwater organisms that are very common in ponds and small bodies of water, especially if they are rich in nutrients and consequently high in algae (aka ‘pond scum’). As noted below, *Euglena* itself is sometimes photosynthetic and is a component of the green sludge in such ponds. But at other times it is non-photosynthetic and is a component of the diverse group of organisms that are eating the green sludge or perhaps eating the other things that eat the green sludge.



Taxonomy and Phylogeny

Euglena are in a small group (less than 1000 species), that in the past was claimed by both zoologists (because they are mobile and some are heterotrophic) and by botanists (because some members photosynthesize). Accordingly, the group has sometimes called ‘Euglenozoa’ by zoologists (‘zoa’ refers to animals) and has been called ‘Euglenophyta’ by botanists (‘phyta’ refers to plants). In the past the group has been put in the Protist Kingdom. Recent phylogenetic studies have them diverging very early from other eukaryotes and consequently putting them in a very small group that contains very unfamiliar unicellular organisms. Some close relatives of *Euglena* include the causal organism for sleeping sickness and for Chagas disease. Complicating their taxonomy is the fact that some in the group are clearly composite organisms, being the product of secondary endosymbiosis when a green algal was consumed but not digested by a flagellate.



Structure

Euglena is a unicellular organism with a complex internal structure that includes a contractile vacuole that can expel water and a red 'eyespot'. Photosynthetic forms contain a chloroplast. They possess two flagellae, one long, one short, that can allow the organisms to move. *Euglena* are also able to move by means of changing its shape (see video links). Outside the cell membrane is a flexible, protein-based structure called a pellicle. Although not generally considered a cell wall, it has similar functions in providing some rigidity and strength that the membrane cannot provide. However the pellicle is much more flexible than most cell walls and allows for the change in form that is often seen in *Euglena* motion.

Reproduction

Euglena reproduces asexually when cells divide. No sexual reproduction has been found within the group.

The striations seen on the right side are the pellicle, a proteinaceous coating found in euglenoids.

Matter and energy

Sometimes *Euglena* are a typical photoautotroph s, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and as building materials to synthesize a variety of biomolecules. Euglenoids store carbohydrates in a different glucose polymer than typical starch — the glucose units are combined in a 1,3 linkage, rather than the 1,4 linkage found in normal starch. Euglenoids may also behave like heterotrophs and acquire material by ingestion (phagocytosis) or by absorption of solutes from its aquatic environment. Some forms of *Euglena* lack chloroplasts and are solely heterotrophic.

Interactions

Euglena can be important components of certain aquatic environments and play a role as both a primary producer, eaten by other organisms, and also as a decomposer (heterotroph) that consumes other organisms and breaks them down, or consumes dead organic material and breaks it down.

Certain *Euglena* species (e.g. *Euglena sanguinea)* can turn a pond red and can also produce toxins that kill fish.

Further Reading

- "Introduction to Euglenids (Euglenoids) where some exhibit both Plant and Animal Properties" by Dr. Robert Berdan.
    - https://www.canadiannaturephotographer.com/euglenoids.html
- Hall Group at the Earlham Institute. Euglena gracilis.
    - https://www.earlham.ac.uk/research-group/hall-group

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- Euglena pellicle © Deuterostome is licensed under a CC BY-SA (Attribution ShareAlike) license

GINKGO

Gingko (*Ginkgo biloba*) is a commonly planted tree that many have probably seen but may not have distinguished from other trees. In spite of the fact that its form is very similar to most trees it has a number of distinct features. In particular, most trees are flowering plants (angiosperms) or conifers, ginkgo is neither!

60 million year old ginkgo fossil

Taxonomy and phylogeny

Gingko is unique in all of life's diversity because it is the only species that is the sole member of an entire phylum. While there are numerous examples of a single species as the sole member of a genus, and a few examples of a species as a sole member of a family, still fewer examples of a species being the sole member of an order, etc., etc., there is only one example of a species being the sole member of a phylum, in this case the Ginkgophyta. What this means is that ginkgo is distinctly different in a number of ways from all other plants, and in particular from all other seed plants. Generally seed plants are divided into five groups, one of which is the Ginkgophyta; the others are: flowering plants, conifers, cycads and gnetophytes. Ginkgo is an ancient group—the figures above shows a modern leaf and also a fossil exposed in 60 million year old rock. The genus is actually over four times this age with recognizable leaves in 250 million year old deposits.

Structure

Ginkgo looks like a typical tree and, from a distance, because of its broad leaves, would be considered to be more closely related to angiosperm trees like oak and maple than to conifers like pine and hemlock. However, the wood of ginkgo, like that of pines, hemlock and all conifers, contains no vessels or fibers, only tracheids and parenchyma cells. Gingko, like some conifers (e.g., larch) , has 'short shoots' (very slow growing shoots) and 'long shoots' (faster growing shoots). The short shoots look like spurs on the stems and make identifying ginkgo easy in the winter.

Sex and reproduction

Ginkgo produces seeds that develop in the female 'cones', which resemble olive fruits. The species is dioecious, i.e. it has separate male and female plants. Male plants produce pollen in cones. The pollen is dispersed to female cones by the wind. Like *Ephedra* in the Gnetophyta group, the female cones of ginkgo produce a drop of liquid that helps to capture pollen. This drop, containing pollen, is pulled into the cone by capillary action as the drop dries. Once in the cone, the opening to the outside is closed and the pollen germinates and produces a small, fungal-like structure, the male gametophyte, which acquires nutrition from tissues of the ovule. The male gametophyte matures and releases mobile, flagellated sperm into the liquid that is present in the 'canal' at the end of the ovule. These swim to the female gametophyte and fertilize the egg to form a zygote. Flagellated sperm are present in all ferns, mosses, and liverworts but are extremely rare in seed plants, being found only in Gingko, the cycads and some gnetophytes.

Matter and energy

Ginkgo is a typical photosynthetic autotroph, capturing the energy of sunlight in carbohydrates and then using these carbohydrates both as a source of materials and a source of energy. It is a C3 plant that acquires carbon dioxide as it diffuses through stomates from the air into the leaves Interestingly, in the Mesozoic, when carbon dioxide levels were much higher than now, its stomatal density was much lower and some have speculated that rising carbon dioxide levels might allow Ginkgo to expand its range from surviving only where it is planted.

Interactions

Ginkgo are extensively planted as a shade tree. It has an appealing form and grows well in a variety of habitats, including urban ones where pollution and asphalt produce an environment where many trees fare poorly. A significant, but not well explained, feature of the plant, is that it grows well when planted but does not establish itself on its own. Many workers feel that there are no 'naturally-occurring' ginkgos, i.e. that it is only found where it has been planted and its current existence is due solely to the fact that humans have been planting them for the last 10,000 years, most of that time in China, but more recently world-wide.

The 'fruits' (female cones) of ginkgo produce a foul smell (butyric acid) when ripening. In the past the female trees were sometimes removed when they were old enough to produce fruit but modern horticulture has allowed plants to be cloned and most of the trees now planted are male.

The leaves of ginkgo are thought by some to be an herbal medicine that improves brain function. Conclusive evidence of this is lacking.

Further Reading

- *Ginkgo: The Tree That Time Forgot* by Peter Crane, Yale University Press, 2013
- "Ginkgo Biloba Leaves Show Climate Over Millions Of Years" by Kristin Strommer-Oregon on Futurity.org

  - futurity.org/climate-change-over-time-ginkgo-biloba-2365722

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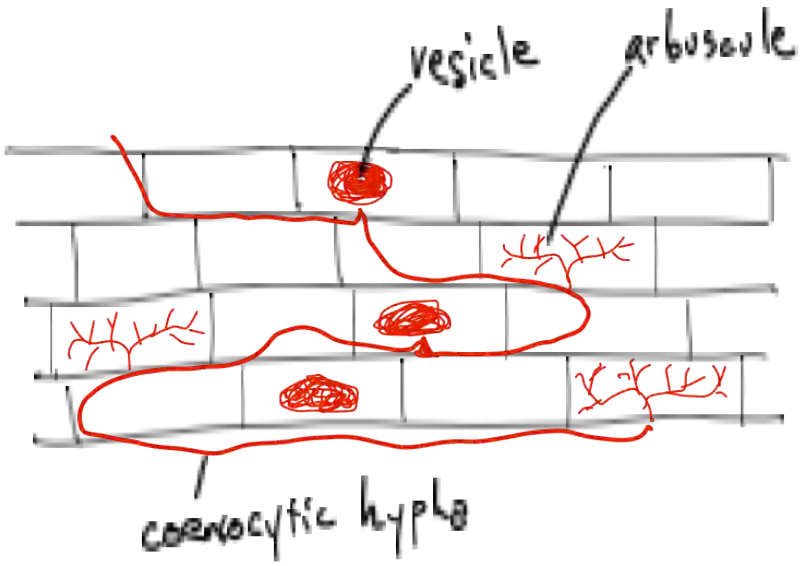
- Landau Ginkgo Goethepark © Rudolf Wild is licensed under a CC BY-SA (Attribution ShareAlike) license

GLOMEROMYCOTA: IMPORTANT MYCORRHIZAL FUNGI

The Glomeromycota are a very common, yet rarely seen, group of fungi. They are ubiquitous partners with angiosperms, forming associations called mycorrhizae, more specifically 'endomycorrhizae', also called vesicular/arbuscular (VA) mycorrhizae. Most plants (more than 80%) are mycorrhizal and most of these form endomycorrhizae with a fungal associate in the Glomeromycota.



A plant root (rectangular cells) infected by Glomeromycota filaments, showing both a vescicle, the round structure, and an arbuscule, the tree-like structure.

Taxonomy and Phylogeny

The Glomeromycota have long been considered a part of the bread mold (Zygomycota) group because of structural similarities (see below) , but recent studies, in particular molecular studies, have indicated that they are distinct from the bread molds and are closer to club fungi and sac fungi than to the bread molds. They are not a very diverse group (less than 500 species in the whole phylum) and morphologically they do not exhibit a great deal of variation.

Structure

Like most fungi, the Glomeromycota generally exist as filamentous hyphae, and like the bread molds, the hyphae have no cross-walls, i.e. the members are coenocytic. Commonly the hyphae produce relatively large spores. Unlike the club fungi and cup fungi they do not produce fruiting bodies. When inside plant cells most Glomeromycota produce characteristic structures called arbuscules that function to transfer materials between the fungus and plant. Also produced are vesicles, which are enlarged spherical parts of the hyphae where materials are stored.

Reproduction

Glomeromycota are strictly asexual. They produce spores but they do not appear to have any sexual process.

Matter and energy

Most, but apparently not all, members of the group are mycorrhizal (endomycorrhizal) and obtain carbohydrates from their photosynthetic associate (usually an angiosperm but there is one documented case of an association with a filamentous blue-green algae). All apparently obtain nutrients (i.e. minerals) from the soil and there is eviden ce that although most species are mycorrhizal, a few species also obtain food (i.e. carbohydrates) from the soil.

Interactions

Glomeromycota interact with many (nearly all) plant species and it is increasingly apparent that they significantly affect the behavior of their hosts, generally allowing them to grow more vigorously. The group was probably significant in the colonization of land by autotrophs and thus the origin of plants.

Further Reading

- USDA publication on endomycorrhizae
- “MYCORRHIZAL ASSOCIATIONS: The Web Resource” by Mark Brundrett
    - http://mycorrhizas.info/vam.html#look

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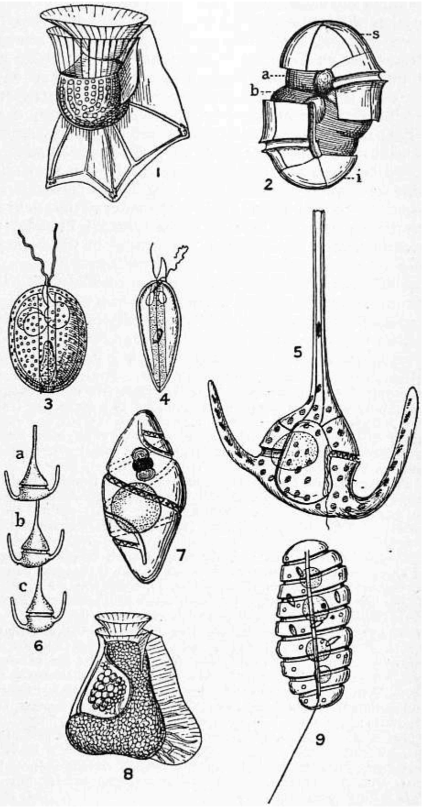
GONYAULAX: A DINOFLAGELLATE

Gonyaulax is representative of a n important group of unicellular organisms, the Pyrrophyta (sometimes called Dinophyta). The common name for the group is the dinoflagellates. Like the Euglenophyta, the group contains both photosynthetic and non-photosynthetic forms. *Gonyaulax* and several other dinoflagellates are notable for their association with two familiar phenomena: ocean bioluminescence and red tides, although most dinoflagellates are not. And both bioluminescence and ‘red tides’ (algal blooms) are not restricted to dinoflagellates.. The group as a whole is extraordinarily diverse in terms of their biology, interactions with other species and evolutionary history.



Taxonomy and Phylogeny

Because of certain ‘prokaryotic’ features associated with their nucleus and DNA, the dinoflagellate group was once were once thought to be a ‘transitional’ group between prokaryotes and eukaryotes but workers now believe that these features are ‘ derived’ (i.e. appeared after the group originated) and not ‘ancestral’ (present in the original dinoflagellates). That is, it is thought that the dinoflagellates diverged from other eukaryotes and then developed these ‘prokaryotic’ features. Modern treatments often lump the dinoflagellates with two other unicellular groups that are completely heterotrophic: the ciliates (including *Paramecium*) and the ampicomplexans (mostly parasites, including *Plasmodium,* the causal organism for malaria). There is evidence that the ancestor of all these groups was in fact photosynthetic, the result of a secondary endosymbiotic event between a red algae and a heterotrophic eukaryote, but that photosynthetic ability was lost in all of these groups, only to be regained in some dinoflagellates by a another endosymbiotic event that apparently has occurred multiple times, with (photosynthetic) diatoms, cryptomonads and green algae.

Structure

Dinoflagellates are unicellular and range tremendously in size, from 5 um to 1mm. They also vary tremendously in form although many are spherical with 'horns'. Many have a complex boundary, called a 'theca' between it and the outside that consists of several large, cellulose plates enclosed in vesicles, just inside the outermost membrane. Most possess two flagellae, one long and one short and have a characteristic 'whirling' motion as a result of flagellar movement.

Reproduction

Most reproduction is asexual and the sexual process has not been found in most of the members of this group. When there is sex the diploid cell quickly undergoes meiosis; therefore finding the diploid cells is rare.

Matter and energy

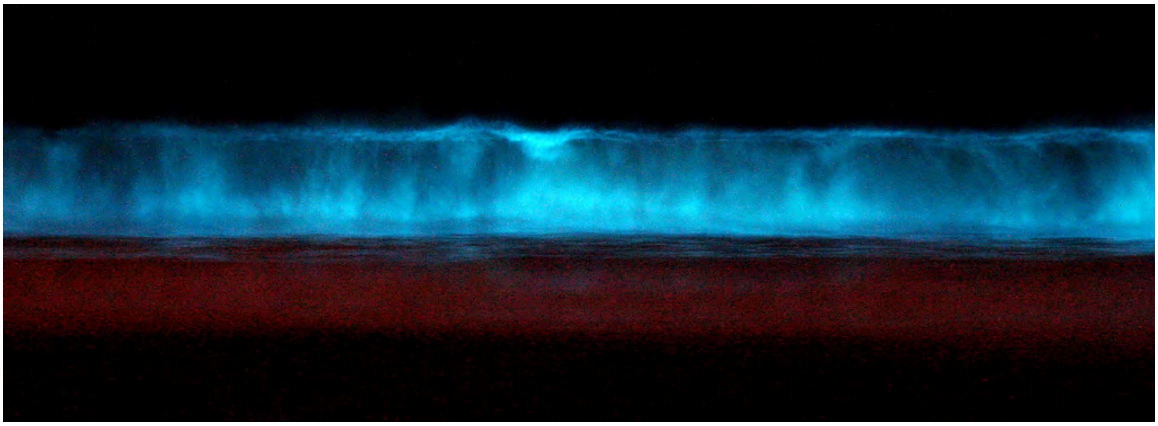
Dinoflagellates occur both as photoautotrophs and as heterotrophs. The heterotrophs may be predatory (i.e. kill and consume other living things), parasitic (i.e. live in, and sometimes, but not always, kill its host) or saprophytes (feeding on dead organic matter). Dinoflagellates also serve as the photosynthetic component for a number of symbiotic associations, in particular in corals, and thereby allow these associations to be photoautotrophic.

Interactions

Dinoflagellates are found primarily in marine systems but some are in fresh-water. A number of species produces a toxin which can kill fish and invertebrates and may kill humans if they eat organisms, in particular shellfish, that have consumed the dinoflagellates. Dinoflagellates sometimes have population spikes causing what are known as 'red tides', so named because of the of a red carotenoid pigment often present in the cells.

Dinoflagellates are also significant in producing the chemical dimethylsulfoniopropionate (DMSP), a chemical that is eaten by bacteria and is significant not only to their nutrition, providing carbon and reduced sulfur. As a consequence of bacteria eating DMSP, another chemical, dimethyl sulfide, is released and this chemical is thought to be highly significant to global climate because it triggers cloud formation.

Gonyaulax has been used to study the biological clock — it is bioluminescent with a 24 hour periodicity. Additionally, bioluminescence in several species is triggered by agitation as is shown in the picture below where the motion of breaking waves triggers luminescence.



Bioluminescent dinoflagellates (*Lingulodinium polyedrum*) lighting a breaking wave at midnight. The blue light is a result of a luciferase enzyme acting on a luciferin molecule. Although both fireflies and dinoflagellates exhibit bioluminescence, the luciferase enzyme and the luciferin substrate are both distinctly different, i.e. this is a case of convergent evolution. In fact bioluminescence appears to have evolved multiple times. The light emitting molecule in dinoflagellates is structurally related to chlorophyll, a light absorbing molecule.

Further Reading

- “Evolution of Dimethylsulfoniopropionate Metabolism in Marine Phytoplankton and Bacteria” by Hannah A. Bullock, Haiwei Luo, and William B. Whitman
    - https://www.frontiersin.org/articles/10.3389/fmicb.2017.00637/full
- “Tree of Life – Dinoflagellates” by Mona Hoppenrath and Juan F. Saldarriaga
    - http://tolweb.org/Dinoflagellates/2445

Media Attributions

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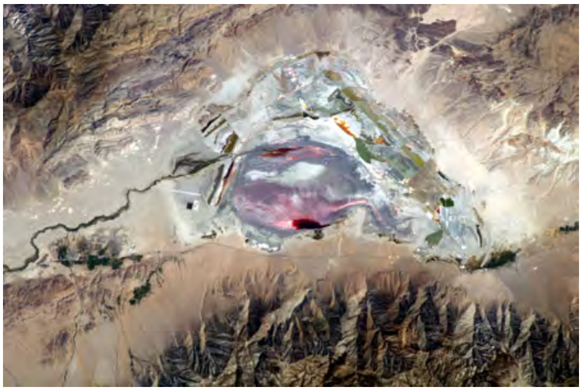
- Dinoflagellate bioluminescence © Mike / Red Tide at midnight is licensed under a CC BY-SA (Attribution ShareAlike) license

HALOBACTERIUM

Halobacterium is one of several organisms that can color high salt environments red, e.g., the hypersaline pools in Owens Lake, California. *Halobacterium* is significant not just for its tolerance of extreme salinity but also because it is a member of the Archaea and because it has some peculiar metabolic abilities.



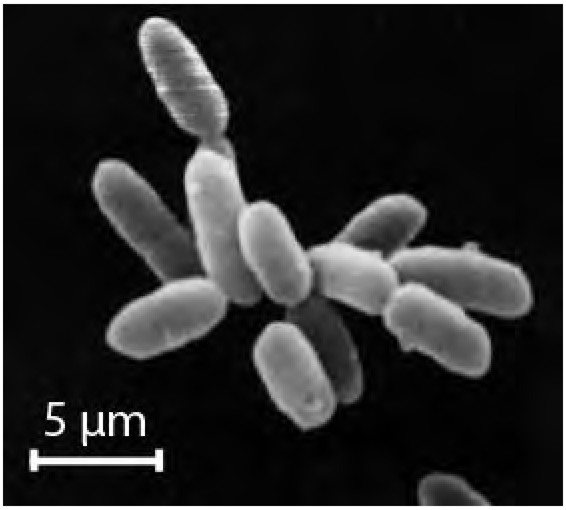
Owens Lake viewed from an orbiting satellite. The red color in the center is caused by the presence of Halobacteria.

Phylogeny

Halobacterium is an oxymoron, because it is not a bacterium, it is an archaeon, a member of the Archaea, a group of prokaryotes that in 1977 was distinguished from the rest of prokaryotes (organisms lacking cellular organelles) by virtue of a suite of characteristics, in particular the sequence of bases in the 16s ribosome (actually the sequences of bases in DNA that codes for the RNA of the 16s ribosome). Thus most workers now describe two groups of prokaryotes, Archaea and Eubacteria. Although initially thought to be representative of the most ancient forms of life (hence the name Archaea) workers now believe that the Archaea were derived from Eubacteria. Based on metabolic pathways and genes, it appears that and that eukaryotes and Archaea are more closely related than eukaryotes and Eubacteria.

Structure

Cells are rod-shaped and roughly 2-5 um in length with a single lipid bilayer membrane surrounded by a glycoprotein cell wall. Archaea cell membranes are made of phospholipids that are distinct from those found in bacteria and eukaryotes. *Halobacterium* cells are flagellated and capable of moving towards a source of light, especially light in the in



the yellow-green, around 560 nm, which is where its photosynthetic pigment (bacteriorhodopsin, see below) has peak absorbance.

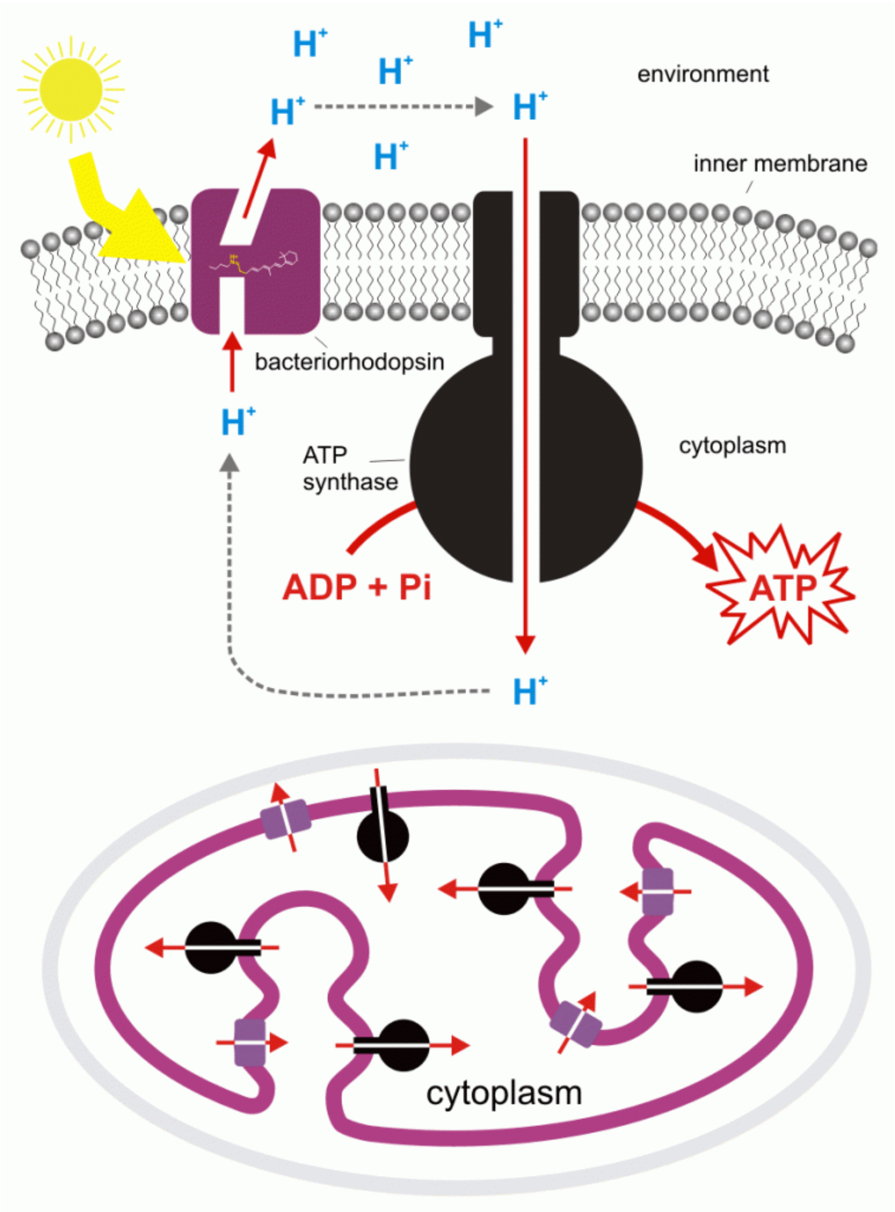
Sex and reproduction

Like all prokaryotes, *Halobacteria* are not sexual but they are capable of exchanging genetic material by other means. They reproduce by cell division but, like all Archaeons do not produce endospores.

Matter and energy

Halobacteria are photoheterotrophs. Like other heterotrophs they need to eat (i.e. assimilate) organic compounds to provide themselves with material to grow, but they also use light energy to generate ATP. In contrast, photosynthetic organisms are autotrophic: they make food (carbohydrates) and then 'eat' some of it to make ATP and use the rest as building material. Regular heterotrophs 'eat'both to acquire material for growth and to obtain energy, usually via cellular respiration. . If *Halobacteria* are deprived of light they need to eat more because they will behave like a 'normal' heterotroph, using the food they eat both to make themselves bigger and also to provide for their energetic needs.

The pigment that interacts with light is bacteriorhodopsin, a form of rhodopsin, the same pigment that our eyes use to see. In both instances light causes a conformational change in the protein. In our eyes this causes a nerve impulse to be transmitted; in *Halobacterium* it causes protons to accumulate on one side of a membrane, and proton flow down the gradient that has been created allows ATP to be synthesized. *Halobacterium* also possesses a second protein pigment, halorhodopsin, that can use light energy to pump chloride ions into the cell, increasing the solute concentration and preventing excessive water loss.



Bacteriorhodopsin is a membrane-spanning protein that can acquire protons in the cytosol, change conformation due to the absorption of light and release protons on the outside of the membrane. Protons then flow into the cell, down their electrochemical gradient, in a process that is associated with ATP formation.

Interactions

Halobacterium is a classic example of an 'extremophile', an organism that exists under extreme conditions, such as high temperature, high salinity, high acidity. *Halobacterium* can live, and indeed requires, salt concentrations far exceeding the tolerance levels of most other organisms. They can even survive in saturated brine solutions. Because of this, they can actually be 'fossilized' in salt deposits and stay alive for thousands, perhaps millions of years. Tolerance of extreme conditions probably means reduced competition in such habitats.

Although many archaeons are extremophiles, not all are; and there certainly are extremophiles that are not archaeons (one you should be aware of is the bacterium, *Thermus aquaticus)*. Another non-archaeon that lives in high salt conditions is the uni-cellular green algae *Dunaliella salina* which can produce large quantities of the pigment beta-carotene and at one time was once thought to be the source of red coloration in hypersaline lakes. Most workers now believe that archaeons like *Halobacterium* are what make the lakes red, but that *Dunaliella* may be responsible in making flamingos pink, a result of their consumption of brine shrimp that have feasted on the beta-carotene loaded *Dunaliella*.

Further Reading and Viewing

- "Halobacterium" on Cronodon.com
    - https://cronodon.com/BioTech/Halobacterium.html
- "The Immortal, Halophilic Superhero: Halobacterium Salinarum – A Long-lived Poly-extremophile" by Terry J. McGenity
    - https://microbiologysociety.org/publication/past-issues/real-super-heroes/article/the-immortal-halophilic-superhero-i-halobacterium-salinarum-i-a-long-lived-poly-extremophile.html
- "Archaea Are More Wonderful Than You Know" by Jennifer Frazer
    - https://blogs.scientificamerican.com/artful-amoeba/archaea-are-more-wonderful-than-you-know/
- "General Microbiology – Archaea" by Linda Bruslind. Archaea membranes.

  - https://open.oregonstate.education/generalmicrobiology/chapter/archaea/

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- Halobacteria with scale © Vojtěch Dostál is licensed under a Public Domain license
- Bacteriorhodopsin chemiosmosis © Darekk2 is licensed under a CC BY-NC-SA (Attribution NonCommercial ShareAlike) license

HEMLOCK

Eastern hemlock, the state tree of Pennsylvania. This picture was taken in early summer when this year's growth is a bright green. Of the fifty state trees, 19 are conifers including nine different species of pine. The next most common genus is oak, occurring seven times.

A tale of two Hemlocks

Eastern hemlock (*Tsuga canadensis*) is a common tree in the northeastern U.S. It is the only conifer that is common in eastern deciduous forests. Other conifers do occur in the eastern forests, on sites where they have been planted, or in specific habitats (higher elevations in the mountains, areas with sandy or boggy soils) , or early in a successional sequence where they are eliminated with time. Western Hemlock (*Tsuga heterophylla*) is found in the Pacific northwest and generally occurs in coastal temperate rainforests. Other hemlock (*Tsuga*) species occur in Japan/China/Korea.

Distribution of western hemlock.

Distribution of eastern hemlock.

Taxonomy and phylogeny

Hemlock is a gymnosperm, a seed producing plant that does not have flowers. Gymnosperms are not considered monophyletic and therefore it is not a phylogenetic entity. The four groups that used to be lumped as gymnosperms (conifers, ginkgo, cycads and gnetophytes) are no longer grouped together unless the largest seed bearing group, angiosperms, is included as well. Hemlocks are in the pine family (Pinaceae) of the conifer phylum (Coniferophyta); other members of the Pine family are pines, firs, spruces and larch and other members of the Coniferophyta are junipers, redwoods and cedars. There are about ten species in the genus *Tsuga*.

Structure

Hemlocks are typical woody plants, with a main trunk capable of extensive secondary growth and reaching substantial girths and heights. Eastern hemlock can often reach 30 m and western hemlock more than twice that height, making it one of the tallest tree species. These are long-lived organisms, with Eastern Hemlock reaching over 500 years in age and western Hemlocks over twice that age.

Sex and reproduction

Hemlock produces seeds in small (~2 cm), woody cones that earlier are the site of meiosis and female gametophyte development, including the production of eggs. Male gametophytes (pollen) are produced in separate cones that are much smaller. Pollen is dispersed by the wind and completes its development inside the female cone, producing sperm that fertilize the egg. The seeds are small (1-2 mm), winged, and dispersed by the wind.

Matter and energy

Hemlock is a typical photosynthetic autotroph. Western hemlock occurs in coastal evergreen rainforests in habitats with relatively mild winter temperatures and where being evergreen has a distinct advantage.   Eastern hemlock is unusual in being an evergreen species in a forest that is dominated by deciduous trees. It may gain some advantage by being able to acquire carbon in the winter but often photosynthesis is limited by low temperatures and especially by reduced water transport when it is below freezing and water transport is restricted. Both species are known for being extremely shade tolerant, meaning that they can stay alive (have a positive carbon budget) in spite of low levels of light, this would require low respiration rates.

Interactions

An introduced insect species, the hemlock wooly adelgid(HWA), is causing significant mortality of eastern hemlocks, especially in the southern part of its range. The HWA exclusively feeds on hemlock species. Closely related to aphids, adelgids are sedentary insects that feed on phloem sap, using a stylet to penetrate phloem sieve tubes. They then acquire carbohydrates when the pressurized phloem sap is pushed into the insect's body, similar to the way that pressurized capillaries of mammalian circulatory systems allow mosquitoes to acquire a blood meal. In neither case is the insect 'sucking' fluids, it is merely tapping a pressurized 'pipe'. In the far east, where the HWA is native, its population are controlled by predatory insect species and there is hope that introduction of these predators may help control the pest in North America.

Although a common tree, the eastern hemlock is not commercially useful. Its wood has a number of features that make it ill-suited as lumber or pulp (for making paper). In contrast, the western hemlock is a highly desirable lumber species with considerable strength and a straight grain. Western hemlock pulp makes high quality paper. In the 18th and 19th century the bark of eastern hemlock was a source of tannins. Tannins are group of chemicals that are important both to the plants that produce them and for humans utilizing the plants. For plants, tannins are bitter tasting and deter feeding because of this. However, if eaten, tannins can interact with digestive enzymes and thereby impede digestion. Herbivore avoidance of tannin containing plants may be a learned and/or evolved consequence of these effects and not simply a 'dislike' for the taste. To humans, tannins actually provide a desirable bitterness to (at least some) humans and consequently are desirable at a certain level in tea, chocolate, wine and other consumables. Another use for tannins is the process of tanning leather, where the ability of tannins to interact with proteins, specifically the collagen found in animal skin, a llows tanning to make animal hide more supple and less prone to decay.

Gamoderma tussle

Some fungi apparently like the taste of hemlock, *Gamoderma tsugae*, the hemlock varnish fungus, is distinctive because of its shiny, glossy surface. As the name implies, it grows (i.e.

eats) hemlocks, although it occasionally is found on other conifers. *Gamoderma tsugae* is closely related to *Gamoderma lucidum*, known as Lingzhi (Ling Chih) in China and Reishi in Japan which is highly valued medicinally.

Further Reading

- "Tannins" by the US Forest Service
  - https://www.fs.fed.us/wildflowers/ethnobotany/tannins.shtml

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HORSETAILS, THE GENUS EQUISETUM

Horsetails, the genus *Equisetum,* are a very easily recognized group of plants that are commonly found throughout the world. They represent a very small remnant, only a single genus with less that 100 species, of a group that in the Paleozoic was a much more conspicuous component of the earth's flora. From 100 million years, ending 250 million years ago, this group was a dominant in terrestrial habitats world wide and the group is responsible for much of our coal and oil deposits. They are common in most of the United States, sometimes as a roadside weed or in wet habitats.

Taxonomy and Phylogeny

The genus traditionally had been put in a phylum all by itself but more recent treatments lump the horsetails in the fern phylum (Pterophyta), usually putting them in an order (Equisetales) distinct from other fern groups. When treated this way, the orders of the Pterophyta diverged in the late Paleozoic era. Whether you consider horsetails to be a phylum by themselves or an order within the Pterophyta, they still are very easy to recognize because of their distinct structure.

Structure

Horsetails have a very distinctive form–they have jointed stems with small and inconspicuous leaves that appear as scales at the base of each section of stem. The stems are hollow and ribbed. The successive sections of stem get shorter and shorter, reminiscent of a logarithmic scale and there is a claim (I haven't been able to verify this) that the plant was an inspiration to John Napier to invent logarithms. Napier invented logarithms in the 16th century to make calculations easier (many biology students don't believe that logarithms make calculations easier!!). The stems sometimes have whorled branches (in which case they look a bit like a horse's tail) but sometimes don't (in which case they really do not look at all like a horse's tail!). Horsetails have extensive underground horizontal stems (rhizomes) off of which emerge roots and vertical above ground stems. The commonly seen plant is a sporophyte that produces spores in a terminal cone or strobilis. Some species are dimorphic, with vegetative stems that are green and photosynthetic but produce no spore-producing strobili, and fertile stems that are brown (no chlorophyll, no photosynthesis) but do produce strobili and thus are only involved in reproduction. Fossil members of the group had secondary growth and grew up to 18 m in height, with stems a half a meter across. These plants were significant components in the deposits that yield coal and oil.

Reproduction

Like all plants, *Equisetum* exhibits alternation of generations. They have a easily visible sporophyte and hard-to-find gametophyte. Spores are produced in 'cones', terminal portions of stems where certain cells undergo meiosis to produce a 'tetrad' of four spores. The spores have extensions of the cell wall called elaters that move in response to humidity changes and provide some motility to the spores (see video below). The spores germinate and produce haploid gametophytes that are bisexual (thus the plants are homosporous, producing only one type of spore). Equisetum gametophytes are small, uncommon produce archegonia, that produce eggs, and antheridia, that release haploid, flagellated sperm that are chemically attracted to the archegonia and fertilize the eggs, forming a zygote that grows into a diploid sporophyte that soon overgrows the gametophyte.

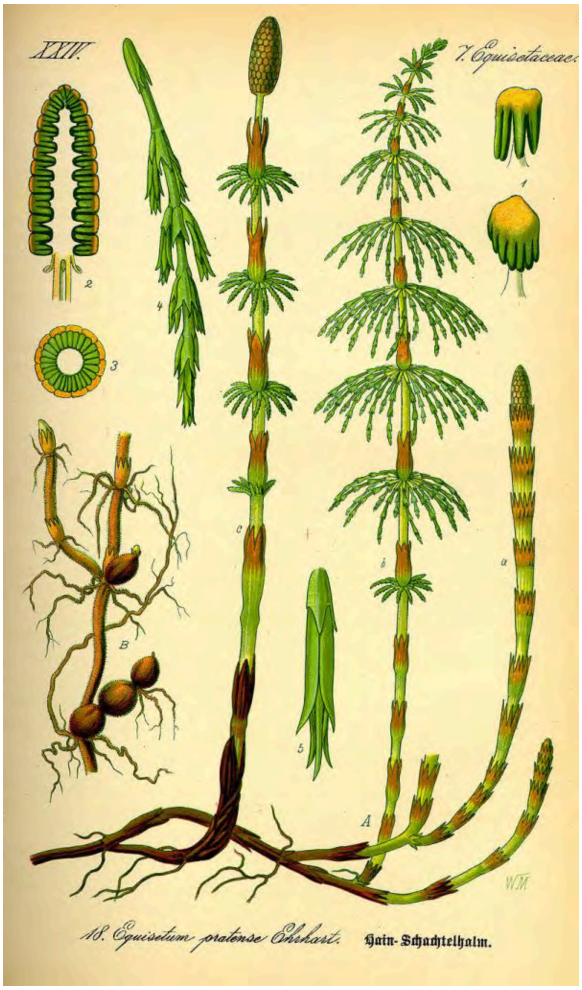
Matter and energy

Dimorphic stems of Equisetum ravens—the green stems are sterile and photosynthetic, the brown ones are fertile and non-photosynthetic

Equiesetum (both the sporophyte and gametophyte) is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and water and then using the carbohydrates as an energy source in cellular respiration and as building material to synthesize a variety of biomolecules. Note that for dimorphic species the spore bearing stems are photosynthetic only briefly and are 'fed' by the photosynthetic branches for most of their existence. Significantly, the energy captured by horsetails 300 million years ago is now being utilized when coal and oil are burned, releasing carbon that has been trapped in molecules that were transformed into fossil fuels. The plant has a fairly unusual nutrient requirement, silicon, which most plants do not have (many plants may take up and contain silicon but it is not a required element, i.e. they can grow without it). Silicon is also required by the diatoms (phylum Bacillariophyta), a group of unicellular algae. The presence of silica dioxide deposits in the cell walls of horsetails makes the stems particularly tough and accounts for the common name 'scouring rush' because pioneers used the stem of the plant as a scrub brush.

Interactions

Equisetum plants are commonly encountered both in ‘weedy’ habitats (the plant can be a problem in agricultural situations) and also in less disturbed habitats. The group generally requires high light conditions and most species are shaded out when trees are present. Like the clubmosses, they do not appear to suffer much from herbivory; this is perhaps because of the silica deposits in the cell walls.



Dimorphic stems of Equisetum arvense. The brown stems bear sporangia at their tips but are non-photosynthetic; the green stems bear no sporagia but are photosynthetic

Further Reading and Viewing

- “The anomaly of silicon in plant biology” by E. Epstein
  - https://www.pnas.org/doi/abs/10.1073/pnas.91.1.11
- “The walk and jump of horsetail spores (Equisetum) [Better sound]” by Philippe Marmottant. Video of horsetail spores moving by elaters.
  - https://www.youtube.com/watch?v=ZALgWLpanEo

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- Equisetum arvense (Field Horsetail) © Mike Dickison is licensed under a CC BY (Attribution) license
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JUNIPER

Juniperus

Juniper with berries

Junipers are a widely distributed group of plants that are used extensively in landscape gardening, especially in commercial and academic settings where their diversity in form and texture are appealing to landscapers. As a result, they are seen by most people in the United States although many may not recognize what they are seeing except that they are evergreens. They may be a small tree or an upright or prostrate shrub.

Taxonomy and Phylogeny

Junipers (the genus *Juniperus)* are conifers (Phylum Coniferophyta) and generally put into the Cupressaceae (cedar) family whose members generally have very small leaves that overlap one another, making it hard discern the individual leaves. Other members of the group include: cedars, incense-cedars, cypress and redwoods. The family appeared in the Triassic, around 200 million years ago, but junipers are much more recent additions.

Juniper leaves—needle like on the left and scale like on the right. At the tips of some branches on the right are male cones.

Structure

Juniper is a woody, slow growing plant that sometimes grows as a small tree and sometimes is shrub-like with multiple stems and extensive branching. There also are a number of forms that have been selected for their prostrate growth, producing stems less than 30 cm tall and spreading along the ground. Generally the leaves are small (2-3 mm) and 'imbricated' (overlapping like shingles on a roof). A few species have longer needles that extend extend outward from the stem. And there are a few species produce both types of leaves with the pointy needles occurring on younger growth. The leaves generally senesce as a group, with entire branches browning and abscising rather than individual leaves

Reproduction

Like all seed plants, Junipers produce female gametophytes inside ovules. The zygote is formed when the egg, produced by the female gametophyte, is fertilized by a sperm nucleus produced by the male gametophyte (pollen). Pollen is produced in minute (1-3 mm) male cones. The zygote develops into a new sporophyte embryo that is packaged inside a seed, a mature (fully developed) ovule. Junipers produce 'berries' that are a good example of convergent evolution. Technically, berries are fruits and fruits are only produced by flowering plants as a result of development of the ovary of the flower following fertilization. In many cases fruits have characteristics (rewards) that attract frugivores to come and eat the fruit and subsequently disperse the seed, present in the fruit, by defecating somewhere distant from the plant where the fruit was collected. Juniper 'berries' are actually cones, like those of pine and hemlock, but the cone scales are not woody but are thick, fleshy and aromatic and attract frugivores who disperse the seeds. Fleshy fruits are found in some other non-flowering seed plants (gymnosperms) including ginkgo and some species of Gnetophytes (*Ephedra)* .

Juniper cones have scales that are thick and fleshy and often blue-black with a whitish bloom. The seeds are produced on the upper surface of the cone scales.

Matter and energy

Juniper is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and also as building materials to synthesize a variety of biomolecules. The wood of juniper is infused with chemicals that deter the growth of decomposer organisms, hence the carbon captured by junipers may last for a long time before be released back to the atmosphere. Some juniper individuals live for thousands of years.

Interactions

In arid parts of western North America at the lower elevations of mountains there exists a shrub-land, the 'Pinyon-Juniper'zone, named for its two dominant species, pinyon pine and juniper. Because of their abundance in these areas junipers have significant interactions with herbivores and other organisms. Because pinyon juniper woodlands are poor habitat for cattle, areas of pinyon-juniper are sometimes destroyed to promote the growth of grasses and shrubs that cattle prefer to eat.

Pinyon juniper community in Nevada

Juniper is an alternate host for a rust species that also affects apples and hawthorns. Juniper berries are used to flavor gin and also as a spice in cooking.

Due to its resistance to decay, juniper stems have often been used as fenceposts. The wood is often used in the making of 'cedar chests' for clothing because the aromatic wood repels moths.

Media Attributions

- Juniper berries © Quadell is licensed under a CC BY-SA (Attribution ShareAlike) license
- Juniper leaves © MFP is licensed under a CC BY-SA (Attribution ShareAlike) license
- Juniper cones © Hardyplants is licensed under a Public Domain license

Further Reading and Viewing

- “Western Jumper Factsheet” by Oregon State University – College of Forestry. Nursery presentation on junipers.
    - https://juniper.oregonstate.edu/node/6

KELP: LAMINARIA, A BROWN ALGAE

Like *Fucus* (rockweed) *Laminaria* is representative of an interesting group of organisms that are commonly seen in the intertidal zone and washed up on beaches. Most of the organisms called ‘seaweeds’ are brown algae, although some are red algae and a few are green algae. Like most (but not all) brown algae, *Laminaria* is a large, multicellular organism that well-adapted to life in intertidal and shallow coastal waters, most commonly in relatively cool waters.

Taxonomy and Phylogeny

The brown algae are a small group of eukaryotes who traditionally were placed in their own phylum, the Phaeophyta, sometimes along with two groups of primarily unicellular algae, the golden algae and the yellow-green algae, based on similarities in pigmentation and other factors. Most modern treatments do not elevate this group to the phylum level but combine it with other ‘heterokonts’, a group defined by having two characteristic flagella, one longer than the other. The heterokonts (sometimes called the Stramenopiles) also includes diatoms and the heterotrophic water molds (Oomycota). The pigmentation of photosynthetic stramenopiles is similar to that of the haptophytes like coccolithophores and the cryptophytes. This may not represent a common phylogeny but instead that all three groups separately became photosynthetic by acquiring the same photosynthetic endosymbiont. The photosynthetic members of these groups are thought to have been produced by secondary endosymbiosis and their chloroplasts have four membranes (see discussion in the article on diatoms*)*.

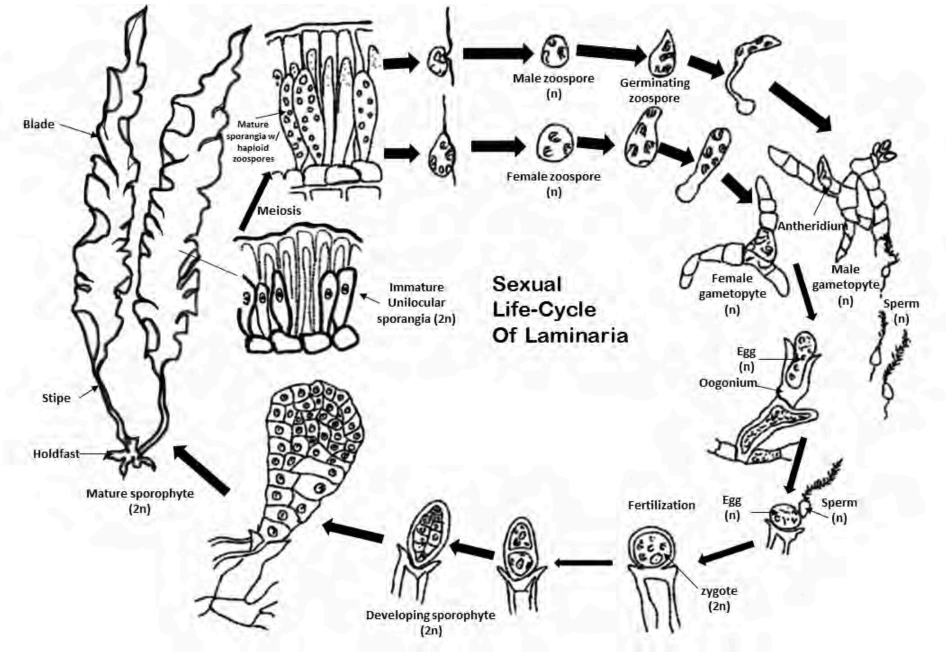
Structure

Typical of most brown algae *Laminaria* is truly multicellular, and has three distinct multicellular organs: a holdfast, that attaches the organism to a substrate, a broad flat blade that carries out the bulk of photosynthesis, and a stipe (stalk) that connects the blade to the holdfast and is long enough to allow the blade to obtain light. Many brown algae also have 'floats', air filled bladders that cause the blade to be elevated. Brown algae have transport systems that allow photosynthate from the blade to be distributed throughout the plant.

Brown algae, *Laminaria*

Reproduction

Most brown algae are sexual and exhibit alternation of generations. The 'dominant' (i.e. larger and more visible) stage is usually the sporophyte (diploid) stage but there are some brown algae that show isomorphic alternation of generations (the sporophyte and gametophyte look identical) and a few where the gametophyte stage is dominant. Another brown algae, rockweed (*Fucus),* shows a life cycle like humans, with no alternation of generations and where the only haploid cells are gametes. Gametes are sometimes distinct from one another (egg and sperm) and sometimes all look the same (isogametes). Flagellated cells are common and include sperm, isogametes and zoospores, mobile cells that can attach to a substrate and grow into a new organism.



Matter and energy

Laminaria is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and as building materials to synthesize a variety of biomolecules. The brown algae produce a distinct form of a carbohydrate storage polysaccharide called laminaran, made up of glucose units connected by a *beta* 1-3 linkage, rather than the *alpha* 1-4 linkage found in starch. They also have high concentrations of mannitol that serves as a transport carbohydrate, a role occupied by sucrose in most plants.

Interactions

Laminaria is an important member of cool, shallow coastal waters. Along with other members of the brown algae they form 'kelp forests', providing food for a number of organisms and habitats for others. Rockweed (*Fucus*) is especially important in the intertidal zone for similar reasons.

Further Viewing

- "Underwater Kelp Forests" by usoceangov
    - https://www.youtube.com/watch?v=GcbU4bfkDA4

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- Laminaria Life Cycle © Aivaldez94 is licensed under a CC BY-NC-SA (Attribution NonCommercial ShareAlike) license

LUNGWORT LICHEN (LOBARIA PUMONARIA)

Lungwort lichen

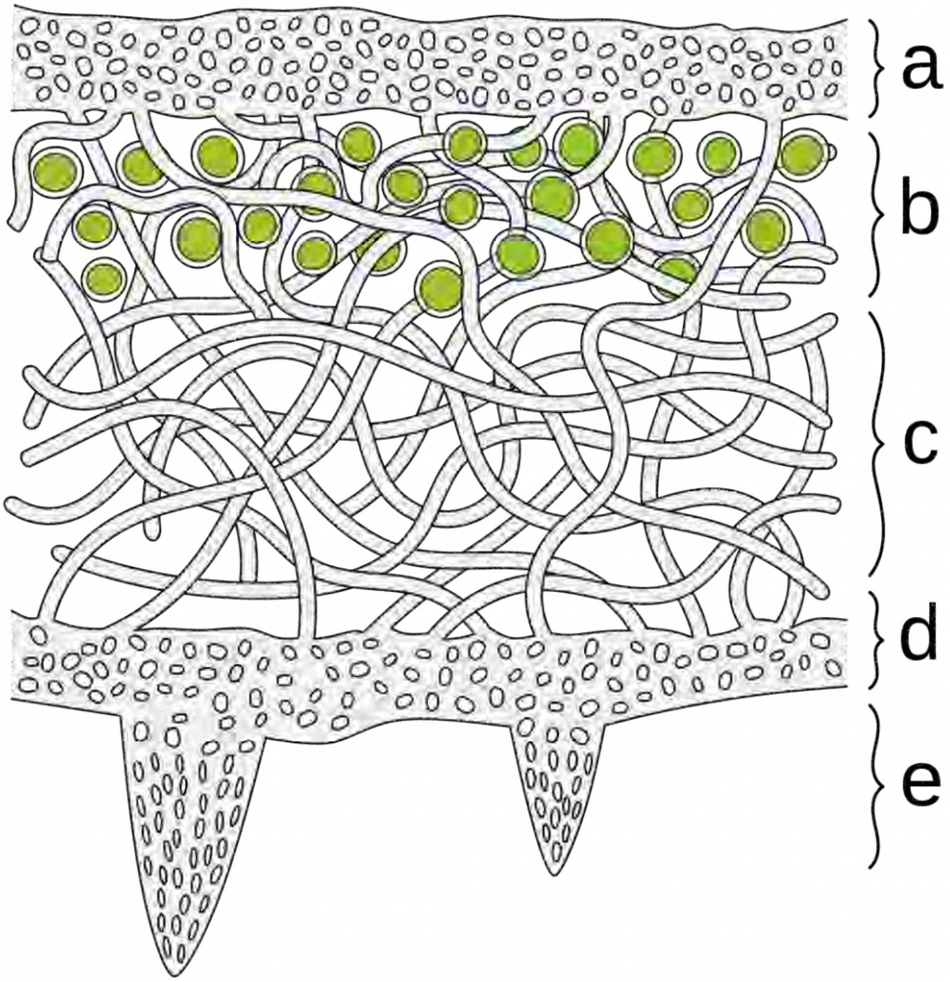
Lungwort lichen is unique among the groups considered here because it represents a very different biological entity that the others. Lichens are communities, assemblages of organisms and communities are generally not given genus and species names and are generally not considered to be organisms. But the definition of 'organism' is not rigid (see Chapter 1) and certainly lichens can be considered organisms. The fact that they can be given scientific names attests to this. Like 'regular' organisms, they are distinct in time and space. The boundary between the lichen and its environment is very evident and one could follow its development, if you live a long time and are patient, from its initiation to its demise. Traditionally, lichens were considered to have two components: a photobiont, either a unicellular green algae or a cyanobacterium (bluegreen algae) and a fungus. Recent work has ind icated that lichens also contain another fungus, one that is unicellular fungus i.e., a yeast. And some lichens, including lungwort have two photobionts, meaning that it is a community of at least four organisms.

Taxonomy and Phylogeny

Lichens are able to be classified because of characteristic form, color and structure. While each component of the lichen may have an evolutionary history (phylogeny), it would be difficult to track the phylogeny of the composite organism. Lichens are generally classified on the basis of their fungal component but the same fungus can produce marked different structures depending upon its algal symbiont and other features. Thus although lichens can be classified based on form ('looks', including chemical 'looks')) but this does not pin down the entity to specific components.

Structure

Lichens are typically grouped (see this the US Forest Service site for images) as 'foliose '— having flattened leaf-like features (like lungwort), 'fruticose '— having extensions that are typically round and stem-like, not leaf like, and 'crustose'— forming a crust, typically over a rock. Especially in foliose and crustose lichens there is an upper and lower layer of dense fungal hyphae all glued tightly together, with a middle layer where the fungal hyphae are more loosely arranged and where the photobiont is found. The fungal component of most lichens is an ascomycete fungus and commonly one can find cup-shaped apothecia, a structure associated with the sexual reproduction of ascomycetes (aka cup-fungi) on the lichen. The algal component is unicellular and usually a cyanobacterium or a green algae. Lichens are often very colorful with the coloration generally being determined by the photobiont.



Cross-section through a heteromeric lichen thallus. Such thallus is usually divided in these layers: a) upper cortex b) layer containing the photobiont (in this case alga) c) medulla / loosely packed hyphae d) lower cortex e) rhizines

Sex and reproduction

Lichens reproduce asexually by fragmentation, and this is often promoted by the production of soredia, small pieces of lichen that are easily dislodged and dispersed. The fungal component of the lichen is capable of sexual reproduction, as evidenced by the production of ascocarps, but to recreate the lichen requires the acquisition of the photobiont.

Matter and energy

Note the cup-like apothecia of this lichen.

The lichen can be considered a photosynthetic autotroph, using sunlight to capture carbon dioxide and form carbohydrates that are then used (1) structurally to make more lichen (both the photobiont and the fungus) and used (2) energetically to power the metabolism of both the photobiont and the fungus. It is thought that the fungus manipulates the photobiont to make it more likely to 'leak' carbohydrates. The other 14 elements (besides carbon, hydrogen and oxygen) required to make more lichen come from rain water, perhaps modified as it descends down tree trunks and acquired by the fungal component.

Interactions

Lichens are extremely common components of the landscape, be it forest, desert or tundra. Although they are rarely eaten, they often provide materials for birds to build nests. They are significant to soil development both by providing organic material and also by breaking down rocks.

Further Reading and Viewing

- Forest service site on lichens.
  - https://www.fs.usda.gov/wildflowers/beauty/lichens/about.shtml-https://www.fs.usda.gov/wildflowers/beauty/lichens/biology.shtml
- "Yeast emerges as hidden third partner in lichen symbiosis" by Natalie van Hoose. A discovery of a third component, yeast, in lichens.
  - https://www.purdue.edu/newsroom/releases/2016/Q3/yeast-emerges-as-hidden-third-partner-in-lichen-symbiosis.html

  - https://www.sciencedaily.com/releases/2016/07/160721151213.htm

Media Attributions

- Lichen cross section – heteromeric thallus © Nefronus is licensed under a CC BY-SA (Attribution ShareAlike) license
- Green lichen © Umberto Salvagnin from Italy

MARCHANTIA: THALLOID LIVERWORT

Marchantia, a ‘complex, thalloid’ liverwort

Marchantia is one of the most commonly encountered liverworts. It has a wide distribution (arctic to tropics) and is relatively large and with a distinctive form. It is often encountered in seeps near steep rocky outcrops next to brooks and streams.

Marchantia gametophyte, a prostrate (ground-hugging) thallus that bifurcates (forks) as it grows.

Taxonomy and phylogeny

Marchantia is in the Phylum Hepatophyta in the Plant Kingdom. In the past, the three groups of non-vascular plants (mosses, liverworts and hornworts) were grouped together into some taxonomic entity, often a phylum, but recent studies have supported placing the three groups into three separate phyl a, reflecting a view that the liverworts, mosses and hornworts are not obviously connected with each other, other than all being plants.

The 9000 species of liverworts are usually separated into three groups, one of which contains *Marchantia* and other ‘complex thalloid ‘forms, described below.

Structure

(Gametophyte)—Of all the plant groups, the liverworts show the most diversity in form. While some liverworts bear a resemblance to mosses, having a stem axis with appendages (‘leaves’), *Marchantia* is representative of a group of liverworts described as having ‘complex thalloid’ structure, consisting of a flattened body (a thallus) that generally spreads across the ground surface and is differentiated into a top and bottom. *Marchantia* is characterized by repeated branching into two parts. The thallus has multiple layers of cells. The top layer has permanently open pores (visible to the naked eye as minute dots) that allow for carbon dioxide entry. Below this skin (dermal) layer lies a layer of chlorophyll containing cells that are loosely arranged with lots of air space to allow for the diffusion of carbon dioxide. Below this is a (usually) thicker layer of cells that lack chlorophyll, and finally the lower skin (epidermis) which has multicellular fish-scale like structures that help attach the liverwort to the substrate, and also rhizoids, cells with thread like extensions that also attach the liverwort to a substrate. The **sporophyte** is hard to find, being small (less than 1 mm) and imbedded on the underside of archegoniophores (see below).

Sex and reproduction

Like mosses, liverworts show alternation of generations with a ‘dominant’ gametophyte (dominant = more visible, longer lasting). Under the appropriate conditions the gametophyte of *Marchantia* (and some other liverworts) grows two types of vertically oriented, umbrella/mushroom shaped structures: antheridiophores and archegoniophores, both roughly 1 cm in height. The antheridiophores produce male structures that produce sperm on the upper surface of the umbrella.

The archegoniophores, which are like umbrellas that lack the webbing between ribs produce female structures, archegonia, on the underside of the ribs.

On the underside of the female structures are produced flask-shaped archegonia, at the base of which is a single egg. When mature, an opening (‘canal’) develops from the egg to the tip of the archegonia, providing a route for the sperm to access the egg and allowing for fertilization. After fertilization a small (barely visible to the naked eye) sporophyte is produced, embedded in the tissue that produced the egg. Spores from the sporophyte are

Antheridiophores of Marchantia. These extend above the main body of the thallus which is barely visible. On the upper surface of these structures are produced antheridia that produce sperm that eventually are released and swim towards egg-containing archegoniophores.

dispersed in the air and germinate to produce more gametophytes. *Marchantia* has separate male and female gametophytes (some liverworts have bisexual gametophytes).

Marchantia also reproduces asexually, producing small cup shaped 'splash cups' with clusters of cells (gemmae) at the base. These can be ejected by rain drops and are capable of producing new gametophytes if the end up in a favorable location.

Archegoniophores of Marchantia. These extend above the main body of the thallus, the flat part running horizontally. On the lower surface of the 'ribs' are produced archegonia that produce egg that, if fertilized will grow into minute sporophytes still embedded in the ribs of the archegoniophore.

Matter and energy

Liverwort gametophytes are photosynthetic autotrophs. Minerals are obtained from the absorption of solutes in rainwater. The sporophytes are totally dependent on the gametophyte for nourishment.

Interactions

Marchantia generally appears to require moisture and a lack of competition. It is found on rocks in places where water is seeping through the substrate, or perhaps gently falling from above. Although *Marchantia* can grow on moist soil it probably is eliminated

Gemmae cups on the upper surface of the gametophyte. At the base of the cups are clusters of cells that are dispersed by the force of raindrops and are capable of forming into new plants.

by organisms (vascular plants) that can grow upwards and outcompete them for light. However, these competitors generally cannot grow without soil, which is probably why *Marchantia* is usually found on rocks. Although it can grow in full sunlight if moisture is available it often is found in shady conditions. *Marchantia* benefits, as do most non-vascular plants, from being small and being able to function in conditions where small stature is useful. *Marchantia* contains a variety of secondary plant compounds that may explain the fact that it apparently is rarely eaten.

Further Reading and Viewing

- “What is a liverwort?” by Australian Bryophytes. Good discussion of liverworts from an Australian site.
    - https://www.anbg.gov.au/bryophyte/what-is-liverwort.html
- “Ohio Liverwort Diversity” by Ohio Moss & Lichen Association. Pictures and descriptions the of liverworts of Ohio.

  - https://ohiomosslichen.org/ohio-liverwort-diversity/

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- Marchantia polymorpha male © Plantsurfer is licensed under a CC BY-SA (Attribution ShareAlike) license
- Moos_5772-1
- Common Liverwort (Marchantia polymorpha) © Ryan Hodnett is licensed under a CC BY-SA (Attribution ShareAlike) license

MARSILEA: THE 4-LEAF CLOVER FERN

Marsilea is a genus of ferns that don't look much like fern s. Its leaves look more like a four-leaf clovers than the typical fern leaf. There are a number of species of *Marsilea* and it is common throughout temperate and subtropical regions of the world, usually growing in shallow water with a stem rooted to the bottom and leaves that extend up and float on the surface. In North America *M. quadrifoliata* is considered a weed, although it is commonly grown intentionally in water gardens. It is sometimes found emerging from moist soil as well.

Phylogeny and taxonomy

Marsilea is in a group (generally considered an order — the Salviniales) that is known as 'water ferns' in the Phylum Pterophyta (ferns), the group that includes most seedless vascular plants (the other group of seedless vascular plants are the clubmoss group, Lycopodiophyta). Some water ferns, including mosquito fern and azolla, are floating aquatic species, while *Marsilea* is rooted and can tolerate seasonally dry conditions.

Structure

Marsilea produces a horizontally running stem across the surface of the substrate (which may be underwater). Like sensitive fern and some of the horsetails, water fern is dimorphic and the horizontal stem produces two types of leaves, green, photosynthetic leaves and non-photosynthetic leaves associated with reproduction. The vegetative leaves look like shamrocks. These elongate and make it to the surface of the water or, if growing on moist soil, grow to a height of ~ 10 cm. A second type of leaf is much smaller, with a shorter petiole ending in a sporocarp, a brown circular seed-like structure that dries out completely.

Sex and reproduction

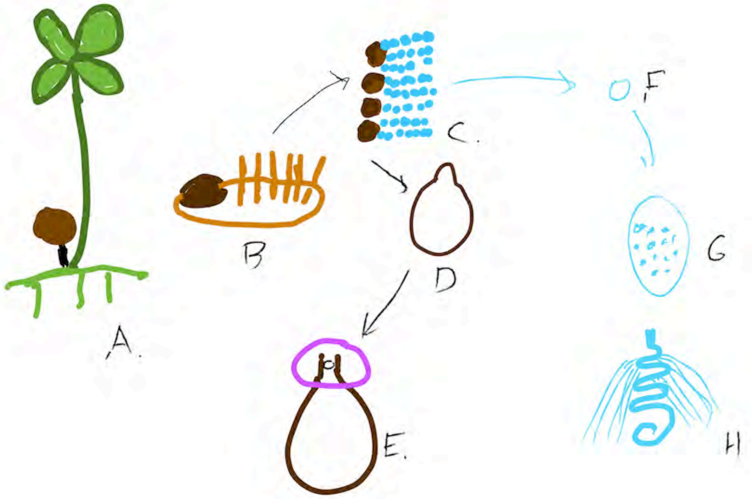
Like all plants, *Marsilea* alternates between a haploid and diploid stage. And like all vascular plants, it is the diploid, spore producing, stage that is most visible. The sporocarp is seed-like in looks and behavior, but developmentally is something very different. The sporocarp is a highly modified spore-bearing leaf that develops to a certain point and then becomes dormant and dries out and is therefore capable of being dispersed. Eventually, when the hard coating of the sporocarp becomes scarred, either by mechanical forces (abrasion) or by biotic forces (decomposition), water can enter and hydrate the spore bearing leaf, which then emerges from the sporocarp. The leaf looks nothing like a regular leaf, it is very small and non-photosynthetic, but bears two types of sporangia, producing two types of spores: larger spores (megaspores) that develop into female gametophytes inside the spore case (endosporically) and smaller spores that release flagellated sperm.

Matter and energy

Marsilea sporophytes are photosynthetic autotrophs. The gametophytes live solely off material from the sporophyte incorporated in the mega and microspores.

Interactions

Marsilea sporocarps (the seed-like structures) are eaten by aboriginal Australians, although proper preparation is important. The plant produces an enzyme, thiaminase, that breaks down vitamin B1 and if this enzyme is not de-activated vitamin B1 deficiency and death can result. This same enzyme is also found in bracken fern, some horsetails and also in carp and goldfish.



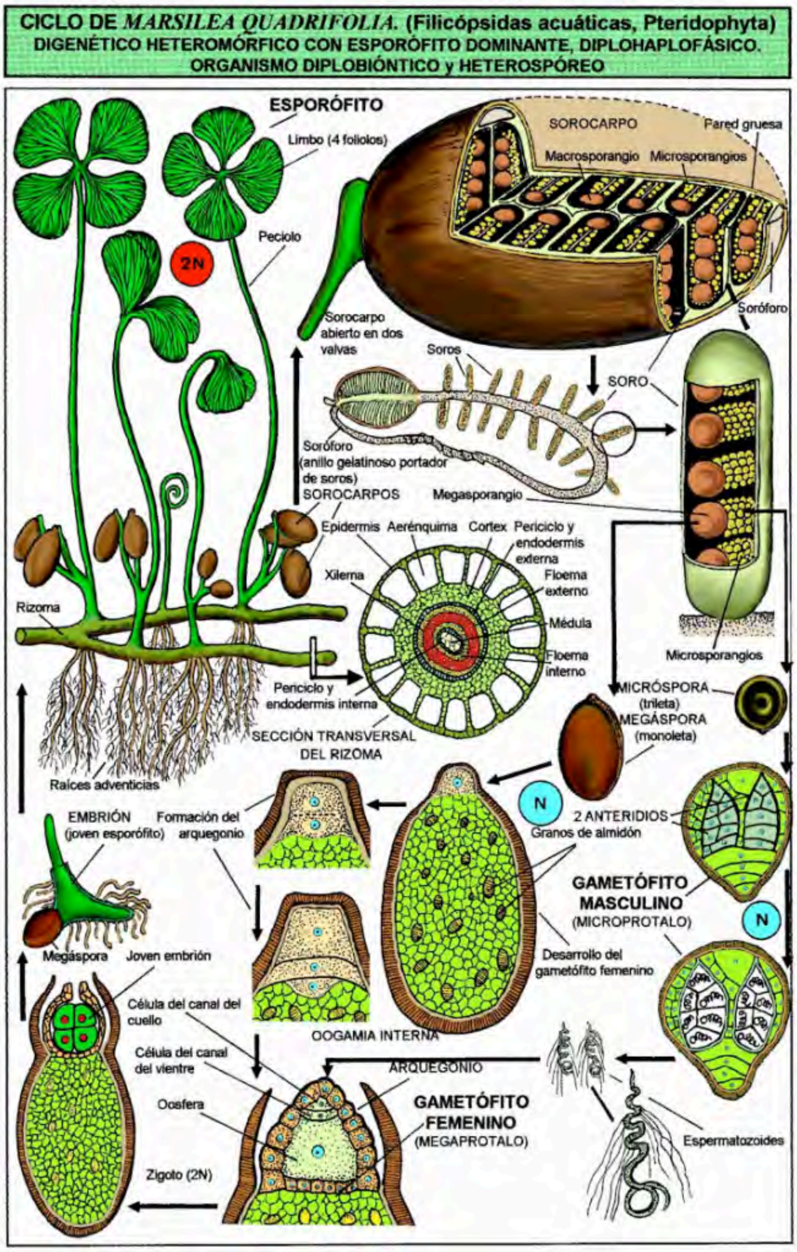
Life cycle of Marsilea: A-sporophyte plant, with a vegetative and a reproductive leaves (sporocarp). B- germinated sporocarp exuding a gelatinous ring with sori (spore producing structures (roughly 5 mm in size) C-closeup of the heterosporous spore-producing structures that produce two types of spores, larger megaspores (brown) and much smaller microspores (blue). D-megaspore, in which the spore germinates and produces E-a small female gametophyte still enclosed by the spore wall (endosporic development) with an egg-producing archegonium (circled), F- microspore also develops endosporically producing 32 or 64 cells (G) that develop into spermatozoids (H) and are chemically attracted to the archegonia when they are released.

Further Reading

- "Marsilea – Classification, Structure of Sporophyte, Reproduction, Structure of Gametophyte and Fertilization" by Prema Iswary. Good discussion of Marsilea biology.
    - http://premabotany.blogspot.com/2018/12/marsilea.html

Media Attributions

- Marsilea quadrifolia colony © Show_ryu is licensed under a CC BY-SA (Attribution ShareAlike) license


CICLO DE *MARSILEA QUADRIFOLIA.* (Filicópsidas acuáticas, Pteridophyta)
DIGENÉTICO HETEROMÓRFICO CON ESPORÓFITO DOMINANTE, DIPLOHAPLOFÁSICO.
ORGANISMO DIPLOBIÓNTICO y HETEROSPÓREO
ESPORÓFITO
Limbo (4 foliolos)
2N
Peciolo
SOROCARPO
Pared gruesa
Macrosporangio
Microsporangios
Soróforo
Sorocarpo abierto en dos valvas
Soros
SORO
Soróforo (anillo gelatinoso portador de soros)
SOROCARPOS
Megasporangio
Epidermis
Aerénquima
Cortex
Periciclo y endodermis externa
Xilema
Floema externo
Médula
Floema interno
Rizoma
Periciclo y endodermis interna
Microsporangios
MICRÓSPORA (trileta)
MEGÁSPORA (monoleta)
SECCIÓN TRANSVERSAL DEL RIZOMA
Raíces adventicias
N
2 ANTERIDIOS
Granos de almidón
EMBRIÓN (joven esporófito)
Formación del arquegonio
GAMETÓFITO MASCULINO (MICROPROTALO)
N
Megáspora
Joven embrión
Desarrollo del gametófito femenino
Célula del canal del cuello
OOGAMIA INTERNA
Célula del canal del vientre
ARQUEGONIO
Oosfera
GAMETÓFITO FEMENINO (MEGAPROTALO)
Espermatozoides
Zigoto (2N)

METHANOGENS: ARCHAEA WITH INTERESTING CHEMISTRY

Methanogens are what make ‘biogas’ fuel (methane) possible. Like the nitrifying bacteria, methanogens are a group that are united by what they do rather than by their phylogeny. As the name implies, methanogens make methane. This is significant for multiiple reasons: methane can be burned (oxidized) and is the main component of ‘biogas’ (made from sewage) and also ’natural gas’ (mined from underground deposits) that are used industrially. Methane is also a ’greenhouse gas’ impacting global energy budgets.

Methane gas generated by a landfill is recovered, treated and piped to Tucson Electric Power where it is used to generate electricity.

Methanogens are significant biologically because of their role in ruminant digestion, allowing herbivores to acquire more nutrition from the food that they eat. More generally they allow organic material to be more fully 'digested' i.e. broken down, in land fills and swamps, ultimately allowing the recycling of nutrients. Finally, methagens are included here because of their unique abilities and what they can teach students about energy and organisms.

Taxonomy and Phylogeny

All methanogens are archaea, beyond that they don't fall into a phylogenetic entity. And, as discussed below, they differ substantially in their lifestyle, albeit unified by producing methane. Many methanogens are extremophiles, living under extreme conditions of heat, cold and acidity.

Structure

Methanogens are not distinguished by structural features. The are 'typical' archaea in their shape and internal composition.

Matter and Energy (see Chapter 21)

Organisms are constructed of 'reduced carbon compounds', primarily carbohydrates, and it is generally the case that organisms, both autotrophs and heterotrophs, obtain energy in the process of cellular respiration whereby reduced carbon compounds are oxidized to carbon dioxide. This reaction is energetically 'downhill', i.e. thermodynamically favored, and the usual assumption is that reduced carbon compounds 'have more useful energy' than carbon dioxide and that this energy is what allows ATP production. Given this assumption the reverse reaction by methanogens, converting carbon dioxide to methane (a reduced carbon compound) would seem to be energetically unfavorable. But it is important to look closely at the overall reaction of cellular respiration:

reduced carbon compound + oxygen—>water + carbon dioxide

The presence of oxygen is critical, not just to the reaction (as a reagent) but also to the description/assumption that reduced carbon compounds 'have energy'. They 'have energy' only when oxygen (or some other oxidizing agent, e.g. nitrate) is present. In the absence of oxygen and with an abundance of hydrogen it turns out that reduced carbon compounds are now energetically 'downhill' of carbon dioxide and therefore organisms can take advantage of this by converting carbon dioxide to methane and obtaining energy (ATP) in the process.

For some methanogens the significance of the reaction is simply the ATP obtained that can then be used metabolically in a variety of ways. Like *Halobacterium*, some methanogens are heterotrophs for carbon but can obtain energy without oxidizing carbohydrates. While *Halobacterium* uses light energy to make ATP and might be considered a 'photoenergetic heterotroph, these methanogens might be called chemoenergetic heterotrophs.

Other methanogens are like the nitrifying bacteria, 'chemoenergetic autotrophs' (chemosynthetic autotrophs), autotrophs like plants that make food and then eat themselves, but not using the energy of sunlight for energy, instead utilizing energy obtained from chemicals in their environment (CO_2 and H_2).

Interactions

Methanogens are common in a variety of habitats where organic matter has accumulated and oxygen is absent (because it has been utilized by heterotrophs): swamps, landfills, the stomachs of ruminants. In these habitats methanogen action is important to other organisms that are present because it consumes hydrogen, whose build-up retards the chemical reactions of decomposition. Methanogen activity thus allows the continued breaking down organic material. In cow's stomachs this results in the production of materials that the cow can absorb and utilize. In swamps it allows for the recycling of nutrients. In both places the methane leaks into the atmosphere.

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- Cow © Kim Hansen is licensed under a CC BY-SA (Attribution ShareAlike) license

MOLDS: UBIQUITOUS FUNGI

The common molds *Aspergillus* and *Penicillium* are of tremendous importance to human endeavors for both positive and negative reasons.

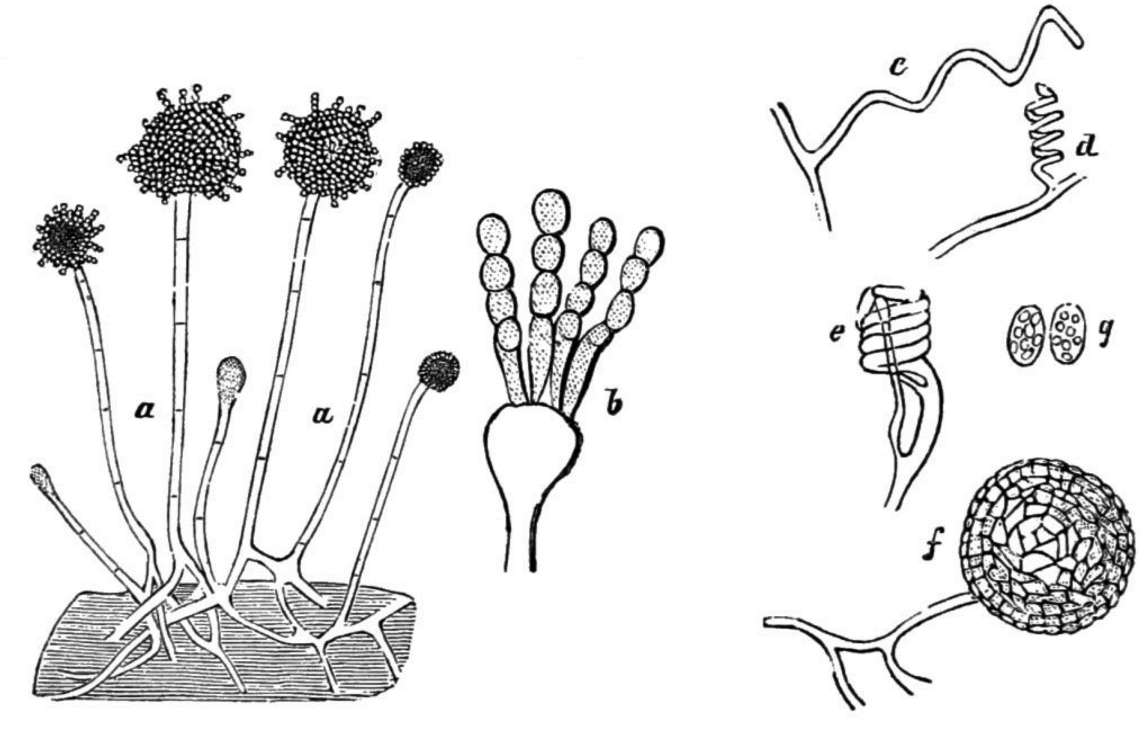
Both are ‘spoilers’ that can destroy crops before harvest or, more commonly, during storage. They also can spoil all sorts of non-food items: leather, clothing, shoes, carpeting, paintings, etc.. Members of both genera produce chemicals that are toxins to other species, including humans. Most well known of such chemicals is the antibiotic penicillin, which is a toxin to many bacteria but is not toxic to (most) humans. Another chemical produced by molds is aflatoxin, which doesn’t affect bacteria but is a toxin and a carcinogen in mammals, including humans. Both genera are of commercial importance in several ways: enzymes from *Aspergillus* are used to produce citric acid, an additive in soft drinks and a variety of candies, it is also used to produce soy sauce, a fermented liquid used as a flavoring. Besides being used to make antibiotics, *Penicillium* is used to produce brie, camembert and blue cheese.

Phylogeny and taxonomy

Most of the species in the genus *Aspergillus* and some of the genus *Penicillium* are fungi for which there is no known sexual stage. Until relatively recently, fungal classification was based almost exclusively on characteristics of the sexual stages. Consequently, fungi lacking sexual stages could not be categorized and were put into a category of their own called the Deuteromycetes or the Fungi Imperfecti. With the use of molecular characteristics these fungi can now be put into phylogenetic categories, and both *Aspergillus* and *Penicillium* have been put in the same family in the Ascomycete phylum.

Structure

As Ascomycetes, both genera are septate fungi that have a typical filamentous structure of hyphae that form mycelia. The relatively few members that reproduce sexually (usually only rarely) produce small spherical closed fruiting bodies called cleistothecia. What are much more commonly seen are the asexual reproductive structures called conidia. *Penicillium* produces minute 'paint-brush' conidia, with each 'hair' on the brush producing small, spherical conidiospores, while *Aspergillus* produces spherical structures with linear extensions of conidiospores.



Conidiophores of *Aspergillus*: (a) vertically oriented conidiophores, (b) thin section through the with conidiospores breaking off the top (c-e) development of sexual structure showing two separate hyphae interacting and eventually fusing to form a dikaryon structure and eventually a 'fruiting body' where meiosis occurs and asci are formed, (f) the fruiting body of Aspergillus (cleistothecium), (g) asci with ascospores are inside.

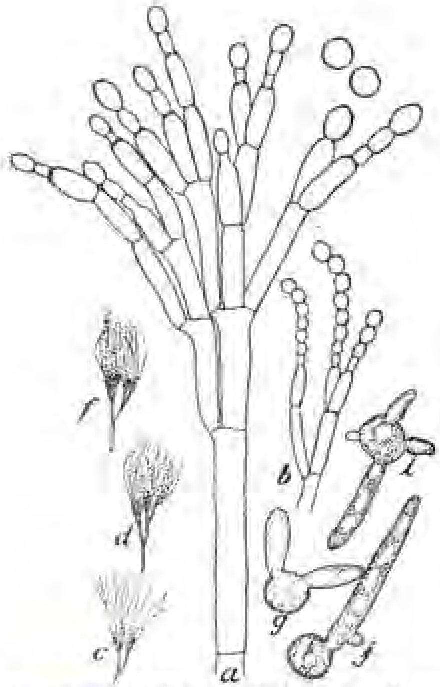


Fig. 245.—*Penicillium Camemberti.* *a*, Conidiophore with common type of branching with conidiospores; *b*, a common less-branched form; *c, d, f*, diagrams of large fructifications; *g, i, j*, germinating conidiospores. (*From Bull.* 82, *Bureau of Animal Industry, also After Thom.*)

Conidiophores of *Penicillium* with conidiospores breaking off the top. Image is of the species used to make Camembert cheese.

Sex and reproduction

All members of these two groups primarily reproduce by means of conidia, asexual spores. The ones that reproduce sexually exhibit sexual reproduction typical of Ascomycetes: dikaryon hyphae are produced after plasmogamy of two different strains; asci are produced in which karyogamy and meiosis occur, followed by mitosis to produce eight haploid ascospores.

Matter and energy

Both *Aspergillus* and *Penicillium* are generalist heterotrophs, i.e. can feed on a wide-variety of materials, including most crops species. It is a common pest, spoiling corn and other grains while in storage.

Blue cheese, made with Penicillium roqueforti, whose hyphe make the blue coloration.

Interactions

Aspergillus and *Penicillium* are both fast growing and more tolerant of lower humidity levels than most fungi. This allows them to grow in drier situations than other fungi. Additionally, some species can tolerate growth on media that have a high solute content, e.g. the high sugar levels on jams and jellies (high sugar contents generally act as preservatives because many bacteria and fungi cannot tolerate the 'dry' conditions that result from high solute levels). Molds might be considered 'weedy' fungi, because they grow on a wide variety of materials, in contrast to many fungal species that are much more discriminating in terms of where they will grow and what they will eat. However, weeds are often poor competitors (Chapter 29) yet some species of *Penicillium* compete very well, at least with bacteria, because they produce a chemical (penicillin) that deters the growth of many bacteria that might be competing for the same food source.

As mentioned above, both genera are used extensively in the production of foods and beverages. While *Penicillium* is mostly associated with the production of cheeses, *Aspergillus* is used to make sake (rice wine), soy sauce and miso. In all of these, the fungus is capable of converting starch in the rice to sugars which are then used to produce alcohol and flavorings.

Aspergillus is occasionally a human pathogen, primarily in people with weakened immune responses.

Further Reading and Viewing

- "Discovery and Development of Penicillin: International Historic Chemical Landmark" by ACS: Chemistry for Life.
    - https://www.acs.org/content/acs/en/education/whatischemistry/landmarks/flemingpenicillin.html
- "Making Traditional Japanese Sake" by 2 Guys & a Cooler. Making sake (rice wine).
    - https://twoguysandacooler.com/making-traditional-japanese-sake/

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- Blue Stilton Penicillium © Dominik Hundhammer is licensed under a CC BY-SA (Attribution ShareAlike) license

NITRIFYING BACTERIA: CHEMOENERGETIC AUTOTROPHS AND HETEROTROPHS

Nitrifying bacteria are a group of bacteria that are capable of utilizing ammonia and nitrite as energy sources that allow them to synthesize carbohydrates from carbon dioxide. They are highly significant to the global nitrogen cycle and to the existence of plants. They are autotrophs (they eat themselves) and they make 'food '(carbohydrates) by utilizing energy from chemicals rather than from light as photosynthetic autotrophs do.

Taxonomy and Phylogeny

Nitrifying bacteria are not unified by phylogeny and the taxonomic entity 'nitrifying bacteria' is totally artificial. The group includes bacteria from several unrelated groups and also includes some archaea (i.e. organisms that are not bacteria). The group includes organisms that: (1) convert ammonia to nitrite, (2) convert nitrite to nitrate and (3) recently discovered organisms that can do both reactions, converting ammonia to nitrate.

Structure

Consistent with their phylogenetic diversity, these bacteria exist in a variety of forms: rods, spheres and spirals. Many have extensive internal membrane systems that probably are significant to the biochemistry they accomplish.

Matter and Energy

Most organisms obtain energy through cellular respiration, a series of biochemical reactions that remove hydrogens from carbohydrates (oxidizing them) and transfer them to oxygen, forming water. In the process, the energy from carbohydrates is transferred to ATP. One can think of ammonia as 'food', comparable to carbohydrates in being a chemical that can be oxidized in a process that allows its energy to be 'captured'. Some nitrifying bacteria are 'ammonia oxidizing bacteria' and they obtain energy as the ammonia is oxidized to nitrite (NO_2^-).

In a similar process, the nitrite (NO_2^-) formed by ammonia oxidizing bacteria can be further oxidized by 'nitrite oxidizing bacteria', converting the nitrite (NO_2^-) to nitrate (NO_3^-).

Each of these groups have members that can do more than just acquire energy in the form of ATP as they carry out these oxidations. Both These reactions can also be part of a process that allows carbohydrates to be formed from carbon dioxide. Recall that this happens in the Calvin cycle of photosynthesis where NADPH (a source of electrons, i.e. reducing power) and ATP are inputs in a process that reduces carbon dioxide, forming carbohydrates. In nitrifying bacteria the net effect of the process is a transfer of electrons from either ammonia or nitrite to CO_2:

$$\text{ammonia} + CO_2 \text{ —-> } NO_2^- + (CH_2O)_n \quad \text{(ammonia oxidizers)}$$

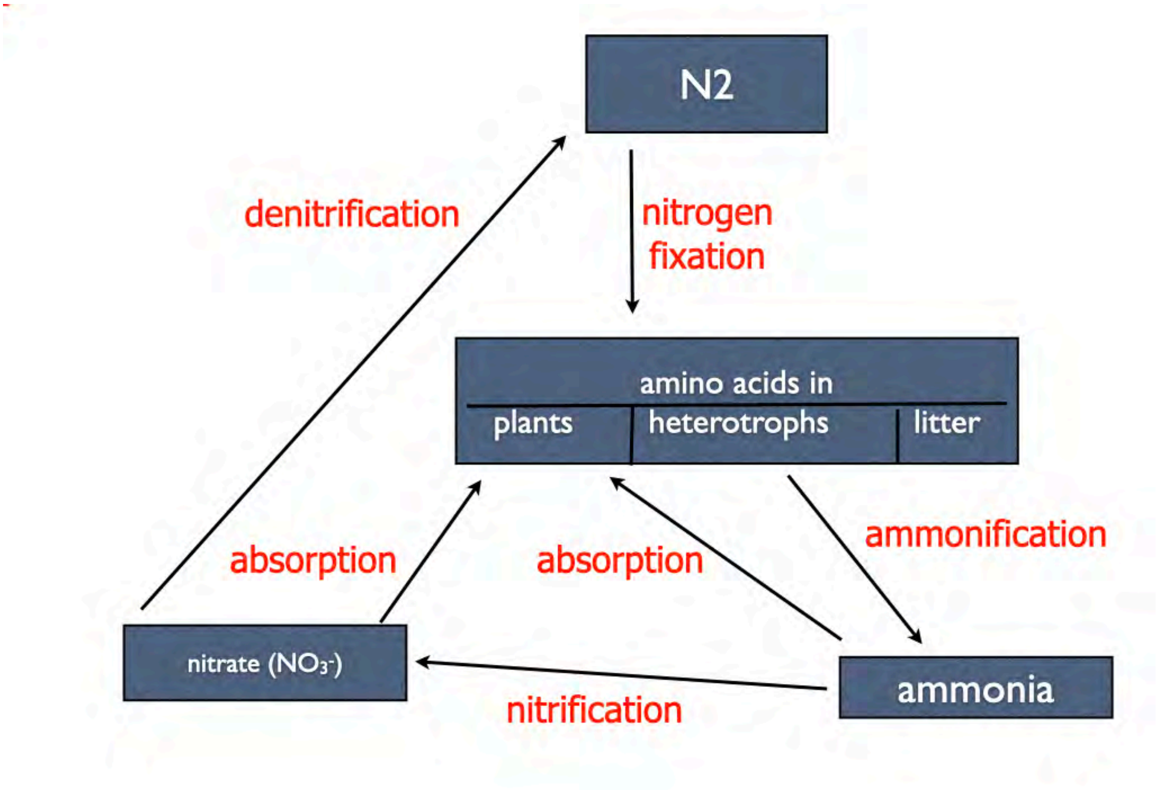
$$NO_2^- + CO_2 \text{ —-> } NO_3^- + (CH_2O)_n \quad \text{(nitrite oxidizers)}$$

$$\text{ammonia} + CO_2 \text{ —-> } NO_3^- + (CH_2O)_n \quad \text{(comammox)}$$

Organisms that carry out these reactions are considered autotrophs because they eat self-made food and they could be called 'chemoenergetic autotrophs' because they utilize chemical energy to make their on food (similarly plants could be considered 'photoenergetic autotrophs'). Other organisms in these groups do not make their own food but simply use ammonia and nitrite as a food source to get energy. They need to acquire reduced carbon to satisfy their material carbon needs. They could be considered chemoenergetic heterotrophs.

Interactions

Nitrifying bacteria are extremely important to all vascular plants by providing the preferred form of nitrogen (nitrate) to the soil and allowing nitrogen to cycle rapidly from plants to heterotrophs to nitrifying bacteria and back to plants (Chapter 22).

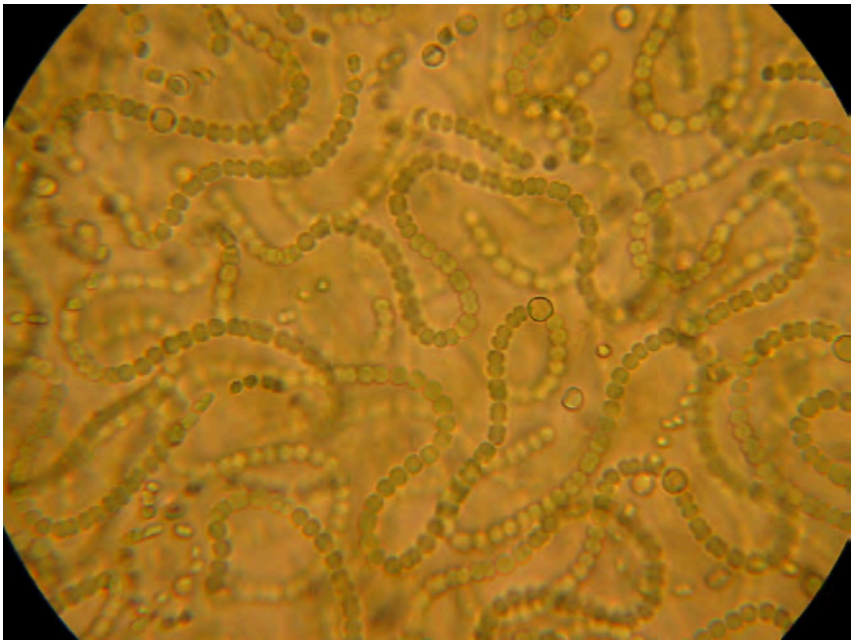


Nitrifying bacteria conserve nitrogen in the soil because ammonia is volatile and escapes to the atmosphere, although in acid soils it gets protonated to ammonium (NH_4^+) that is not volatile.

Media Attributions

- Nutrient cycles

NOSTOC: THE SMALLEST MULTICELLULAR ORGANISM



Filaments of Nostoc imbedded in a gelatinous polysaccharide. Enlarged heterocyst cells are frequently present.

Nostoc is a genus of cyanobacteria that is common in a variety of habitats: soil, ponds and growing on the surface of rocks and soil if they are kept moist. It also lives symbiotically inside of other organisms. Because of its ability to metabolize nitrogen (see below) it can be significant to ecosystems and to the organisms it associates with. As discussed in Chapter 5 it might be considered multicellular because it has multiple cell types that communicate and cooperate with each other.

Phylogeny

Nostoc is in the group with the common name 'blue-green algae', a group often called cyanobacteria. In a five-kingdom classification they are in the Kingdom Monera, Phylum

Cyanobacteria. In other classification systems they may be put in Domain Eubacteria, Kingdom Bacteria, Phylum Cyanobacteria. Cyanobacteria are thought to be the endosymbiont that became the chloroplast of eukaryotic photosynthetic organisms.

Structure

Cyanobacteria occur in a number of forms: single cells, filaments and groups of cells in a variety of colonial shapes. *Nostoc* are filamentous with roughly spherical cells. In addition to the normal cells, they also produce two larger specialized cell types: heterocysts, which are cells specialized to fix nitrogen; and akinetes, which are a type of spore that is resistant to environmental extremes. Cyanobacteria, like gram negative bacteria, have a layer of peptidoglycan sandwiched between and inner and outer membrane. However, the peptidoglycan layer is much thicker in cyanobacteria than typical gram negative bacteria. *Nostoc* typically produces a large amount of polysaccharide mucilage that forms a sheath around the filaments and occasionally form hollow balls and other amorphous shapes that are up to several cm in size.

Sex and reproduction

Like all bacteria, *Nostoc* are not sexual but they are capable of exchanging genetic material by other means. Reproduction is solely asexual. In addition to simply producing new cells by cell division, they also produce akinetes, an enlarged cell that because it is tolerant of desiccation and other extremes it can therefore be dispersed through unfavorable space or unfavorable times

Matter and energy

Nostoc and the cyanobacteria are an important group of organisms that ‘can do it all’, being able to acquire **both** carbon (via photosynthesis) and nitrogen (via nitrogen fixation) from the atmosphere. Nitrogen is acquired by the reduction of dinitrogen gas into ammonia that is subsequently used in forming amino acids. Although they lack chloroplasts, their photosynthesis is basically the same as that found in eukaryotic organisms and it produces oxygen. More so than most organisms, they can ‘live on their own’, acquiring carbon and nitrogen with out requiring the intermediaries of other organisms.

Irregular gelatinous masses of Nostoc. Sometimes these occur as spherical balls 5-20 mm in diameter.

Interactions

Nostoc forms associations with several plants, including hornworts (a group of non-vascular plants), liverworts, ferns, and some flowering plants. Nitrogen fixation by *Nostoc* can be an important source of nitrogen in soils that are young and have few plants growing on them and therefore little nitrogen availability via the normal route, i.e. as a result of the decomposition of organic material. *Nostoc* is occasionally eaten by humans, particularly in Asia, although there are some reports of it producing toxins.

Some cyanobacteria can form toxic algal blooms on lakes, causing health officials to close beaches.

On a global scale, cyanobacteria like *Nostoc* were the cause of the 'Great Oxygenation Event' starting about three billion years ago Oxygen produced by the photosynthetic process started to accumulate in the atmosphere, causing a biological catastrophe by eliminating much of the life present at the time whose metabolism was poisoned by oxygen.

Further Reading and Viewing

- "Blue-green Algae (Cyanobacteria) from Pond to Lab – Pondlife, Episode #2" by American Museum of Natural History. Nice video on cyanobacteria.
  - https://www.youtube.com/watch?v=ZRgeh7cN9PQ
- "The Origin of Oxygen in Earth's Atmosphere" by David Biello. Origin of oxygen in the atmosphere.
  - https://www.scientificamerican.com/article/origin-of-oxygen-in-atmosphere/

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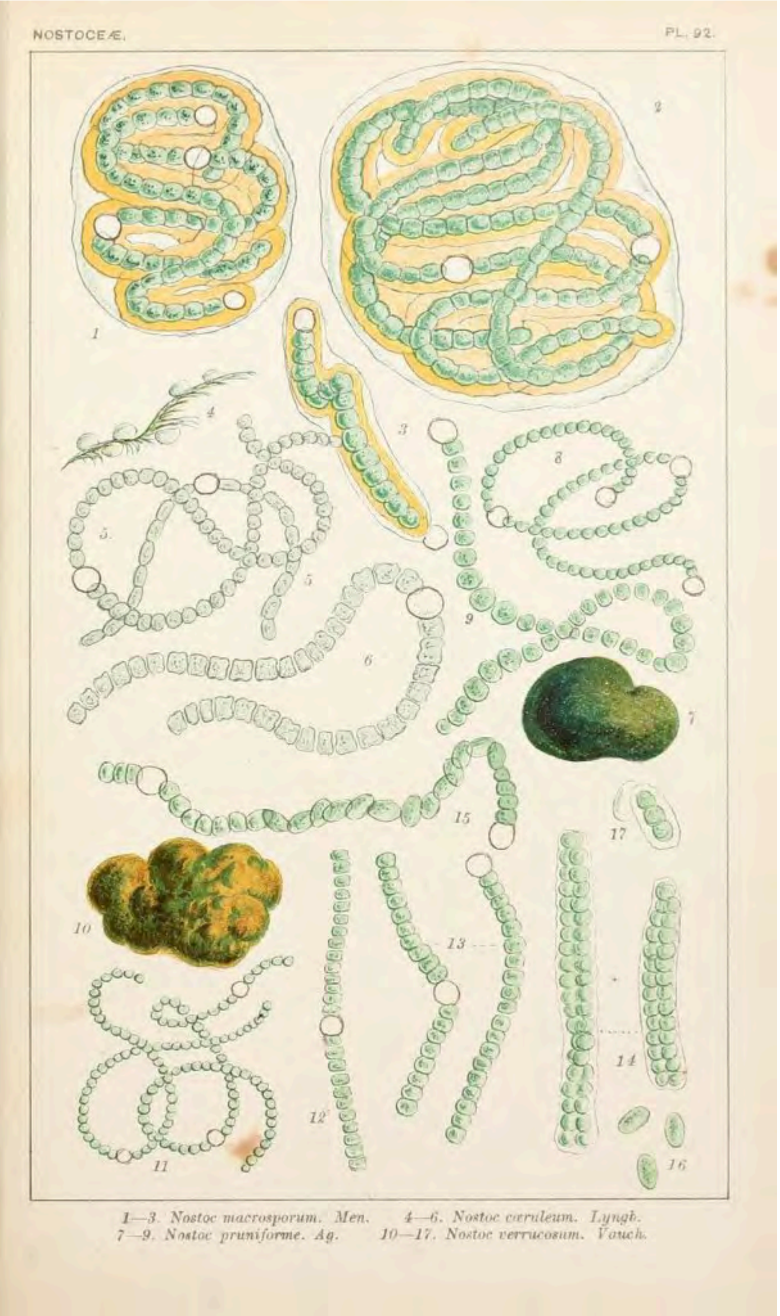
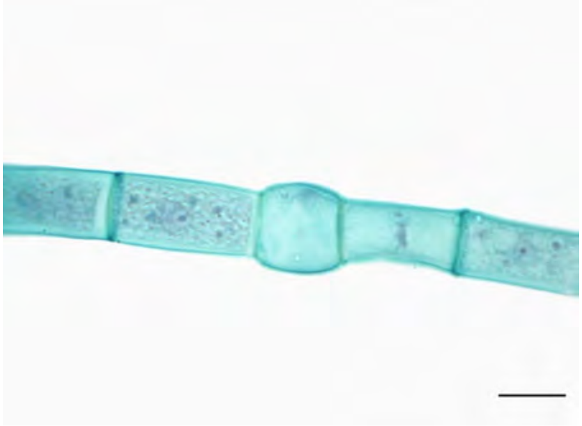
- British fresh-water algae © Cooke, M. C. (Mordecai Cubitt) is licensed under a Public Domain license



1—3. *Nostoc macrosporum. Men.* 4—6. *Nostoc cœruleum. Lyngb.*
7—9. *Nostoc pruniforme. Ag.* 10—17. *Nostoc verrucosum. Vauch.*

Nostoc filaments, the irregular structures represent globular cluster of filaments surrounded by polysaccharide.

OEDOGONIUM: A FILAMENTOUS GREEN ALGAE



Oedogonium is representative of a number of organisms in a very diverse group, the green algae (Chlorophyta). In this book we consider several members of the green algae that illustrate a range in form and structure. Other members of the green algae group are *Chlamydomonas* (small and unicellular), *Acetabularia* (large and unicellular) and *Caulerpa* (large and coenocytic) , which are quite different in form and structure.

Taxonomy and Phylogeny

The green algae (= Chlorophyta) are a group of eukaryotes that have some characteristics in common with plants (they are photosynthetic, possess both chlorophyll a and b, generally store carbohydrate as starch and have cellulose cell walls). But they also differ from plants in several ways: almost all are not multicellular, being either unicellular, siphonaceous or filamentous; they do not retain embryos inside the previous generation as all plants do; few grow on land as almost all plants do. Because land plants are thought to have originated from ancestral 'green-algal like organisms' separating green algae and plants in separate kingdoms, as is done in the 'five-Kingdom' classification, with a Protist Kingdom that includes green algae and a separate Plant Kingdom, is very artificial. One remedy is to put green algae in the plant kingdom and some observers do this. Another alternative is to simply throw out the Kingdom level of taxonomy and this is what many modern treatments do. If this were done then one might split the green algae into two phyla, one that includes land plants (Streptophyta) and one that doesn't (Chlorophyta), which would include *Oedogonium*.

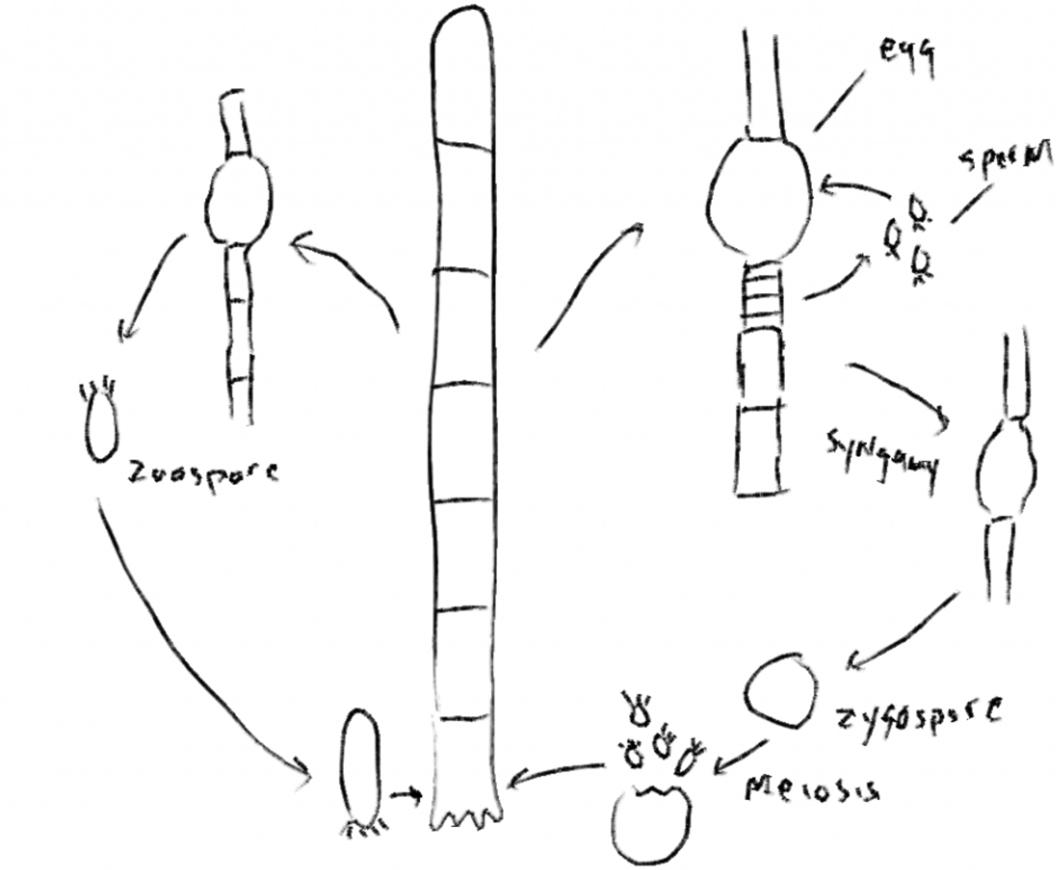
Structure

Oedogonium forms elongate filaments of cells, m ost of which are non-flagellated, cylindrical and have a cell wall that contains both cellulose and chitin. These cells are vegetative, i.e. are not associated with reproduction but only associated with photosynthesis and growth of the filament. Several additional cell types are produced that bring about reproduction and sex:

- zoospores — mobile, flagellated cells do not have cellulose cell walls. Zoospores are released from parental cells and can attach to various substrates, becoming immobile and dividing to form new filaments. Zoospores have contractile vacuoles; why do you think this is the case?
- oogonia — large cells that develop a pore in the cell wall that allows flagellated sperm cells to enter the cell
- sperm — mobile, flagellated cells that are released from parental cells and swim to the oogonia
- zygospores — produced after sperm fertilize eggs, these cells develop a thick cell wall. They eventually undergo meiosis and break open to release flagellated zoospores.

Reproduction

Oedogonium reproduces asexually via mobile zoospores and sexual ly via sperm, oogonia and zygospores. Sperm are released from parental cells and are chemo-attracted to the oogonia that house an egg. A pore in the oogonium cell wall allows the sperm to enter the oogonium and fertilize the egg. Fertilization occurs and the oogonium develops a thick wall, forming a structure called a zygospore. Eventually the cell inside the zygospore undergo meiosis and haploid daughter cells are released as mobile zoospores, which, like the zoospores produced asexually, swim to a substrate and attach themselves and elongate into filaments.



Matter and energy

Oedogonium is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and as building materials to synthesize a variety of biomolecules.

Interactions

Oedogonium is common in in fresh water habitats. It is eaten by a variety of herbivores including fish, mollusks and other invertebrates.

Further Reading

- "The Filamentous Algae" on *Micrographia*
  - http://www.micrographia.com/specbiol/alg/filamen/fila0100.htm (*Spirogyra*)
- Oedogonium Image-based Key
  - http://cfb.unh.edu/phycokey/Choices/Chlorophyceae/filaments/unbranched/OEDOGONIUM/Oedogonium_key.html (note epiphytic diatoms)
- Observations of *Oedogonium* and chytrids
  - https://microscopesandmonsters.wordpress.com/tag/oedogonium/
- Article on the evolution of green algae
  - https://www.researchgate.net/publication/24188801_Streptophyte_algae_and_the_origin_of_embryophytes

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PHYSARUM: A PLASMODIAL SLIME MOLD

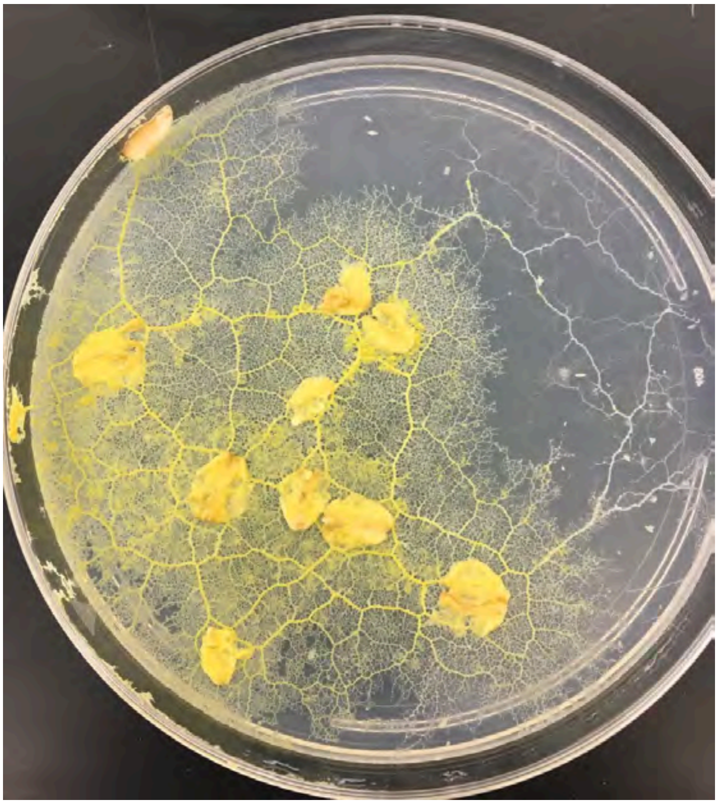
Physarum: a plasmodial slime mold

Physarum polycephalum

Physarum is a member of a group that is unfamiliar (to most) but whose members are actually relatively common. They can commonly seen on mulch used in landscaping and occur as a large thin, amorphous 'blob' of yellow or cream colored material that usually hardens in a day or two. They also are commonly found on decaying wood in the forest.

Phylogeny and taxonomy

Since they are heterotrophic, mobile and (generally) unicellular they used to be considered 'protozoa'; other early treatments put them with fungi because they produce spores and fruiting bodies. Like a number of other 'misfit' groups, the plasmodial slime molds can be placed in the Protist kingdom, a heterogenous assemblage of eukaryotic groups that do not readily fall with animals, plants or fungi. In certain stages plasmodial slime molds look like a giant, multinucleate amoebae and they are sometimes grouped with other similar looking things (including the amoebae often seen in introductory biology classes, as well as cellular slime molds (see *Dictyostelium*) in a group that may be called the Amoebazoa. However, looks can be deceiving and apparently not all amoebae-like things belong (phylogenetically) together, i.e. amoeboid 'looks' evolved more than once and a group with all amoebae-like things (e.g. the Rhizopoda) is paraphyletic (i.e. grouping together organisms with different origins). Consequently, the Amoebazoa does not include all amoebae-like things.



Physarum growing on 4" petri dish with flakes of oatmeal for food

Structure

Physarum is eukaryotic and is capable of ingesting material by phagocytosis. The cells are multinucleate (coenocytic), forming a thin film called a plasmodium that spreads across its substrate, often with visible branching channels occurring within the structure. They often can become several centimeters in size, flowing over a substrate (soil, leaves, branches or logs. They exhibit an easily seen (with a hand lens or dissecting scope) cytoplasmic streaming, the result of the interaction of motor proteins with microfilaments (actin filaments). Their normal food is bacteria or other minute organisms. They also can live off of dead organic matter (e.g. oatmeal, which is often used to feed it in the laboratory). Under adverse conditions the cytosol thickens and dries out forming a structure called a sclerotia that can survive in an inactive state for a prolonged period.

Reproduction

The large cell often reproduces by fragmentation, which can also happen with the dried sclerotia. The plasmodium can also dramatically transform from a blob of cytoplasm to a rigid structure consisting of numerous sporangia, often stalked structures with a round capsule (sporangium) at their top, in which are formed haploid spores created as the result of a meiotic cell division that occurs in the developing sporangium. The spores are dispersed and, when they germinate, form uninucleate amoeboid (haploid) cells that grow and divide and can develop, also lose, a flagellum. At some point some of these cells are capable of fusing with each other and having their nuclei also fuse. This diploid cell is capable of growing and forming a large, multinucleate cell, the plasmodium.

Close up of plasmodium growing on oatmeal agar, showing channels and fan-like growth ~ 1 cm in extent.

Mature fruiting bodies

Plasmodium just starting to coalesce to form fruiting bodies

Matter and Energy

Physarum is both predatory heterotroph, capturing (by phagocytosis) other living organisms (primarily bacteria) and also a saprophyte, feeding on dead organic material. In either case they break down their food's biomolecules into simple sugars, amino acids, etc. and reform them into their own biomolecules. That is, they are typical heterotrophs.

Interactions

Plasmodial slime molds interact in a trophic manner with their prey and with organisms that eat them (either the plasmodium or the spores). They need moist conditions to grow and changes in their growth pattern (spore germination, formation of sporangia and sclerotia) are triggered by environmental conditions.

Dog vomit 'fungus' (actually slime mold) is fairly commonly seen growing on bark compost. This organism is just starting to sporulate and in a day will be dried out with a relatively solid structure.

Further Reading

Plasmodial slime molds have been shown to be capable of a type of 'reasoning' (depending upon how one defines it–see the first link. In addition to the links listed below, YouTube also has several excellent videos of slime molds.

- "Brainless Slime Mold Physarum polycephalum Shows Intelligence"
    - scitechdaily.com/brainless-slime-mold-physarum-polycephalum-shows-intelligence
- "Life Cycle of *Physarum polycephalum*"
    - http://www.educationalassistance.org/Physarum/LifeCycle.html
- Hunting Slime Molds
    - https://www.smithsonianmag.com/science-nature/hunting-slime-molds-38805499/
- "Life Cycle of Physarum"
    - http://www.biologydiscussion.com/fungi/life-cycle-of-physarum-with-diagram-fungi/63114

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PHYTOPHTHORA

Model of late blight of potato infecting a potato leaf. (note that the leaf is upside down.) The hyphae can enter the leaf through stomata or the cuticle; they infect and kill cells and spread throughout the leaf. Fruiting structures emerge through stomata into the air and release zoospores that can swim through films of water to infect additional leaves and plants

Phytophthora is an example of the water mold group—the Oomycetes (Oomycota). They are highly significant to humans as pathogens of plants, in particular late blight disease of potatoes, but also the pathogens that cause sudden oak death syndrome, downy mildew and 'damping off' diseases. There are a few oomycetes that are pathogens of animals, in particular the fuzzy mold that is sometimes seen on fish (just before they die).

Phylogeny

Because of its structure, water molds were once considered to be fungi. However, a variety of features do not match with fungi and recent work either puts them as a distinct phylum in the Kingdom Protista, or in a separate Kingdom altogether (the Chromista or the Stramenopiles or heterokonts). They have affiliations with a number of photosynthetic groups (diatoms, brown algae, golden algae) and there is some debate as to whether the group started out without chloroplasts or whether the ancestor of the water molds lost chloroplasts.

Structure

Like the bread molds, most water molds have a filamentous structure where cells are not delineated with cross walls (i.e. they are siphonaceous). Although water molds exhibit a filamentous structure like fungi, the cell walls are composed of cellulose, not chitin as is found in fungi. The filaments explore the habitat (which is sometimes water and sometimes the inner part of other organisms) and obtain nutrients; in the case of *Phytophthora*, the habitat is the inside of potato leaves or potato tubers

Reproduction

Phytophthora can spread very rapid in moist weather using mobile zoospores, flagellated cells that can swim through the water. Although they are not long distance swimmers, movement of water by splashing, or by the wind and animals walking through vegetation, can aid in their dispersal. *Phytophthora* also reproduces sexually, producing large, immobile eggs and smaller, mobile sperm. Unlike the fungi, the typical (i.e. most commonly encountered) cell of a water mold is diploid.

Matter and Energy

Phytophthora is a typical heterotroph, needing to find organic material as a source of matter and energy. For part of its life, *Phytophthora* is what is known as a 'biotroph' which means that it associates with living cells and is able to acquire matter (sugars, amino acids) from them using a structure called an haustorium, a structure that penetrates the cell wall, associates with the host cell membrane and is able to induce materials to move from the cytosol of the host plant to the cytosol of the parasite. With time, this drain on plant nutrients can kill the host plant cells and the fungus necessarily shifts from being a biotroph, to a necrotroph, an organism that kills its food and then eats it, similar to killer whales, lions and spiders. Significant to researchers is the fact that biotrophs are impossible to culture without living plant cells, i.e. you cannot simply have a medium with 'good stuff', like sugars and amino acids, and culture *Phytophthora* on it.

Dead oaks (all the grey regions) in California caused by a 'sudden oak death syndrome, a disease caused by a *Phytopthora ramorum*.

Interactions

There are a substantial number of *Phytophthora* species, mostly known because they affect a number of crop species (potato, leek, cucumbers, squash, soybean, cocoa) or ornamental species (rhododendron, azalea). These species are found in the wild, not just in agriculture, and affect wild relatives of these crops. Moreover, epidemics caused by *Phytophthora* do occur in the wild (sudden oak death syndrome in California), not just in planted monocultures.

One species of *Phytophthora*, *P. infestans* has had a particularly significant influence on human history, being the cause of the potato famine in Ireland in the 1850's that killed over a million people and caused roughly twice that number to emigrate to the United States, significantly affecting the history of the U.S. (see last link below).

Further Reading

- "Introduction to the Oomycota" by Brian R. Speer
    - http://www.ucmp.berkeley.edu/chromista/oomycota.html
- "Oomycota" on Microbe Wiki
    - http://microbewiki.kenyon.edu/index.php/Oomycota
- "*Phytophthora infestans*" by Tom Volk
    - http://botit.botany.wisc.edu/toms_fungi/mar2001.html

Media Attributions

- Modell eines Querschnitts durch ein Kartoffelblatt mit Phytophthora infestans (Kartoffelpilz) © David Ludwig is licensed under a CC BY-SA (Attribution ShareAlike) license
- Sudden oak death © Hemhem20X6 is licensed under a Public Domain license

PINUS: PINE TREES

Most pine needles differ from other conifers (e.g. hemlock) because they are much longer and occur in clusters, with the needles per cluster depending upon species.

Pine trees should be familiar to just about everyone although some might confuse them with other evergreen trees. Most pines are distinct from other evergreens by the fact that their needles are longer, often 10 cm long or more, and they almost always occur in clusters (bundles), typically in groups of two, three or five with the number of needles per group being a useful identification aid.

Phylogeny

Pines belong to a distinct phylogenetic entity, the conifers, a group that is usually placed at the phylum level (Pinophyta). They have vascular tissue and produce seeds but do not produce flowers. Sometimes conifers and the other seed plants without flowers (e.g. cycads and ginkgo) are grouped as gymnosperms but most workers do NOT consider this to be a sound phylogenetic entity, i.e. they are not a group unified by their evolutionary history. Conifers are by far the most commonly encountered gymnosperm and pines (the genus *Pinus)* are probably the most frequently encountered conifer. They are the largest genus within the phylum, containing over 100 of the approximately 600 species in the group.

Structure

Almost all pines are typical woody trees (a few might be considered large shrubs) with a branched, dendritic form that through time and with secondary growth produces the typical form that we recognize as trees. While some pines and most other conifers (spruces, firs and douglas fir) produce a 'Christmas tree' form, with triangular crowns that are usually quite steep, pines often have a broader base and less steep sides.

Sex and reproduction

Pines reproduce by seed, a multigenerational unit, which in the case of conifers contains both an embryo and the female gametophyte that produced the egg that was fertilized to form the zygote that grew into the embryo. Both these entities are packaged in a seed coat constructed of cells derived from the tree that produced the cone. Significant to the story is that pines, like ferns and mosses and also like wheat and aspen, **do** produce spores, i.e. seeds do NOT replace spores. Most species of pines have seeds that are winged and dispersed by the wind, but a few species have adapted to dispersal by birds (see below).

Matter and energy

Pines are typical photosynthetic autotrophs, acquiring carbon dioxide from the air and converting it into carbohydrates to be converted back to carbon dioxide in cellular respiration (yielding ATP) or to be used to synthesize biomolecules. The shape of of conifer leaves (cylindrical), coupled with a thick cuticle reduces water loss but also slows carbon dioxide acquisition when compared to a broad-leafed plant with a much greater surface area to volume ratio and thinner cuticles. In spite of the fact that individual leaves of pines and most other conifers have a much smaller surface area than broad-leaved plants, the total leaf area per branch may exceed that of broad-leaved plants because there often are lots of needles. Two other features are significant to the matter and energy relations of pines (and other evergreen conifers): (1) their evergreen life-style allows for year-round photosynthesis if conditions are appropriate, (2) leaves with longer lifespans are potentially beneficial to nutrient status because absorbed nutrients have a longer residence time in the plant.

Interactions

With climate:

Pines are primarily distributed in the northern hemisphere, and primarily occur at latitudes north of the tropics. They are particularly abundant in mountain habitats, as are other conifers. Many are tolerant of extreme cold and can live at upper elevations (e.g. lodgepole pine in the western US, Swiss pine in the Alps). As a group they are also tolerant of dry conditions, in particular seasonally dry conditions. P ines are often associated with sandy soils, which hold less water than other soils.

With disturbance:

Many pines are 'fire-adapted' and are associated with habitats that burn frequently, e.g. long-leaf pine, found in the southeastern US; ponderosa pine, found in the western US. ; pitch pine, found in the eastern US (e.g. in the Albany Pine Bush and the Pine Barrens of New Jersey). All these pines have features that actually promote fire, in particular their needles are flammable and they also have behaviors and anatomy that allow them to tolerate fire. These species are likely to be eliminated from sites if fires are suppressed.

Ponderosa pine stem showing multiple fire scars. The tree started growth in 1639 but 44 years later (1683) a fire destroyed two-thirds of the vascular cambium. The tree survived and subsequent growth was able to repair some of the damage. Other fires occurred in 1693, 1747, 1795 and 1861.

With seed predators (i.e. things that eat seeds):

A number of pines have interesting relationships with birds, such as the Clark's Nutcracker, that feed on their seeds. The seeds of these pines are particularly large and are NOT winged. The birds have morphological features that allow them to easily extract the seeds from the cones and they also exhibit a 'caching' behavior: much like some squirrels, they bury their food for consumption later in the year. The birds make caches that are some distance from where they forage. This, coupled with the fact that they generally bury more seeds than they end up eating, means that the birds both disperse the seeds and also plant them.

Most pine seeds are wind dispersed, with a prominent thin wing and a relatively small seed.

With humans:

Pines are an important timber species and chemicals from their 'sap' are useful in a variety of ways: as waterproofing, as organic solvents (turpentine), to improve grip for baseball hitters (pine tar on the bat), for baseball pitchers (resin bags), and for violin bows (rosin—to improve their 'grip' on the strings), pine tar is sometimes used medicinally. The seeds of a number of pines are eaten (pignoli).

The seeds of pines dispersed by animals have no wing and are much larger. The Clark's nutcracker has just harvested a seed from a limber pine. Another animal dispersed pine, pinyon pine, is shown below.

Seeds of a pinyon pine are similar to that of the limber pine that Clark's nutcracker harvests. They have no wing and are much larger than typical pine seeds

Further Reading

- The Gymnosperm Database at conifers.org is a good site on conifers.
    - https://www.conifers.org/
- "Longleaf Pine Ecosystem" by Albert Way
    - http://www.georgiaencyclopedia.org/articles/geography-environment/longleaf-pine-ecosystem
- "Restoring a Disappearing Ecosystem: the Longleaf Pine Savanna" by Noreen Parks in *Science Findings*
    - https://www.fs.fed.us/pnw/sciencef/scifi152.pdfhttps://www.nps.gov/romo/learn/nature/clarks_nutcracker.htm
- "Clark's nutcracker" by John Fraley
    - http://fwp.mt.gov/mtoutdoors/HTML/articles/portraits/nutcracker.htm
- Photos and videos of Clark's Nutcracker in Macaulay Library
    - https://www.allaboutbirds.org/guide/Clarks_Nutcracker/mediabrowser/443726

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- Seed pinus sylvestris © Beentree is licensed under a CC BY-SA (Attribution ShareAlike) license
- Pinyon cones with pine nuts © Dcrjsr is licensed under a CC BY (Attribution) license

POLYTRICHIUM: HAIRY CAP MOSS

Polytrichium is a common moss that occurs across all of North America. It is large for a moss and regularly exhibits both the haploid and the diploid phases of its life cycle. Thus it is a useful example of what mosses are about. It is generally found in forests but can also be found on soil or gravel in open areas.

Gametophyte plants (green), a few with sporophytes emerging from the top of female plants.

Phylogeny and taxonomy

In the past, the three groups of non-vascular plants (mosses, liverworts and hornworts) were put together in a taxonomic unit (Division Bryophyta = 'Bryophytes' = non-vascular plants), but there is little evidence that this is a unified group other than they are all plants. Mosses are distinct from the other two non-vascular groups and vascular plants are probably more closely related to liverworts than to mosses. Mosses are now generally put into their own division, the Bryophyta, distinct from the division of liverworts (Hepatophyta) and hornworts (Anthocerophyta). Within the Bryophyta there are around 12,000 species.

Gametophyte plants (green) and sporophytes (brown) of Polytrichium.

Structure

The gametophyte (haploid form) of mosses is the form that is usually seen. It is green, (photosynthetic) and lives for several years. *Polytrichium* has an erect unbranched stem with small pointed 'leaves' emerging off the sides. Technically it lacks 'true' vascular tissue because it lacks lignin. But it does produce cells, comparable to vascular cells, that are specialized for transport. Even without lignin for support *Polytrichium* can produce a stalk standing 4-10 cm tall. The plants have thread-like rhizoids emerging from the base of plant and attaching it to the substrate.

The gametophyte gets its name because it produces gametes. *Polytrichium,* but not all mosses, is dioecious, meaning that it has separate male and female plants. The gamete-producing organs appear at the tips of the stems, in structures (antheridia) that produce many mobile (flagellated) sperm on the male plants and structures (archegonia) on the female plants in which are produced a single, immobile egg.

The diploid form of the plant is called a sporophyte and it grows out of the structure that produces the egg (the archegonium). It has a typical spore-producing structure (cf. that of the cellular slime mold, *Dictyostelium,* or mushrooms) with a stalk (often over 5 cm) elevating a spore producing capsule at its top. The elevation provided by the stalk (seta) allows the spores to be more readily dispersed by the wind. Most moss capsules have one or two rings of teeth surrounding the opening of the capsule that can open and close, releasing spores under favorable (dry) conditions when they will be transported further by the wind.

The tips of male gametophytes of Polytrichium. The reddish structures are clusters of sperm-producing antheridia, surrounded by sterile appendages.

Reproduction

Mosses exhibit the typical plant sexual life cycle that involves an 'alternation of generations', alternating between a haploid gametophyte and a diploid sporophyte, and the sexual cycle requires both. Unlike familiar animals who reproduce by directly making replicas of themselves, plants, including mosses like *Polytrichium,* alternate between two forms: the sporophyte makes gametophytes and the gametophytes make sporophytes. Note that, if one rigidly holds to a definition of organisms being entities distinct in space, then the sporophytes produced by gametophytes are not 'new individuals', just appendages off of old ones! The gametophyte of most mosses can reproduce asexually both growing in a clonal manner. Some mosses also can reproduce asexually by producing groups of cells (gemmae) that break off and can be dispersed, but these are not found in *Polytrichium.* In *Polytrichum,* only one sporophyte is produced for each female gametophyte. In some other mosses a single gametophyte may produce a several sporophytes but for all mosses it is the sporophyte generation does the bulk of the reproduction, producing many, many spores. Of even more significance, the production of spores is what allows the moss to spread to new areas, i.e. performs a dispersal function.

Matter and Energy

Hairy cap moss is a photosynthetic autotroph, it makes food (carbohydrate) through the process of photosynthesis and then uses this carbohydrate both as a material to make biomolecules and also to provide energy for metabolic activities. For the gametophyte, this is true throughout its existence. The sporophyte is usually only photosynthetic during its period of growth, if at all, and often loses its chlorophyll, and thus its ability to feed itself, as it matures, becoming dependent upon the gametophyte that it is growing out of for its food.

Mineral nutrition of mosses is different from that of vascular plants whose roots obtain nutrients from the soil solution. The rhizoids of mosses are limited in extent and lack the ability of transporting nutrients to the above ground portion because they specialized cells for transport. Most of the nutrients obtained by mosses probably comes through the leaves of the gametophytes that provide substantial surface area and, unlike the leaves of vascular plants, are generally not coated with a waterproof cuticle that retards absorption of water or dissolved solutes. The nutrients in the solution surrounding the leaves are provided by dust particles blown in the wind, solutes dissolved in precipitation and solutes added to precipitation as it flows down the trees and shrubs in the forest canopy (if there is one), as well as solutes that may be carried up with capillary water from the substrate that the moss is growing on. Sporophytes of mosses lack leaves and are not in contact with the soil and thus probably obtain all their nutrients from the gametophyte that they grow out of.

Interactions

Mosses are very common in a variety of habitats and are particular significant in some of them (e.g. Sphagnum moss in bogs). They are rarely eaten extensively and generally (with the significant exception of *Sphagnum*) produce very little biomass compared to vascular plants, thus their contribution to the trophic structure of most ecosystems is slight. However, they do provide habitat for a number of small invertebrates (see the article on tardigrades linked below), they can sequester nutrients, including carbon, and are often very important in soil formation on sites that previously have lacked a soil, i.e. in primary succession.

Further Reading

- Great book on mosses.
    - *Gathering Moss* by Robin Wall Kimmerer ISBN 0879714993
- General information at Wikipedia.
    - https://en.wikipedia.org/wiki/Moss
- *Bryophyte Ecology* by Janice Glime. A tremendous source of information on moss ecology.
    - http://www.bryoecol.mtu.edu
- “Tardigrades” by William Randolph Miller. An interesting article on tardigrades, fascinating tiny animals that often live in the environment surrounding moss leaves.
    - https://www.americanscientist.org/article/tardigrades

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POPULUS

Aspens, cottonwoods, poplars: the genus *Populus*

Trembling Aspen (*Populus tremuloides*) is the most widely distributed tree in North America, occurring from the east coast to the west coast and from Alaska to Mexico. The genus *Populus*, which includes several other aspen species and also cottonwoods, has a world wide distribution in the northern hemisphere. While cottonwoods, like *P. deltoides* and *P. fremontii* are typically found along streams and rivers, aspens like *P. tremuloides* and *P. grandidentata* are found in a variety of upland habitats, often forming monotypic stands because they grow clonally (see below).

Phylogeny

Populus is a genus of flowering plants in the willow family with around 25 species, many of which are familiar and are commonly seen. The willow family is a taxonomic grouping that used to be small (three genera), but recent studies using molecular information have enlarged the family greatly (56 genera) by merging it with several other families. Although the group was once thought to be primitive, based on floral characteristics, including the fact that most are wind-pollinated, most plant taxonomists now consider the family to be of relatively recent origin.

Structure

Most members of this genus are fast-growing and relatively short-lived trees. They exhibit typical tree-like above-ground form but are relatively unusual because of their below-ground behavior, producing underground stems (rhizomes) that spread horizontally below ground and sporadically produce vertical shoots that form new trees. As a consequence, several members of the genus (especially aspens) are typically found as clones, stands of genetically identical individuals all connected (or previously connected) by below-ground structures. Some other trees that behave similarly are black locust and beech. This kind of growth pattern with spreading below ground stems is also found in shrubs (e.g., creosote bush of the M ojave desert) and herbaceous (non-woody) plants (e.g., goldenrod, Kentucky bluegrass, a common lawn grass).

Although individual aspen trees (above ground stems) are relatively short lived (typically less than 200 years) aspens clones represent some of the longest-lived organisms. One of the best-studied clones lives in Utah and has been named ‘Pando’. It is estimated to weigh over six million kilograms, extend over 43 hectares, and may have an age of 80,000 years (see link below).

Reproduction

As described above, aspens ‘reproduce’ asexually by spreading below ground, although one could argue that this isn’t reproduction at all, it is simply organismal growth. Aspen is also capable of the sexual reproduction typical of angiosperms, producing mobile male gametophytes (pollen) which are dispersed to the location of the female gametophytes (the ovules of flowers). The gametes that are subsequently produced unite to form a zygote that grows and is packaged into a seed. One relatively unusual feature for *Populus,* compared to most flowering plants, is that individual trees and (therefore) clones are unisex-

Male flowers of aspen. Both male and female flowers occur in long clusters that hang below branches early in the spring.

ual; the flowers are unisexual and any one tree/clone produces only one kind of flower, either male or female. Both the male and female flowers occur in catkins, drooping clusters of flowers that lack obvious petals. Cottonwoods (*P. deltoides*) in particular but all members of the genus are known for producing copious quantities of seeds, each packaged in a cottony tuft of hairs.

A ‘snow’ of cottonwood seeds.

Matter and Energy

Aspens are typical photosynthetic autotrophs. Individual plants accumulate carbon dioxide from the atmosphere and use it to form carbohydrates that are both used to enlarge the plant (i.e., grow) and also to be ‘burned’ in cellular respiration to provide energy for the plant. Aspens are typical seed plants, requiring 17 elements: carbon, hydrogen and oxygen (obtained as carbon dioxide and water) , plus an additional 14 ‘minerals’ that are obtained from the soil solution by the root system.

Interactions

Because it is a common, wide-ranging genus there is a multitude of interactions that aspens exhibit. Among them are the following:

Fire ecology

In parts of its range aspen depends upon fire to eliminate competitors. Conifers (e.g., spruce and fir) do not grow as fast as aspens but can grow taller and can eventually outcompete aspens by shading them out, killing trees and root sprouts. Fire can kill conifer competitors while only eliminating the above-ground part of aspens. Thus, fire allows aspens, sprouting from underground stems, to quickly re-colonize the area. In western North America, avalanches may serve as a different form of disturbance that eliminates aspen competitors and facilitates continued aspen presence.

Beaver interactions

Beaver are herbivores that feed primarily on tree bark and shoots. They are particularly fond of aspen and some of its relatives. As a consequence, beaver can have a very substantial influence on forest composition, drastically decreasing the occurrence of aspen and increasing the frequency of species less desirable to beaver. Because beaver can significantly affect communities by building dams and flooding areas, the preference for aspen can influence what areas get flooded as a result of beaver activity.

Further Reading

- ‘Pando’ and large organisms
  - https://www.nationalforests.org/blog/unforgettable-experiences-pando-aspen-clone
  - https://www.nationalforests.org/blog/tree-profile-aspen-so-much-more-than-a-tree
  - https://en.wikipedia.org/wiki/Pando_(tree)
- Ecology of aspen—Bryce Canyon National Park
  - http://www.nps.gov/brca/naturescience/quakingaspen.htm
- Ecology of aspen
  - https://www.fs.usda.gov/wildflowers/beauty/aspen/ecology.shtml
- Ecology of aspen and beaver
  - https://western-aspen-alliance.org/files/briefs/

WAA_Brief6_Beaver_final_.pdf

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- Catkin being pollinated © Wolfmann is licensed under a CC BY-SA (Attribution ShareAlike) license

POTATOES: SOLANUM TUBEROSUM

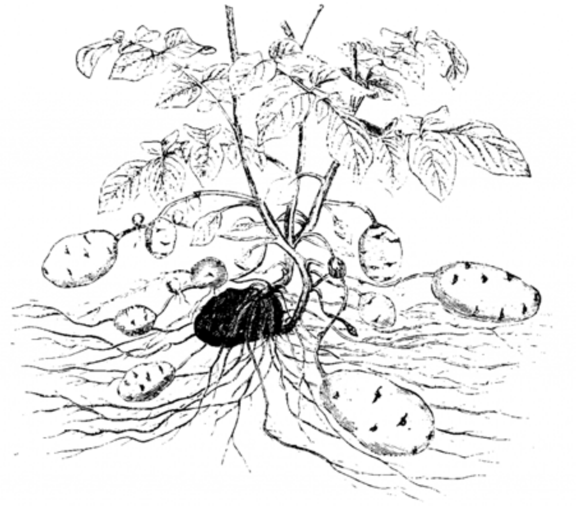
Potato plants in flower. Europeans recognized the floral structure to be similar to some poisonous plants and were resistant to eating them when introduced from South America in the 18th century.

Potatoes (*Solanum tuberosum*) are an herbaceous plant, native to South America, that has been cultivated by indigenous peoples for five to ten thousand years but only became cultivated world-wide in the last 500 years. Grow ing at high elevations of Peru and Bolivia, it was a staple crop of the Incas, who developed a freeze-dry preservation technique, producing 'chuno'. This was possible in these high elevation sites (10,000 feet or more) where the combination of clear nights and bright sunny days allowed for the freezing and drying. The spread of potato in Europe was slowed because people recognized that it was related to plants that were known to be poisonous, e.g. several species of nightshade. The potato family is interesting in that it has produced a number of important crops (potato, tomato, pepper, eggplant) and also important poisons and drugs (nicotine, novocaine, atropine).

Phylogeny

Potato (*Solanum tuberosum*) is a flowering plant (angiosperm) and would typically be classified as: Plant Kingdom, flowering plant phylum (Magnoliophyta = Anthophyta), dicot class (now usually considered the Eudicot class), potato order (Solanales), potato family (Solanaceae). Other members of this family include: tomato, pepper, tobacco, nightshade, jimsonweed and petunia.

Structure



Note that the potato produce underground stems that are much enlarged at their tips.

Potato is an herbaceous plant with a typical plant structure of below-ground roots and above-ground shoots with leaves. Like tulips and a number of other plants, the above-ground stem and leaves are 'annual', i.e. they die every year. The plant is perennial because a below-ground portion survives and perpetuates the organism. The perennating part is a structure called a tuber, a branch shoot that is produced and remains below ground. These stems do not grow upwards and do not produce leaves but their tips swell and produce tubers. These results from the production of much more parenchyma tissue than is found in a normal stem. Tubers (or functionally similar, but anatomically different, structures called corms and rhizomes) are a common feature that allows plants to survive in areas where the above ground climate is hostile (cold or dry) for part of the year. The above ground portion of the plant dies, but the below-ground part, present in the more favorable (i.e. warmer/moister) environment of the soil, is able to survive and can sprout new 'normal' (i.e. upward growing) branches when it 'knows' that favorable above-ground conditions have returned. Parenchyma cells of the tuber possess numerous starch storing plastids (amyloplasts) that provide material and energy to power growth when it resumes. The 'stem nature' of a potato tuber is revealed in its 'eyes', which are lateral buds, i.e. embryonic branches. They, like the leaves and branches of the above ground stems, are distributed in a spiral fashion around the shoot. Farmers vegetatively propagate potatoes by cutting the tubers into sections with at least one eye and planting them.

Sprouting ‘eyes’ of a potato—these are branch shoots that can produce new above ground growth.

Sex and reproduction

Potatoes reproduce sexually by flowers (the flowers are basically the same structure as petunias, a close relative) but are generally propagated vegetatively from the tubers. Although it is grown as an annual crop, it is perennial in the wild.

Tubers are planted in the spring and the tubers are harvested in the fall after the annual shoots have died.

Matter and energy

Like most plants, potatoes are photosynthetic autotroph s, acquiring carbon from the atmosphere, water from the soil and another 14 essential elements from ions and solutes dissolved in soil water.

Interactions

Potato 's interactions with humans have been extremely significant, both by being the primary food source for several regions and also for the disruption caused when crops failed, disruptions whose consequences were felt for many years in multiple regions (read about the Irish potato famine and its effects on the United States). The causal organism for the famine is late blight of potato (*Phytophthora infestans)*, and the interaction between late blight and potato reveals some interesting features significant to disease interactions specifically and biotic interactions in general:

The interaction involves three 'players' (the disease triangle, see Chapter 30):

- the host —*Phytopthora infestans* infects potato (*Solanum tuberosum*) and also tomato (*Solanum lycopersicon*). Within both host species there are varieties that are more and less susceptible but as yet, no variety that is completely resistant.
- the parasite—Interestingly, it appears that *Phytopthora infestans* originated outside the native range of either of its current-day primary hosts (potato and tomato), feeding on other species of *Solanum* . Host and parasite were brought together when potato cultivation spread from its origin in South America into Central America and the parasite 'jumped' hosts.
- the environment—outbreaks of the disease are associated with cool and moist conditions, conditions that favor the growth, reproduction and spread of the parasite.

Other interesting interactions involving potato are:

The Colorado potato beetle shows some similarities to late blight of potato: it feeds on (i.e. 'has a taste for') a group of related plants: potato, tomato, pepper, indicating that diet preferences are probably related to the secondary chemistry of the hosts. Like late blight, the beetle originated in an area where potato/tomato was not present but, given the opportunity, developed a taste for these new arrivals.

Tuber formation in potato, something essential for its utility as a crop, involves a complex combination of interactions with the conditions the plant encounters. Tuber formation is is promoted by short day photoperiods, cool night temperatures, and relatively low soil nitrogen levels.

There are many, many varieties of potato and only a small portion of these are available commercially in the U.S. Among other differences (such as color and shape) potatoes also vary in the type of starch present and this can impact their utility in cooking: some potatoes (considered 'starchy') have almost all of their starch as unbranched polymers of glucose — this produces a potato better suited for mashing or baking. Other potatoes (considered 'waxy') have a greater portion of their starch existing as branched polymers of glucose, which allows the potato to retain its shape and firmness even after cooking and is better suited for use in potato salads and other situations where it is desirable for the potato to maintain its shape (e.g. in a soup or stew).

Further Reading and Viewing

- "Discovery: How Colorado Potato Beetles Beat Pesticides" by Joshua E. Brown. Colorado potato beetle pesticide resistant and epigenetics.
    - https://www.uvm.edu/news/story/discovery-how-colorado-potato-beetles-beat-pesticides
- "The Many Possibilities of Potato Starch" by Tim Chin. Potato starch and cooking.
    - https://www.seriouseats.com/potato-starch-guide-5204609

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PORPHYRA: AN EDIBLE RED ALGAE

Dried specimens of Porphyra.

Porphyra is representative of a diverse and important group, the red algae (Rhodophyta), one of three algal groups that have members that include multicellular, macroscopic forms (the other two are the brown algae (Phaeophyta) and the green algae (Chlorophyta)). Like the green algae, but not to the same extent, the red algae group also has members that are unicellular or filamentous. Some red algae deposit calcium carbonate in their cell walls and therefore produce a rigid structure that may be a crust on rocks or may form erect branching structures (see link below). Other red algae are significant because the cell walls contains polysaccharides that can be extracted from their cell walls and used to make gels (agar).

Taxonomy and Phylogeny

The red algae are eukaryotes and usually placed in their own phylum, the Rhodophyta. Their affinities with cyanobacteria are reflected in their chemistry (in particular their photosynthetic pigments), but they are clearly eukaryotic with nuclei, chloroplasts and mitochondria. Like the green algae, the chloroplasts of red algae have two membranes, one thought to be the remnant of the membrane of the cyanobacterium that was engulfed during the endosymbiotic event and a second membrane that was produced during phagocytosis when the cell was engulfed, the phagosomal membrane. The chloroplasts of other photosynthetic groups of algae (e.g. diatoms, brown algae) are considered to have been the result of secondary endosymbiosis, a second engulfing (phagocytosis) event where an already eukaryotic cell consumed, but did not digest, another eukaryotic cell that was a red or green algae. These chloroplasts have four membranes, two from the chloroplast of the red/green algae, one from the plasma membrane of the (primitive) red or green algae cell that was engulfed and a fourth membrane, again a remnant of a phagosomal membrane, derived from the engulfing cell.

Structure

Although large, often up to 20 cm in extent, *Porphyra* is not truly multicellular, i.e. parenchymatous (three-dimensional). It has a very simple two-dimensional form, existing as sheets which are either one or two cells thick. The alga does produce filamentous ‘rhizoids’ that attach one end of the sheet to a substrate.

Reproduction

Sexual reproduction in all the red algae is complex and involves alternation of generations, but instead of alternating between a haploid form and diploid form there are three forms: (1) a haploid (gamete producing) form that develops from haploid spores; (2) a diploid form that develops from a zygote, stays attached to its parental gametophyte and produces diploid spores that are dispersed; and (3) a diploid form that develops from these diploid spores and in turn produces haploid spores following meiosis.

Matter and energy

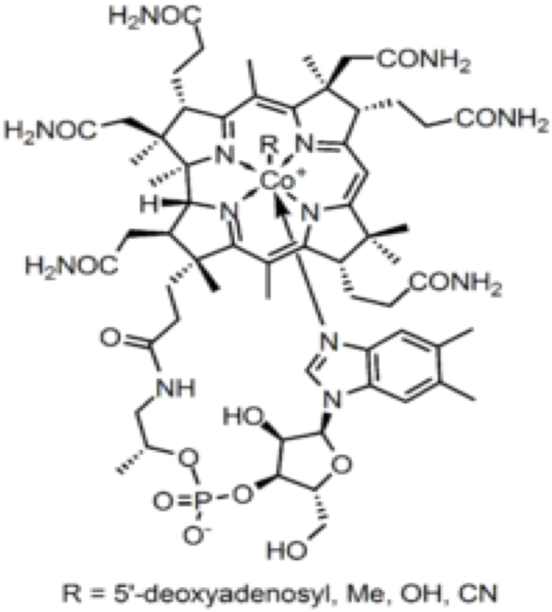
Porphyra is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and as building materials to synthesize a variety of biomolecules. The red algae produce a distinct form of starch, floridian starch, that is not found in other eukaryotes.

Interactions

Porphyra is generally found in cool, marine waters. It is an important component of shallow marine waters into the intertidal zone. As an autotroph it is an important base to marine food chains. It is also a type of 'seaweed' that is commonly eaten by humans and is called 'nori' or 'laver'. More recently it has become popular in the U.S. in sushi. *Porphyra* is cultivated in the oceans off Japan and elsewhere, being grown on rope networks hung in the water.

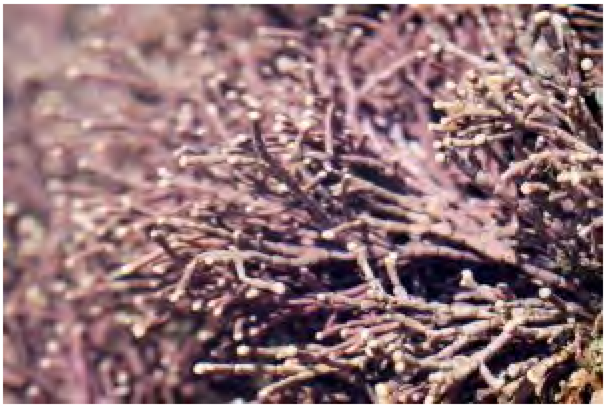
Nori, roasted sheets of Porphyra, used in sushi

Other red algal species are important to humans to produce agar. Polysaccharides in the cell wall are extracted, purified and dried to a powder. This can then be used to make gels suitable for growing a variety of organisms.

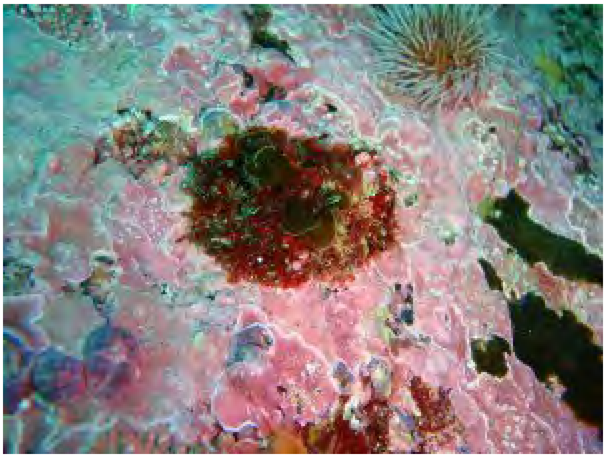


Vitamin B_{12}

For vegetarians *Porphyra* is thought to be a source of vitamin B_{12}, a nutrient usually derived from animal sources. There are some reports that chemical found in *Porphyra*, although similar to vitamin B_{12}, does not perform the necessary functions, but most researchers believe that *Porphyra* can be a source of vitamin B_{12}.



An 'articulated' corraline red algae growing off of a substrate



A crustose corraline algae, forming a coating on the rocky substrate.

Further Reading and Viewing

- "A Brief History of Agar" by Sim Shuzhen.
    - https://www.asianscientist.com/2016/01/columns/history-agar-

microbiology-lab/

- “Red Algae (Rhodophyta)” by Marine Education Society of Australia. Discussion of red algae, including corraline red algae
    - http://www.mesa.edu.au/marine_algae/algae03.asp

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REDWOODS: THE TALLEST AND LARGEST TREES

The name 'redwood' is applied to two distinct entities, both found in California: the 'Coast Redwood' of the northern California and the 'Giant Redwood', or 'Big Tree' or 'Giant Sequoia' of the western slope of the Sierra Nevada mountains in southern California. The habitats of these two areas are significantly different: the Coast Redwood only occurs in areas that are frequently in a coastal fog. The fog significantly alleviates dry conditions and the trees actually obtain moisture from it. The Giant Sequoia occurs in a much drier montane habitat and is a fire-adapted species, having a number of features that allows it to do well in areas that burn. Although both species can become very big, their shapes are distinctly different, with the coast redwoods being taller and thinner. The tallest tree is a coast Redwood with a height of 115.55 m and a volume of 530 m^{3}·. This is about one-third the volume of the largest (by volume) tree, a Giant Sequoia, which has a volume of 1487 m^{3} but is 'only' 84 m tall.

Sequoiadendron giganteum, Big Trees Trail, Sequoia National Park

Phylogeny

Both the coastal redwood and the giant sequoia are sole representatives of their genera (*Sequoia* and *Sequoiadendron*, respectively) with additional species being described from the fossil record. Most workers put these two genera in the Sequoioidae subfamily of Cupressaceae (cedar) family of the conifer group. A third genus in this subfamily is *Metasequoia*, the dawn redwood, a tree that was first described from fossils before living representatives were found. All three genera are endangered and have limited distributions, although throughout most of the Cenezoic era (the last 65 million years) these species were common and much more widely distributed. Other members of the cedar family include junipers and cedars, both of which have small, scale-like leaves that overlap each other on the stem, a feature that is also found in the Giant Sequoia. In contrast, the coast redwood has needles.

Structure

Except for their potential size these are typical woody trees and obviously have extensive secondary growth. The wood that is produced is high in tannins and this accounts for both its durability (i.e. resistance to decay) and color, features that are found in all the members of the cedar family. The cells that conduct water (trachieds) have features that allow them to operate at the extreme tensions that are required to pull water up to the tops of these tall trees. The long distance that water has to be moved, coupled with the fact it is moving against the force of gravity means that the tensions are extreme and the tracheids found in the uppermost leaves have features, including an ability to collapse, that make it possible for the transport system to function.

Sex and reproduction

These are seed-bearing trees that produce seeds in cones, not in flowers. The seeds develop in mature female cones, structures where female gametophytes develop eventually producing eggs that, when fertilized, develop into the embryos present in seeds. These trees also produce male cones where male gametophytes (pollen) are produced and subsequently released. The cones of Giant Sequoia are fire adapted, opening in response to heating created by a fire. Coast Redwood has an ability rarely found in conifers, the ability to sprout from the trunk of the tree if the top is damaged and or killed. Sprouting is the result of the creation and activation of new apical meristems in response to some signal (perhaps reduction in carbohydrate supply) that indicates that the top of the plant is not functioning. As a consequence of this ability one can sometimes find straight rows of Coast Redwood trees reflecting their origin from the trunk of a downed stem, or a ring of trees that have sprouted from the base of a felled tree. Sprouting is fairly common in angiosperm trees but much less common in conifers.

Matter and energy

Redwoods are typical photosynthetic autotrophs.

Interactions

Both species have distributions that reflect interactions with physical conditions: Coast Redwood requires the foggy conditions only found along the coast; Giant Sequoia is a classic fire-adapted species, requiring fire both to open cones and release seeds and also to remove litter from the surface because successful germination requires the seeds to have contact with the mineral soil.

Only recently have ecologists accessed the canopies of these trees and found, especially in those of the Coast Redwood, remarkable communities of lichens, mosses, vascular plants, and associated animals. Some of the needles that are shed from the top of the trees accumulate on the intertwining branches below. Soils actually develop on these sites located 50-100 m in the air and allow for a rich diversity of epiphytes and associated animals. Nearly 200 ‘species’ of lichens and nearly 50 species of bryophytes and a similar number of vascular plants have been found growing in this arboreal environment (http://www.ecology.info/redwood.htm).

Further Reading and Viewing

- The Gymnosperm Database. Good site on conifers.
    - https://www.conifers.org/
- Ecology of coastal redwood canopies.
    - https://www.savetheredwoods.org/grant/sponge-like-mats-make-good-habitat-in-redwood-canopies-wandering-salamanders-benefit/
- *The Wild Trees* by Richard Preston, ISBN 1400064899. Interesting book on the pioneering scientist who climbed into redwoods to study their communities.

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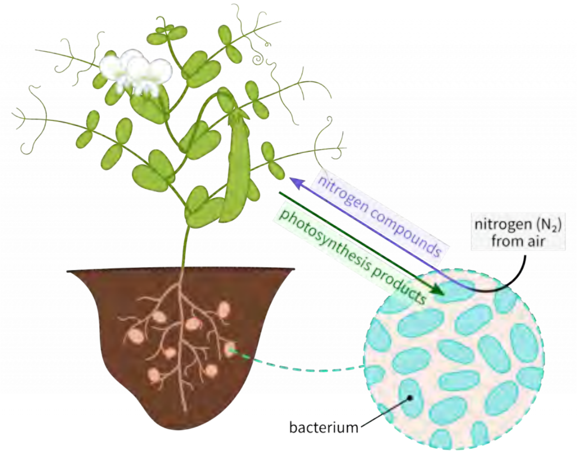
- Closepintree © Boole22 is licensed under a Public Domain license
- Vaccinium ovatum © John Rusk is licensed under a CC BY (Attribution) license

Black Huckleberry (Vaccinium ovatum)—this shrub, along with leather-leaf fern, Polypodium scouleri, are the two most common vascular plants found in the epiphytic communities of the coastal redwoods.

RHIZOBIUM: NITROGEN FIXING BACTERIA



Rhizobia are one of several group of bacteria capable of ‘fixing’ nitrogen, i.e. converting dinitrogen gas into ammonia and then into organic molecules such as amino acids. Because of this ability, nitrogen fixing bacteria are significant conduits between an extremely large pool of nitrogen in the atmosphere and living things who otherwise could only obtain nitrogen by recycling it from existing pools of organic nitrogen (e.g. amino acids, ammonia, nitrate and nitrite). Unlike many nitrogen fixing bacteria that can fix nitrogen when ‘free-living‘ (i.e. when not living inside a host plant) *Rhizobia* can only fix nitrogen when associated with a plant that provides it with carbohydrates. The carbohydrates provide energy for a process that requires substantial inputs of energy (both ATP and the reducing power of NADH). *Rhizobia* only associate with legumes, members of the pea family. (But not all legumes associate with *Rhizobia* and some that have nitrogen fixing associates may have bacteria other than *Rhizobia)*.

Taxonomy and Phylogeny

Rhizobia are members of the Domain Bacteria. They are gram negative bacteria that are usually flagellated and motile. The ability to associate with legumes, like the ability to fix nitrogen, is NOT thought to be significant phylogenetically. The ability to fix nitrogen appears to have evolved separately several times (i.e. convergent evolution) as evidenced by its presence in Archaea, Cyanobacteria (see *Nostoc*) and several other bacterial groups not phylogenetically related. Similarly, the ability to associate with legumes (which might be considered a type of parasitism) is thought to have been transferred horizontally and

consequently is not a good indicator of phylogeny (which reflects vertical gene transfer). The *Rhizobia* group is thus considered to be paraphyletic.

Structure

Rhizobia are rod shaped bacteria, 0.8 um in diameter and 2 um in length, often with flagellae. They assume a different shape when inside their host, being irregularly shaped or often 'Y' -shaped. Their presence nearby a root induces a novel structure within root hair cells called an infection thread. Sensing the presence of *Rhizobia*, root hairs curl and bacteria are lodged in the crook of the curl. At this point the root cell wall is degraded and the bacteria proliferate in a space outside the root hair cell membrane. A tubular 'infection thread' is then produced and grows down the outside of the root hair and into the root itself. The thread is bounded cell wall materials and essentially is an elongate invagination of the cell wall, with materials contributed both by the plant and by the bacteria. The infection thread eventually fuses with cell membrane at its base, adjacent to the root cortex. The infection thread then extends to enter (infect) cortical cells, inside of which the bacteria proliferate. As the thread develops the cortical cells de-differentiated and become meristematic, producing the tumor (nodule) that characterizes *Rhizobium* infection of roots.

Sex and reproduction

Like all bacteria, *Rhizobia* are not sexual but they are capable of exchanging genetic material by other means.

Matter and energy

Rhizobia are heterotrophs that are capable of associating with photosynthetic plants that will provide them with carbohydrates ('food') as well as whatever nutrients (i.e. mineral elements) they need, excluding the nitrogen that they obtain from the air, where it is abundant. Particularly important to the nitrogen fixation process is the element molybdenum. When *Rhizobia* are living outside of a plant they are typical heterotrophs feeding on dead organic material and use the material obtained both as 'building material' for growth and to provide substrates that are oxidized in cellular respiration to provide energy.

Interactions

Group of nodules showing the red coloration of leghemoglobin

The ability to associate with legumes requires elaborate communication (signaling) between *Rhizobium* and its host plant. Factors secreted by both the plant and the bacteria affect the gene expression and behavior of the other. Among other features, the cells of the gall produce a form of hemoglobin called leghemoglobin that is able to bind oxygen and thereby reduce the levels of free oxygen, which is a poison to the nitrogen fixation process. Nodules develop vascular connections, allowing the nodules to be 'fed' with carbohydrates produced by the host plant. These are used primarily to power the substantial energy demands of the nitrogen fixation process but also provide carbohydrate molecules to which the fixed nitrogen is attached. The bacteria acquire N_2 and excrete ammonia that is incorporated by the host plant into organic acids, forming amino acids or other nitrogen containing compounds. There are forms of *Rhizobia* that are complete parasites, being fed by the plant but providing no fixed nitrogen.

Further Reading and Viewing

- “Lifestyle alternatives for rhizobia: mutualism, parasitism, and forgoing symbiosis” by R. Ford Denison and E. Toby Kiers. Lifestyle choices (parasitic vs. mutualistic) in Rhizobia.
    - https://academic.oup.com/femsle/article/237/2/187/528701?login=true
- “Legumes and Rhizobium bacteria – Sharon Long (Stanford)” by iBiology Techniques. Video on nitrogen fixation.
    - https://www.youtube.com/watch?v=zh-YO6wotBs
- Infection Threads by ResearchGate
    - https://www.researchgate.net/figure/Infection-thread-formation-a-A-rhizobium-cell-arrow-makes-contact-close-to-the-growing_fig1_349873219

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- Lotus pedunculatus © Frank Vincentz is licensed under a CC BY-SA (Attribution ShareAlike) license
- Medicago italica root nodules © Ninjatacoshell is licensed under a CC BY-SA (Attribution ShareAlike) license

RHIZOPUS: BREAD MOLD

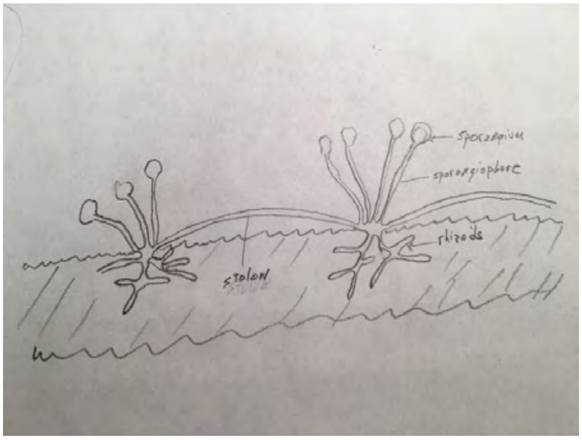
Bread Mold (*Rhizopus*) is one of the most frequently encountered members of the Kingdom Fungi, appearing not only on bread but on a variety of other foods (e.g. strawberries, peaches) if not eaten soon enough.

Taxonomy and Phylogeny

The genus *Rhizopus* has the same common name, bread mold, as the entire phylum, Zygomycota, in which it is found. The Zygomycota are in the Kingdom Fungi, a group unified by two structural features, a filamentous structure and the presence of cell walls formed of the polysaccharide chitin. Within the fungi, the bread molds are one of two groups (the other are the Glomeromycota) that lack of cross-walls (i.e. the filaments are coenocytic) and have a distinctive sexual cycle, see below. Molecular evidence supports both the Kingdom Fungi and the Zygomycota phylum, i.e. both are thought to be a good phylogenetic entities.

Structure

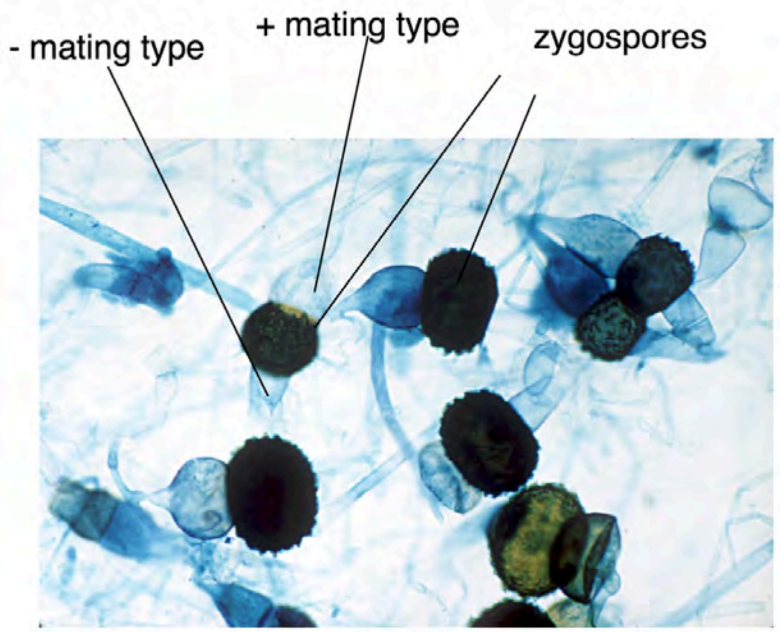
Like most fungi, *Rhizopus* consists of filaments (hyphae) that branch to form a feeding structure, a mycelium. All the bread molds, including *Rhizopus,* are coenocytic, that is, the filaments contain multiple (haploid) nuclei that are not partitioned into individual compartments (cells). The hyphae grow from the tip, extending the filaments, and more nuclei are produced as they grow.



Initially the *Rhizopus* mycelium 'mines' its substrate, acquiring food from whatever it is growing on. Later it produces three distinct structures, all coenocytic: (1) vertically oriented sporangiophores that bear at their tip a round structure that produce numerous asexual spores, (2) root-like 'rhizoids' located below the sporangiophores. They are imbedded in the substrate and allow the sporangiophores to grow upward (3) horizontally running 'stolons' that spread the fungus laterally and produce sporangiophores and rhizoids where they attach to the substrate. Only within the the spore producing structure are cell walls formed around individual nuclei, forming uninucleate cells which develop into spores and are dispersed.

Sex and reproduction

Rhizopus reproduces asexually by producing sporangia at the end of sporangiophores. Sporangia open to release numerous spores. Occasionally hyphae of two different mating types ('+' and '-') encounter each other and, under appropriate conditions, will induce each other to grow together to effect sexual reproduction. The hyphae meet and fuse; cross walls are formed on each side of the junction, creating a cell that contains haploid nuclei from each of the mating types. Pairs of nuclei, one from each mating type, are formed and fuse to form multiple diploid nuclei. All this occurs as the cell containing the now diploid nuclei develops into a zygospore with a thick cell wall with projections extend-



ing outward. The zygospore typically becomes dormant and the hyphae connected to it die. The zygospore can be dispersed by wind or water before any growth occurs. When it germinates a single filament emerges, forming a sporangiophore with a spore producing sporangium at its end. As this develops, the diploid nuclei undergo meiosis, creating haploid nuclei, each of which develop cell walls and forming spores that are subsequently dispersed when the sporangium splits open at the end of its development.

Matter and energy

Rhizopus is a heterotroph, like humans, but it digests food **outside** of the organism, not **inside**, as is the case for most familiar animals. Both fungi and humans secrete enzymes to break down food but humans secrete the enzymes inside a tube running through their body, while fungi secrete enzymes into the environment that they live in. After food has been broken down it can be absorbed by the heterotroph and utilized either materially, to form biomolecules to increase the size of the heterotroph, or energetically, being oxidized in cellular respiration to provide energy sources (ATP and others).

Interactions

Bread molds like *Rhizopus* are very important heterotrophs who collectively eat a great deal of organic material, thereby releasing nutrients that autotrophs can use. But they also destroy substantial quantities of stored food. Occasionally bread molds, including some forms of *Rhizopus*, can cause diseases of both plants and animals. Because *Rhizopus* is relatively easy to culture, it is used industrially to carry out some important chemical conversions, e.g. the conversion of plant steroids into specific chemicals like cortisone and the production of fumaric acid from sugar. *Rhizopus* is also used to produce tempeh, a soybean 'curd' food consisting of crushed soybeans partially decomposed by *Rhizopus* and held together by fungal hyphae.

Further Reading

- "How to Make Tempeh" by Emily Han
    - https://www.thekitchn.com/how-to-make-tempeh-cooking-lessons-from-the-kitchn-202369

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RICE

Rice is our most important cultivated plant, feeding more people than any other crop. It is a n annual or short-lived perennial grass species native to Asia. Its domestication (i.e. cultivation and modification by humans) started 8 to 13 thousand years ago. Much of the world, especially Asia, has rice as its primary food source and rice production is critical for feeding the world. Rice requires warm, moist conditions for growth and is grown world-wide in tropical and warm temperate habitats. As is the case in all 'cereal grains' the 'cereal'— the portion eaten — is a one-seeded fruit with the cells of a very thin fruit fused to those of the seed coat.

Taxonomy and Phylogeny

Oryza sativa is by far to most utilized rice species, although a second species (*Oryza glaberrima*) is grown in western Africa. 'Wild rice' (*Zizania aquatica* and *Z. palustris*) are in the same tribe (a level of classification between genus and family) but are not generally considered a type of rice. Wild rice was and is harvested by Native Americans and has a very limited amount of production, being used primarily for the gourmet food industry. Virtually all of the world's production of rice is *Oryza sativa*, and there are numerous varieties. (The Rice Association states that there are over 40,000 varieties and if you visit a grocery store you might see a dozen or so different types.) *Oryza* is in the monocot group and is in the grass family (Poaceae).

Structure

Rice has a typical grass structure with a series of leaves that form a false stem through which emerges the main stem when the plant flowers and fruits. Although there are some perennial varieties, most rice varieties are annuals with the plant senescing as it develops fruit. The few perennial varieties have annual shoots but are able to sprout new stems from a below-ground shoot system. Particularly significant to its growth in flooded conditions is the fact that the leaves have a thick cuticle and a vertically corrugated surface that allows the grooves to form air-filled capillaries. These allow for the movement of both oxygen and carbon dioxide.

Sex and reproduction

Rice reproduces sexually, producing bisexual flowers that develop into fruits (cereal grains) after pollination and fertilization. As is the case for most grasses, pollination is by the wind and the flower has features to promote pollination: long stamens that are exerted (extended out of) the flower and elongated stigmas that also extend out of the flower. Most rice varieties are annual and show little vegetative spread. But perennial rice varieties do spread laterally below ground and can produce of new erect branches after the first is harvested. In this manner the plant may yield crops for up to 30 years. Rice is difficult to propagate vegetatively and most rice that is planted is first sprouted from seeds and then transplanted as seedlings.

Flowering rice with stamens exerted making wind pollination much more possible. Not shown are exerted stigmas which usually appear after the stamens senesce.

Matter and energy

Rice is a photosynthetic autotroph that uses the C 3 photosynthetic pathway. Like all plants, rice requires 14 mineral elements in order to grow, with nitrogen often being the limiting factor for growth and crop yield. In common with most plants, rice can acquire minerals that are not essential, including minerals that are toxic to the plant and/or toxic to organisms that eat the plant. An example is arsenic. Arsenic is not required by rice or by any plant, but is required in trace amounts by at least a few animals. Arsenic is sometimes accumulated by plants, occasionally to levels that some consider unsafe. Rice is a crop that is much more likely to accumulate arsenic than other crop species, primarily due to the fact that it is usually cultivated in aquatic situations that can promote arsenic availability. While no one is stating that all rice should be avoided, there are some concerns being raised and the arsenic content of rice is being monitored.

Interactions

Like wheat and corn, the most significant of rice's interaction is with humans: their efforts to cultivate rice are of overwhelming significance to the plant. Three other interactions related to its cultivation are worth noting:

- flooding is not required by rice but it is an effective weed prevention technique. Most weeds (and plants in general) do not thrive under flooded conditions, hence the practice of flooding rice paddies cuts down on the number of competitors that rice must face.
- Rice is affected by many pests/diseases including fungi, bacteria and viruses.
- one plant that does thrive in flooded conditions and that is often present in rice

paddies is *Azolla*, a small, floating aquatic fern. *Azolla* harbors a cyanobacterial symbiont that is capable of fixing nitrogen, and *Azolla's* presence can increase rice yield substantially while avoiding the cost of nitrogen fertilizer.

Azolla (sometimes called mosquito fern) is a water fern with very small leaves. It grows on the surface of bodies of water, including rice paddies.

Further Reading

- "How Rice Grows" by ThinkRice. Rice cultivation.
  - https://www.usarice.com/thinkrice/discover-us-rice/how-rice-grows

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RUST FUNGI (ORDER PUCCINIALES, FORMERLY UREDINALES)

Certain stages of rust are often brightly orange colored.

Rust fungi are a common, interesting and economically significant group of fungi. They are obligate parasites of flowering plants, including a number of important crop species: corn, wheat and most cereal grains. Many rust fungi are heteroecious, meaning that they alternate between two hosts. Others are autoecious and only infect one type of host plant. They are particularly challenging to study because, unlike most fungi, which can be cultured on nutrient media, rust fungi can only be grown on living plants, so in order to grow the fungus you have to grow the plant.

Phylogeny

The Pucciniales are an order (i.e. a group of related genera) in the Basidiomycota (club fungi). The group had long been recognized based on their behavior (life cycle) and the structures that they produce on their host plants. Modern molecular studies have confirmed the group as a phylogenetic entity. Many of the structures produced by rusts are orange, hence the common name 'rust fungi'.

Gall caused by a rust fungus on a juniper tree.

Structure

Many of the structures of these fungi are small and not readily observed without a microscope, but some result in the production of characteristic galls on their host plants. A particularly significant feature of these fungi is an haustorium, the structure that occurs inside infected cells and is constructed both of the membrane of the fungus and that of the host plant cell. It is through this haustorium that nutrients pass from the plant to the fungus, allowing it to grow and reproduce.

Sex and reproduction

Rust fungi life cycles are complex. They have multiple stages, typically four or five, that are distinguished by a number of features, including the host plant on which it grows, the structures that are produced, and the 'ploidy' number of the cells (whether they are haploid, diploid or dikaryon). Most of these stages start and end with a type of spore, hence rusts typically produce four or five different spore types and often have a spore produced on one plant species (e.g. hawthorn trees) that is only capable of infecting another species (e.g. juniper trees).

Matter and energy

The brown structures on juniper is a gall produced by a rust fungus that for a brief time in the spring produces large orange colored gelatinous cones (see picture above).

These fungi are heterotrophs that feed upon material produced by other living organisms. They are unusual because they can only be fed by living cells of their host. Even though the nutrients that they need (e.g. sugars, amino acids) might be supplied from non-living sources, these 'obligate biotrophs' cannot absorb nutrients except from the haustorium, the structure produced inside a living cell of its host.

Pictured above is a juniper branch with dormant gall caused by a rust fungus. For a brief period in the spring it turns bright orange (also picture above) and produces 'horns' from which spores are dispersed that infect its alternate host, which may be apple, crab apple, hawthorn or a number of other species. The leaf on the right is a crab apple showing galls on the underside of the leaves. Often the top of the leaf shows orange spots. Spores produced by the galls infect juniper, completing the life cycle.

Galls on the underside of a hawthorn leaf, an alternate host for the juniper rust.

Interactions

Depending upon the rust species, the impact on the host can vary from negligible to devastating. Rust diseases are very significant to several crop species including wheat, corn, coffee and white pine, where they can have serious economic impact. In the northeastern U.S. rust fungi are commonly seen on both hawthorn and its alternate host, juniper, and also on blackberries (this species is autoecious and has no alternate host).

Some of the spores are produced in a sugary substance (nectar) that attracts insects who feed on the nectar and can transport the spores to other plants.

Further Reading

- “The Rust Fungi” by Kolmer, Ordonez, and Groth
  - http://www.researchgate.net/publication/227991330_The_Rust_Fungi
- “Cedar Apple Rust (*Gymnosporangium juniperi-virginianae* Schwein.)” by David Taylor
  - https://www.fs.fed.us/wildflowers/plant-of-the-week/gymnosporangium_juniperi-virginianae.shtml
- “Stem rust of wheat” by Schumann and Leonard
  - https://www.apsnet.org/edcenter/disandpath/fungalbasidio/pdlessons/Pages/StemRust.aspx

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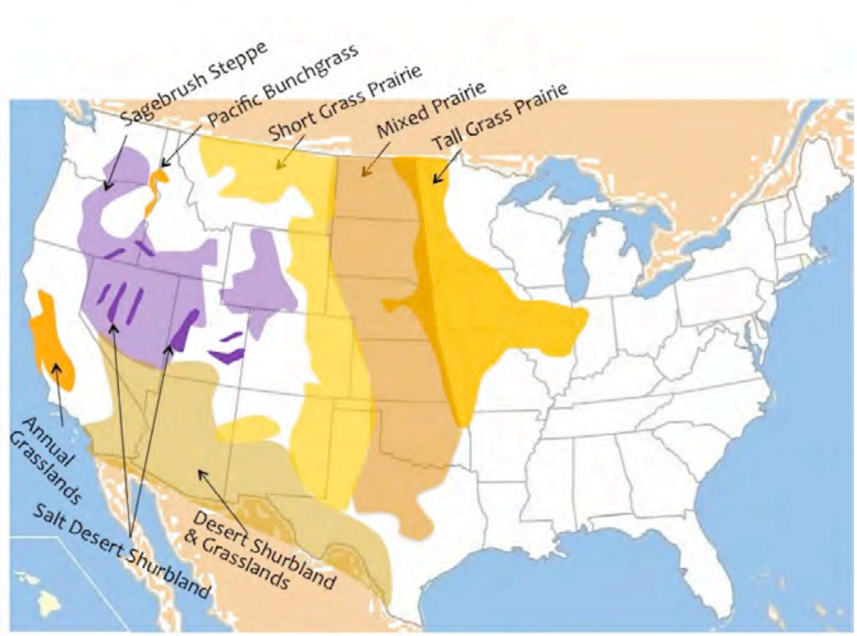
- Cedar apple rust on shimpaku juniper © Littleinfo is licensed under a Public Domain license
- Gymnosporangium juniperi-virginianae gall © Dehaan is licensed under a CC BY (Attribution) license
- Cedar apple rust heavily infected leaf underside © Littleinfo is licensed under a Public Domain license

SAGEBRUSH



Map of rangeland ecosystems of North America.

Sagebrush (*Artemisia tridentata*) dominates large portions of western U.S., regions that are too dry to support forests or grasslands. Similar areas are found in several other parts of the world (central Asia, southern South America, southern Africa) and are sometimes described as a 'shrub-steppe' community. Many of these areas are also described as 'cold deserts' with low rainfall and cold winters. Interestingly, although these areas do not support trees, smaller woody plants with multiple branches (i.e. shrubs) are successful.

Phylogeny

Artemisia is a large genus in the sunflower family (Asteraceae) of the angiosperm (flowering plant) group. There are 200-400 species depending upon how much a worker decides to 'lump' groups together. Many members of the genus are herbaceous, including several cultivated species: *A. drucunculus* is the source of the spice tarragon; *A. absinthium* (aka wormwood) is used to flavor some wines and to produce the liquor absinthe; *A. stelleriana* ('dusty miller') is a common ornamental plant; *A. vulgare* (mugwort), is a common weed. All members of the genus produce chemicals that are aromatic (in an olfactory sense), hence their use as flavorings. Some of the chemicals produced by *Artemisia* have been used medicinally (either directly or after some chemical modification) to treat malaria, internal parasites and morphine addiction. The common name sagebrush comes from the superficial similarity in scent with the herb sage, an unrelated species. The common name sagebrush is applied to a group of roughly twenty species of shrubs found in the western U.S.

Structure

Shrubs are woody plants that have extensive branching and do not grow particularly tall. Sagebrush is rarely over two m tall and, although it often has a main stem, it branches extensively and may send up multiple stems from its base. Because they rarely have taller plants around them, shading is not a problem and their spreading habit allows them to intercept more sunlight. Although woody, they have an unusual pattern of secondary growth where the vascular cambium often does not form a complete ring around the stem/branch, producing branches that are not round in cross section. Sagebrush leaves are evergreen, roughly five cm in length, have three 'teeth' at the end and have a whitish 'bloom', the result of many small hairs. The physical structure of sagebrush is important to a wide variety of other species in providing an improved thermal environment both in the summer through shading, and in the winter by reducing wind speed and convective heat cooling. Sagebrush roots often penetrate several meters into the soil to obtain water. They also produce a root system closer to the soil surface (less than a meter) and studies have shown that at night sagebrush carries out 'hydraulic lift', moving water that actually ends up moistening surface layers of the soil and providing water to both sagebrush and potentially to other plants.

Sex and reproduction

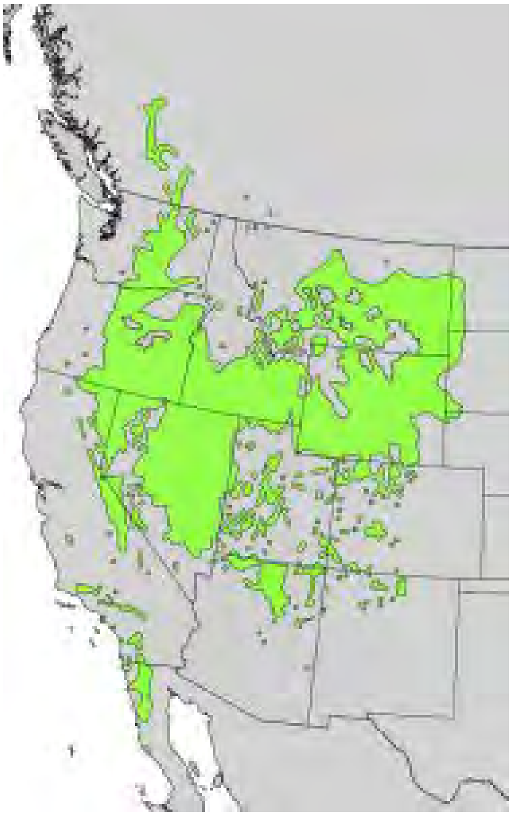
Sagebrush is a typical angiosperm, producing spores in flowers that develop male gametophytes (pollen) that are generally dispersed to other flowers where they complete their development by growing to the location (an ovule) of the female gametophyte (embryo sac) that has developed from a haploid spore. Members of the Asteraceae have ‘flowers’ that are actually inflorescences. Many familiar members of the Asteraceae (asters, sunflowers) have two types of flowers in the inflorescence: ray flowers (‘petals’) and disk flowers. Other members of the family (e.g. dandelion) have only ray flowers. Sagebrush represents a third type of Asteraceae inflorescence, one that has only disc flowers. Sagebrush is also able to reproduce asexually by sprouting from underground rhizomes.

Matter and energy

Sagebrush is a photosynthetic autotroph that uses the C 3 photosynthetic pathway.

Interactions

Sagebrush is often a dominant species in the areas where it grows and is an extremely important species to these communities, providing food for animals including: numerous insects, pronghorn antelope, rodents, and birds (e.g. sage grouse). The plant is not desir-



Distribution map for Big Sage
(*Artemisia tridentata*)

able for ranchers because cattle avoid the bitter foliage and considerable effort has been taken to remove sagebrush and replace it with more palatable species. But efforts are underway to preserve sagebrush and the unique habitat it is associated with, known as 'the sagebrush sea'.

Further Reading and Viewing

- Sagebrush ecology
  - https://cpw.state.co.us/Documents/WildlifeSpecies/Sagebrush/CHAPTER2overviewsagebrushecosystems.pdf
- "Why Care About America's Sagebrush?" by U.S. Fish & Wildlife Service

  - https://www.youtube.com/watch?v=O49OOmMXdZw

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SARRACENIA, A CARNIVOROUS PLANT

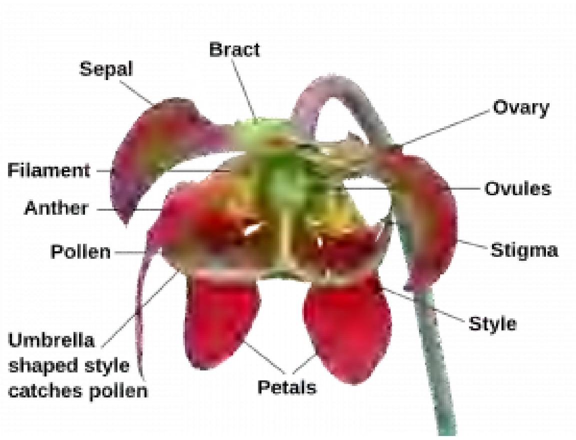
One of the more common groups of carnivorous plants in North America is the genus *Sarracenia*. Carnivorous plants of various types have evolved independently at least seven times. One category of carnivorous plants are those that produce pitchers, a structure that collects water and has other features that enhance the likelihood of trapping insects in that water. Carnivorous plants utilizing pitchers evolved independently in several different plant families. Although insects are the primary 'prey', occasionally frogs and even mice are captured. Death is not directly caused by actions of the plant but is the result of 'drowning' or an inability to escape to feed themselves. Decomposition of the prey is accomplished primarily by microorganisms living in the pitcher but may be aided by enzymes secreted by the plant. In addition to pitchers, carnivorous plants may capture prey by glue mechanisms (e.g. sundews, bladderworts) or mechanical traps (Venus flytrap, bladderworts). Carnivory is associated with habitats that are nutrient poor, generally because the soils are acidic and oxygen-poor (e.g. bogs), conditions where decomposition and the consequent release of nutrients, is limited. The pitchers are habitats on the plant where conditions for decomposition are more favorable and released nutrients are directly absorbed by the plant through the leaves or leaf parts that form the pitcher.

Taxonomy and Phylogeny

Carnivorory is found in over 500 plant species, in over 10 genera and over 10 families in both the monocot and eudicot groups. There is one species of monocots that produces pitchers but most are edicts, found primarily in two unrelated families, the Nepenthaceae, found in Africa, and the Sarraceniaceae, found in both North and South America. The plants described here are in the genus *Sarracenia*, which has about ten species, all in North America.

Structure

The pitchers are highly modified leaves whose margins are sealed for most of its length, creating a water retaining pitcher with a short unsealed terminal portion forming a flange at the top. Leaves occur in clusters on a short vertical stem rising from a rhizome. Flowers are very large and observers often don't recognize that they are part of the same plant that is producing the pitchers.



Reproduction

Sarracenia is a typical flowering plant, producing seeds, composite structures with an embryo, stored food and a protective seed coat. The seeds of *Sarracenia* have a rather limited dispersal ability. It can also spread vegetatively by means of its rhizomes.

Matter and energy

Carnivorous plants nicely reflect the contrast between heterotroph and autotroph nutrition. When heterotrophs 'eat' something, they acquire both food (i.e. carbohydrates and other materials to burn in cellular respiration) and also nutrients (i.e. 14 minerals) that all life requires. In contrast, autotrophs make their own 'food' (carbohydrates), generally in photosynthesis, and need to acquire minerals in a completely distinct process that requires specialized structures, roots. Carnivorous plants don't 'eat' in the same sense as heterotrophs; they derive no carbohydrates from the process. They 'eat' solely to acquire mineral elements because they live in situations where the standard structure of nutrient acquisition (roots) is of limited effectiveness. Pitcher plants have reduced levels of photosynthesis because, although green, leaves are not displayed in a way to maximize light acquisition. If pitcher plants are grown in environments with higher levels of nutrients (available from the roots) they reduce the size and number of pitchers, allowing them to increase photosynthesis.

Interactions

The pitcher provides a habitat for a variety of decomposer organisms: bacteria, protozoans, water molds and others. In fact the pitchers have their own food webs with not only decomposers but also organisms that feed higher up on the food chain: rotifers, midge larvae and others. Several mosquito species specialize in laying their eggs in pitcher plants and their larvae are often the 'top carnivore' in the ecosystem. The midge and mosquito larvae are adapted to aquatic conditions and are not killed in the pitchers.

Further Reading and Viewing

- "Genlisea: A carnivorous plant acting as a trap for Protozoa" by Wilhelm Barthlott et al. A carnivorous plant with a very different type of trap.
  - http://wolfbat359.com/genlisea.htm
- "Plants Are Cool Too! "The Pale Pitcher Plant" (Episode 1 – Sarracenia alata)" by BotanicalSociety
  - https://www.youtube.com/watch?v=uak3m_q-HD0
- "Lifeform of the week: Carnivorous plants" by Alex Reshanov. Site with the discussion of a variety of carnivorous plants.
  - https://earthsky.org/earth/lifeform-of-the-week-carnivorous-plants-are-out-for-blood/?utm_source=EarthSky+News&utm_campaign=16cf37d802-EarthSky_News&utm_medium=email&utm_term=0_c643945d79-16cf37d802-393701925

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- Sarracenia oreophila © Noah Elhardt

SEAWEED, FUCUS: A BROWN ALGAE

Fucus is representative of an interesting group of organisms that are commonly seen attached to rocks and visible at low tide in the intertidal zone. Most of the organisms called 'seaweeds' are brown algae, although some are red algae and a few are green algae. Like most (but not all) brown algae, *Fucus* is a large, multicellular organism that well-adapted to life in intertidal and shallow coastal waters, most commonly in relatively cool waters.

Taxonomy and Phylogeny

The brown algae are a small group of eukaryotes who traditionally were placed in their own phylum, the Phaeophyta, sometimes along with two groups of primarily unicellular algae, the golden algae and the yellow-green algae, based on similarities in pigmentation and other factors. Most modern treatments do not elevate this group to the phylum level but combine it with other 'heterokonts', a group defined by having two characteristic flagella, one longer than the other. The heterokonts (sometimes called the Stramenopiles) also includes diatoms and the heterotrophic water molds (Oomycota). The pigmentation of photosynthetic stramenopiles is similar to that of the coccolithophores (haptophytes) and the cryptophytes. This may not represent a common phylogeny but instead that all three groups separately became photosynthetic by acquiring the same photosynthetic endosymbiont. The photosynthetic members of these groups are thought to be produced by secondary endosymbiosis and their chloroplasts have four membranes (see discussion in the article on diatoms).

Structure

Typical of most brown algae *Fucus* is truly multicellular, and has three distinct multicellular organs: a holdfast, that attaches the organism to a substrate; flattened, dichotomously branching stems/blades (similar to thalloid liverworts) that carry out photosynthesis; and air bladders, often part of the stems, that carry the blades upward in the water column. Brown algae have transport systems that allow photosynthate from the blade to be distributed throughout the plant.

Reproduction

Most brown algae are sexual and exhibit alternation of generations. The 'dominant' (i.e. larger and more visible) stage is usually the sporophyte (diploid) stage but there are some brown algae that show isomorphic alternation of generations (the sporophyte and gametophyte look identical) and a few where the gametophyte stage is dominant. Rockweed (*Fucus)*, shows yet another life cycle, one like humans, with no alternation of generations and where the only haploid cells are gametes. In *Fucus* the gametes are distinct from one another (egg, sperm) and in some brown algae they all look the same (isogametes). Within the brown algae flagellated cells are common and include sperm, isogametes and zoospores, which are mobile cells that can attach to a substrate and grow into a new organism.

Matter and energy

Fucus is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and as building materials to synthesize a variety of biomolecules. The brown algae produce a distinct form of a carbohydrate storage polysaccharide called laminaran, made up of glucose units connected by a *beta* 1-3 linkage, rather than the *alpha*, 1-4 linkage found in starch. They also have high concentrations of mannitol which serves as a transport carbohydrate, a role occupied by sucrose in most plants.

Interactions

Fucus is is especially important in the intertidal zone, providing food for a number of organisms and habitats for others.

Further Reading

- “Fucus” by M.D. Guiry
    - http://www.seaweed.ie/algae/fucus.php

Media Attributions

- Fucus gardneri rockweed © Steve Lonhart / NOAA MBNMS is licensed under a Public Domain license

SENSITIVE FERN

Onoclea sensibilis

Sensitive fern is a very common fern throughout most of the country east of the Rocky Mountains, occurring in wetter spots in the woods. It is an easily recognized fern, with a large leaf that shows the classic 'dissected' leaf pattern. In comparison with other ferns, note that the leaf on the right is dissected once into roughly 17 'leaflets' and that each leaflet is serrated with large rounded teeth. In other ferns the 'teeth' are more distinct, creating a leaf that may be 'dissected' or 'cut' multiple times, i.e. the leaflets have leaflets. Sometimes a fern leaf may be cut as many as four times (the leaf has leaflets, which have leaflets, which have leaflets, which have leaflets). (see wood fern).

Sensitive fern is a perennial plant with a below ground stem that lives for many years, sending up leaves each spring that senesce and wither in the fall.

Taxonomy and Phylogeny

Sensitive ferns clearly belong in the fern group, which most workers consider to be a phylum, the Pterophyta. Among other things the group is united in having vascular tissue but not producing seeds. Recently, many workers have lumped horsetails and 'wisk ferns' together with the ferns. While horsetails (one genus) and wisk ferns (two genera) are very small groups, the fern group is large (over 12,000 species) and possesses considerable diversity in form. Although most of the members of this group look 'fern-like', i.e. they are herbaceous with relatively large leaves that are dissected into leaflets, some ferns look very 'un-fern-like', including some that look a bit like clover (*Marsilea*), some that are tiny/small floating aquatic plants (*Azolla* and *Salvinea*) and some 'tree ferns' that are over

3 m tall and resemble palms because of their dissected leaves. Fern ancestry goes back to the Paleozoic, 350 million years ago.

Structure

Sensitive fern has an underground stem (rhizome) from which emerge the leaves, which, unlike some ferns, are not distinctly clustered together. While most ferns just produce one type of leaf that both photosynthesizes and also can produce spores, sensitive fern is dimorphic, meaning it produces two types of leaves that are specialized in their functioning: green leaves (on the left in the accompanying figure) that photosynthesize but produce no spores and separate spore-producing leaves that do not look much at all like leaves (on the right of the accompanying figure). The below ground stem (rhizome) lives for many years, sending up leaves each spring that senesce and wither in the fall. Other common dimorphic species are Ostrich fern, Cinnamon fern and *Marsilea* (water clover), while a number of other ferns (Christmas fern, Interrupted fern) have dimorphic leaflets, i.e. the leaflets of some of the leaves are specialized for spore production.

Reproduction

Like all plants, sensitive fern exhibits alternation of generations with a visible sporophyte and hard-to-find bisexual gametophyte that is small, uncommonly seen, and quickly over grown by the sporophyte that grows out from the archegonium. Sperm are flagellated and swim to the egg.

Matter and energy

Sensitive fern is a typical photoautotroph, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as both energy source in cellular respiration and as building materials to synthesize a variety of biomolecules. Note that the spore bearing leaf is in a sense a parasite on the photosynthetic part, relying on it for sugars to supply its energy and material needs. The same is true of flowers.

Interactions

Sensitive fern contains a number of toxins and is rarely grazed. It is poisonous to cattle, who by and large avoid eating it. Sensitive fern requires moist, shady conditions.

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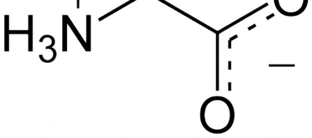
SOYBEANS (AND OTHER BEANS)

The United States leads the world in soybean production

Soybean, *Glycine max,* is an important annual crop throughout much of the temperate regions of the world but especially in the United States, which leads the world in soybean production, followed by Brazil and Argentina. Much of the U.S. production is exported. Soybean is particular notable because of the many ways it is used. It is eaten fresh and dry. The seeds can be processed to yield soy oil or to make soy milk (produced by grinding soy seeds in water, producing an emulsion of protein and oil). Soy milk is used to make tofu. The insoluble remnants of these extractions are used in animal feed.



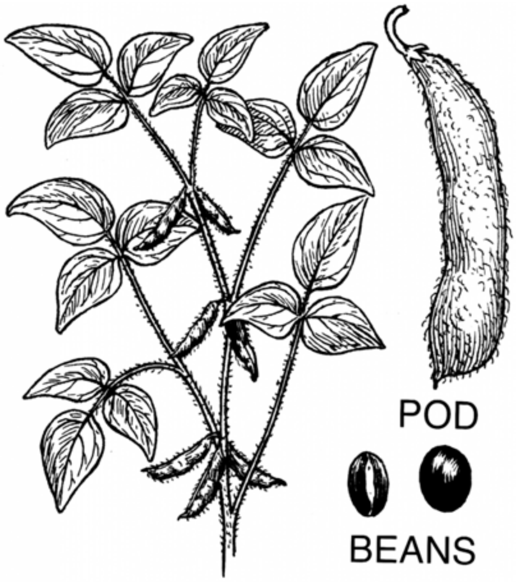
The amino acid glycine

Soybean shares a name (the genus name, *Glycine*) with one of the twenty amino acids, not because soybean is protein rich, although it is, but because of a connection to sweetness. In the 1700's Linnaeus gave a genus of plants the name '*Glycine*' because of the sweetness in the root of one of its species (not *G. max*). In the 1800's the chemical glycine (the amino acid) was isolated from gelatin, and because of its sweetness the chemical was given the name

Tofu

glycine. The sweetness found in plants of the genus *Glycine* is not due to the amino acid, it comes from sugars present in the roots.

Phylogeny



Soybean is a flowering plant (angiosperm) and is a dicot (eudicot) , in the Fabaceae, the pea family, a large and economically important family containing species that are used for food, medicine and lumber plus many species that are important ecologically. The cultivated species is derived from a wild ancestor, *Glycine soja,* which grows wild in Japan, Korea, China and Russia.

Structure

Soybean is an annual herbaceous species that typically grows to roughly one meter in height and may be branched or not depending on the cultivar and planting density. Leaves are compound and generally trifoliate. Small flowers are produced on short branch shoots growing from the axial buds at the base of leaves. Flowers are self fertile and develop into pods (the official fruit name is legume) that are typically less than 10 cm long and contain 2-3 seeds.

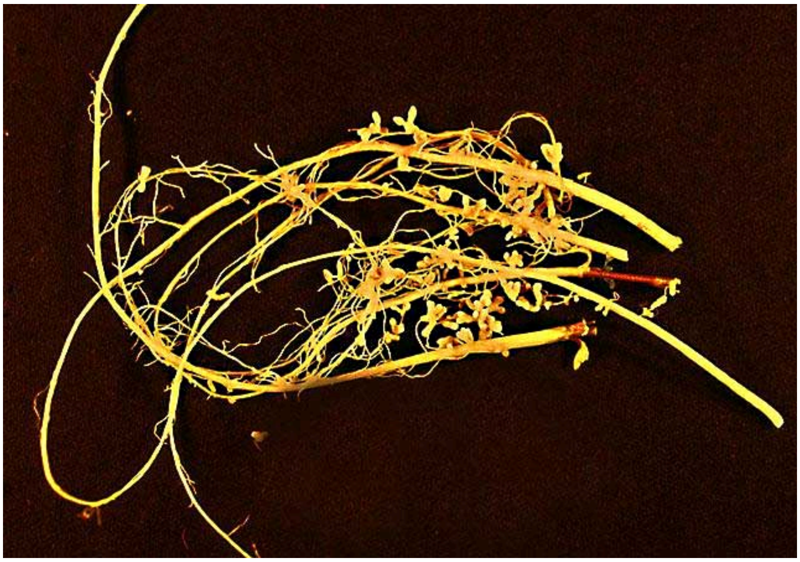
Self fertile flowers of the soybean plant

Sex and reproduction

It is a typical flowering plant with bisexual flowers that produce male gametophytes (pollen) and female gametophytes located in ovules present at the base of the flower, the ovary. The flowers are self fertile; pollen from a flower can be transferred to the stigma of the same flower and it will germinate, grow to the ovule, and fertilize the egg produced by the female gametophyte. Since meiosis does occur in the production of both gametophytes some variability results from the sexual process but much less than would occur if flowers were fertilized by pollen from different plants.

Matter and energy

Soybean is a photosynthetic autotroph which uses the C 3 photosynthetic pathway, producing sucrose that can be used as an energy source in cellular respiration or as a material source, providing carbohydrates. Like many members of the pea family, soybean often houses *Rhizobium* bacteria in nodules (galls) on its roots. The *Rhizobium* bacteria provide



Nitrogen fixing nodules on soybean roots

a source of nitrogen to the plant, but they also represent a sizable drain on photosynthate because substantial amounts are needed to 'feed' the bacteria, mostly to provide energy for the nitrogen fixation process. Whether or not the soybean benefits (grows more) from its interaction with *Rhizobium* depends on the amount of available nitrogen in the soil. But symbiotic nitrogen fixation by *Rhizobium* lessens the nitrogen fertilizer needs for growing soybeans and also enriches the soil with nitrogen for subsequent crops.

Interactions

Soybean is a short-day plant, although the specific requirements vary with cultivar. One of the reasons soybean is not grown near the equator is because the daylength is never sufficiently short to trigger flowering. In addition to the interaction with *Rhizobium,* soybean has significant interactions with a large group of pathogens and herbivores: nematodes, water molds (*Phytophthora*), rust diseases, a variety of bacterial diseases, and a large number of insect herbivores, most of which attack other crops as well.

Soybean leaves with rust disease

Other edible members of the pea family: beans and others

Like the grass family, the pea family (Fabaceae) is the source of a variety of edible crops. These are generally divided into ‘pulse’ crops where the seeds (often called beans) are harvested dry, and green vegetable crops that are harvested and eaten before drying. Some, like soybean and green beans may be harvested both ways.

Harvested green

- *Phaseolus vulgaris* — green bean, string bean
- *Phaseolus lunatus* — lima beans (sometimes called butter bean)
- *Pisum sativa* — peas
- *Glycine max* — soybean, but when harvested green, it is called edamame

Harvested dry

- *Glycine max* — soybean

- *Vigna unguiculata* — cowpea, including 'black eyed peas'
- *Vigna angularis* — adzuki bean
- *Vigna radiata* — mung bean
- *Cicer arietinum* — chickpea, garbanzo bean
- *Phaseolus vulgaris* — pinto bean, black bean, kidney bean
- *Lens culinaris* — lentil
- *Arachis hypogaea* — peanuts
- *Vicia fava* — fava beans

All of the seeds of the Fabaceae family contain secondary chemicals that can have toxic effects on humans, although most of the widely cultivated plants are generally not toxic to most people. Red kidney beans and lima beans should be thoroughly cooked before eating and fava beans are toxic ('favism') to individuals lacking a specific enzyme. Wild members of the pea family are commonly toxic and include 'locoweeds', rosary pea, some species of *Lathyrus*. Note that not all things called 'beans' come from members of the Fabaceae, e.g. castor bean, cocoa bean, vanilla bean, coffee bean.

Further Reading and Viewing

- "How to Make Tofu" by Ashley Adams
  - https://www.thespruceeats.com/how-to-make-tofu-1001574
- "History of Soybeans" by NC Soybean Producers Association
  - https://ncsoy.org/media-resources/history-of-soybeans/
- "Unlocking the Power of the Seed" by National Oilseed Processors Association. Soybean composition and the processing of soybeans.
  - https://www.nopa.org/resources/datafacts/soybean-composition/

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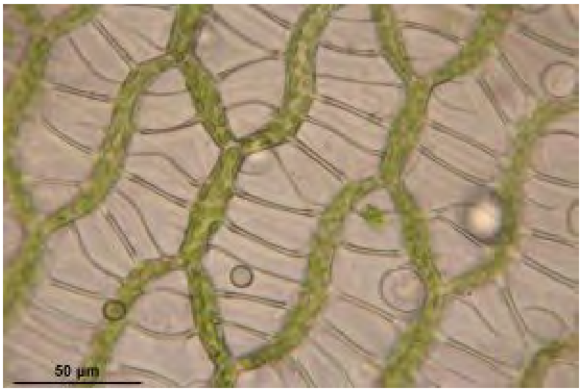
SPHAGNUM-PEAT MOSS

Peat moss

The genus *Sphagnum* is by far the most important non-vascular plant group on earth. The 120 species in the genus are primarily found in cool, moist habitats, mostly in the Northern Hemisphere (northern U.S., Canada, northern Ireland, Scotland, northern Europe, Siberia) but some do occur in the southern part of the Southern Hemisphere (Chile, New Zealand). The genus is important because it can dominate large areas and change conditions at these sites, making them less hospitable for some species and more hospitable for others.

Phylogeny and taxonomy

Sphagnum is the only genus in the family Sphagnaceae, which is the only family in the Class Sphagnales, which is the only class in the order Sphagnopsida, i.e. a single genus is the only representative of an entire Class. *Sphagnum* is distinctive in form. Its distinctiveness is also borne out in molecular studies of the group.



Structure

The gametophyte (haploid form) generally occurs in dense mats. Individual plants may be quite long, over 30 cm, but this is including the slowly decomposing basal parts, with the green portion typically 10 cm or less. Plants are erect and have a cluster of branches near the top that give it a characteristic look. The leaves of sphagnum consist of strands of narrow living cells with abundant chloroplasts, surrounding bands of much larger cells that quickly die after being produced. The ability of sphagnum to hold so much water is related both to the large quantity of non-living cells that can absorb water and also to the fact that the mat of plants itself can hold water in between individual plants.

The sporophyte is less commonly seen and includes a roughly spherical capsule that opens explosively to release spores. In most mosses (e.g. Polytrichium) the sporophytes (the diploid part) have two components: a stalk and a capsule situated at the top of the stalk. However, in Sphagnum the sporophyte is solely the capsule and the stalk that it sits on is haploid and part of the gametophyte.

Reproduction

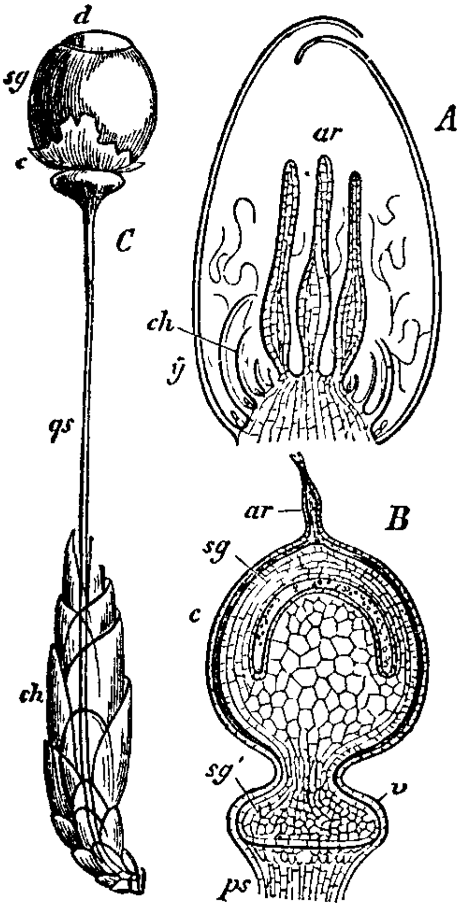
A Sphagnum gametophyte

Sphagnum exhibits the typical alternation of generations found in mosses, with a haploid gamete producing plant (gametophyte) that is relatively large, long-lived and noticeable, and a much smaller, shorter-lived diploid sporophyte that is produced on the gametophyte, produces spores, and then is shed.

Matter and Energy

Sphagnum is a photosynthetic autotroph, it makes food (carbohydrate) through the process of photosynthesis and then uses this carbohydrate both as a material to make biomoleules and also to provide energy for metabolic activities. For the gametophyte this is true throughout its existence. Although the sporophyte of many mosses is green and photosynthetic early in its development, most of the photosynthetic surface is in the stalk. For *Sphagnum* sporophytes with no stalk, the sporophyte contributes little or no carbohydrates to its livelihood and is totally dependent upon the gametophyte throughout its existence.

Mineral nutrition of mosses is different from that of vascular plants, whose roots obtain obtain nutrients from the soil solution. The source of mineral nutrition for most mosses is not the soil, it is precipitation (sometimes altered in chemistry as it flows down tree trunks) and dust. This is especially true for sphagnum moss because it generally occurs as a carpet sitting on top of a large mat of poorly decomposed material (usually sphagnum plants themselves). At least some species of sphagnum are unusual in their ability to use amino acids as a source of nitrogen in addition to nitrate and ammonia.



Sphagnum sporophyte development—A: three archgonia at the tip of a gametophyte stem, B: sporophyte structure, C: sporophyte located at the tip of a gametophyte stalk, labelled (qs). The structure labelled 'd' is the operculum cap that 'blows' off as spores are dispersed. There are two theories of spore discharge, one based on pressurization of the spore capsule as it matures and changes shape, the second argues that drying of the capsule generates tensions that eventually lead to rupture of the capsule. Recent research supports this latter view.

Interactions

Sphagnum interacts with other species a number of ways. Most significant is its ability to alter water and nutrient conditions on a site. Specifically, sphagnum can make areas of land waterlogged, acidic and nutrient poor. This is advantageous for sphagnum because it eliminates competitors that might shade out the sphagnum. It is also significant for other species (e.g. pitcher plants and sundews) that thrive in open, waterlogged habitats, again because potential competitors are kept at bay. Interestingly, not only can sphagnum make terrestrial habitats waterlogged it can also make aquatic habitats (e.g. ponds) somewhat terrestrial, by growing across the surface and producing a mat capable of supporting terrestrial plants, although the habitat is waterlogged and not truly terrestrial.

The remnants of bogs are often 'mined' for the un-decomposed material, called peat, that can be used as a fuel source. Like coal and oil, the energy captured in photosynthesis is still available in the peat because the plant material has not been oxidized in cellular respiration of decomposer organisms. Dried peat is also a common soil additive in gardening.

Further Reading

- "Sphagnum" by the Australian National Herbrarium, from their Australian Bryophytes pages:
  - http://www.cpbr.gov.au/bryophyte/ecology-sphagnum.html
- *Bryophyte Ecology* by Janice M. Glime. A Michigan Tech ebook that is a tremendous source of information on moss ecology.
  - http://www.bryoecol.mtu.edu

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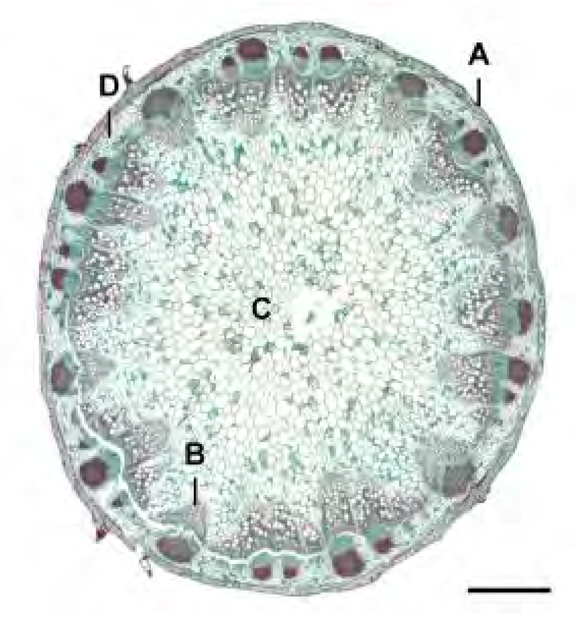
SUNFLOWER: HELIANTHUS ANNUUS

The sunflower is a familiar plant that has the distinction of being the only widely used crop species that originated in North America. Although Native Americans domesticated the plant and selected for plants with single heads and larger seeds, its initial use after being introduced into Europe was primarily as an ornamental plant in gardens. It became popular as a crop plant first in Russia, largely as a consequence of edicts from the Eastern Orthodox Church concerning diet restrictions during Lent. During Lent, consumption of oils from a variety of plants (e.g. olive, palm, sesame) was forbidden, but sunflower, a recent arrival, was not banned and sunflower became an important crop in Russia by being a source of oil during Lent. It is now the national flower of both Russia and the Ukraine. Early in the 20th century sunflower came back to North America as a crop grown primarily for its oil in both the northern U.S. and in Canada. In the southern hemisphere, Argentina is a major producer of sunflower. The oil from sunflower is used both in cooking and also industrially (e.g. as a base for paints). It can be used as a substitute for diesel oil directly or after first being converted to biodiesel. After oil has been extracted the remaining seed can be used for animal feed. To a limited extent sunflower seeds are eaten directly, especially by baseball players!

Phylogeny

Helianthus is a genus in the sunflower family (Asteraceae), one of the largest families angiosperms. There are roughly 70 species, both annual and perennial, with *H. annuus* (an annual) being the most important crop species. A perennial species (*H. tuberosus*), called Jerusalem artichoke, is occasionally grown for its edible tubers.

Structure



Cross section of sunflower stem showing epidermis (A), cortex (D), pith (C) and vascular bundle (B), with large cap of phloem fibers and lignified xylem vessels and trachieds staining red.

Sunflower is an herbaceous annual. Although wild representatives are usually branched, the cultivated form typically does not branch and consists of a single stem that may be well over two meters in height with the single large head whose actions inhibit the production of branches below.. The stem produces a vascular cambium but does not form wood (a continuous cylinder of secondary xylem) instead it adds to the existing vascular bundles. Although it does not produce wood, the stem is remarkably 'woody', meaning tough, durable and resistant to deformation. Most cells in the primary xylem and phloem are extensively lignified and produce a strong stem, able to stand several meters tall and hold a head, that may weigh as much as two kilograms, or multiple much smaller heads. The stem is often more than 5 cm in diameter, with most of the width from primary growth. The bulk of the stem is pith and the strength comes from a ring of vascular bundles near the margin of the stem.

Fields of mature sunflowers are striking because all the heads, regardless of the time of day, are facing the same direction, east. In contrast, younger flower heads, before they start to flower, show a daily movement, tracking the sun from east to west during the day and then returning to the east overnight. The control of the movement probably involves both an endog enous biological clock and a responsiveness to incident light.

The outermost 'petals' are ray flowers, with a large, petals extending radially. In the middle are hundreds of individual disk flowers, arranged in spirals.

The heads of sunflowers are a good place to observe the spirals associated with plant architecture. Spirals rotating in both clockwise and counter-clockwise directions are evident. The number of spirals usually relates to two numbers in the Fibonacci sequence (**momath.org/home/fibonacci-numbers-of-sunflower-seed-spirals/**). See also the following link connecting the Fibonacci series to the 'golden angle', an interesting mathematical and artistic concept (**www.mathsisfun.com/numbers/nature-golden-ratio-fibonacci.html**).

Sex and reproduction

Sunflowers reproduce utilizing seeds produced in the normal pattern for angiosperms. The flowers are characteristic of the Asteraceae family. The 'flower' is actually an inflorescence, a structure of several hundred flowers of two types: the 'petals' of a sunflower are ray flowers, with a large petal that is actually composed of five fused parts and is is asymmetrically oriented, extending out to one side of the flower. Ray flowers are often sterile, lacking both male and female parts. The central disk flowers that make up the bulk of the inflorescence have much smaller petals that are arranged in a ring. They are bisexual and have a distinct phenology (timing). For the head as a whole the central 'disk' flowers mature from the outside inward, i.e. the first flowers to open are on the outside. Each individual flower also has a pattern of development. The anthers mature first, making pollen available to pollinators, primarily bees. After the pollen has been available for several days a stigma pushes up through the ring of anthers. Self-pollination of a particular flower by itself is unlikely unless the flower has not been visited by pollinators, in which case there may still remain pollen that contacts the stigma as it moves upward. While the annual *H. annuus* must set seed to reproduce, the perennial *H. tuberosa* can reproduce via its tubers, which, like potatoes, are produced on underground stems (rhizomes) that allow the plant to spread laterally. This is part of the reason that *H. tuberosa* can be a problem weed.

Matter and energy

Sunflower is a photosynthetic autotroph which uses the C 3 photosynthetic pathway. Among other pathways, the sugars produced in photosynthesis are transported as sucrose from the leaves to developing seeds and then used to construct the oils present in the sunflower seeds. The conversion of sugars to fats requires energy (reducing power and ATP) and this is supplied by the oxidation of sugars.

Interactions

Sunflower probably represents a classic case in the evolution of crops. It is a 'weedy' species in an ecological sense, one that thrives in disturbed habitats. Because of this, it probably frequented the areas close to primitive human habitation. Subsequently humans recognized its utility and started actively cultivating it and thereby developing it as a crop. A similar scenario may also apply to wheat and other crop species.

Helianthus tuberosus flowers

Helianths tuberosus tubers (rhizomes)

Further Reading and Viewing

- “Types of Sunflowers” by Prairie California. Nice discussion of types of sunflower seeds, their oils, health considerations, and crop development.
    - https://prairiecalifornian.com/types-of-sunflowers/
- “How to Count the Spirals” by MoMath: National Museum of Mathematics. Spirals and the Fibonacci series.
    - https://momath.org/home/fibonacci-numbers-of-sunflower-seed-spirals/
- “Nature, the Golden Ratio, and Fibonacci too” by Math Is Fun
    - https://www.mathsisfun.com/numbers/nature-golden-ratio-fibonacci.html
- “Doodling in Math: Spirals, Fibonacci, and Being a Plant [Part 3 of 3]” by Vihart. Very interesting and fast moving video that gets at the mechanisms of the spirals.
    - https://www.youtube.com/watch?v=14-NdQwKz9w
- *The Sunflower* by Charles Heiser, ISBN 0806112299

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TAR SPOT FUNGUS

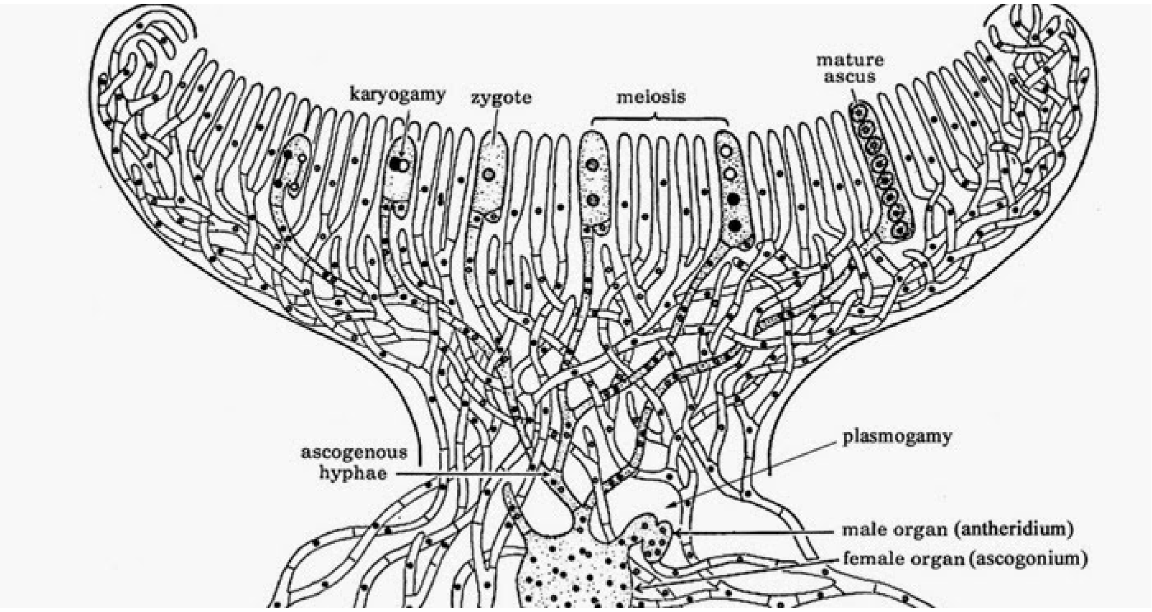
The fungus *Rhytisma* lives inside tree leaves and produces large black spots on the leaves late in the growing season (August and September) as the leaves start to senesce. The most common species in the northeastern U.S. occur on maples but there are other species that occur on other tree species. The black spots form when the fungus produces large black masses of hyphae ('stroma') that break through the epidermis of the leaf. In the spring of the year, spores produced in these black spots are released and can be dispersed by the wind. Some fortunate spores end up on newly produced leaves where they can germinate and penetrate through the epidermis to get inside the leaf. The tar spot fungus is an example of an endophyte, an organism (usually a fungus) that lives inside of plants. Generally endophytes are **not** very apparent and they are not generally thought of as causing disease. Some endophytes are even thought to be a positive presence, providing benefits such as disease and stress resistance while at the same time benefiting from being fed and protected by the plant

Phylogeny and taxonomy

Rhytisma is an ascomycete fungus. As is common for a number of fungi, *Rhytisma* was described with both a sexual form (placed in the Ascomycota) and an asexual form (placed in the Fungi Imperfecti) but it is now recognized that there is one entity that sometimes reproduces sexually and sometimes does not. (Placing fungi into phyla used to require the observation of sexual stages; and fungi lacking sexual stages were placed in the 'Fungi Imperfecti'). With modern molecular techniques fungi can be placed into groups without observation of the sexual stages.

Structure

Tar spot fungus consist of septate hyphae (i.e. filaments with cross walls) that spread through part but not all of the leaf that they have penetrated, typically spreading 1-3 cm. If sexual reproduction is to occur hyphae from two different mating strains need to find each other (i.e. both are present in the same leaf) and some of their hyphae fuse (plasmogamy) to form a dikaryon cell that grows to produce dikaryon hyphae where each cell has two haploid nuclei. In late summer both the haploid hyphae (i.e. those of each mating type) and the dikaryon hyphae intertwine to form a stroma, a thick mass of hyphae. Within the stroma are produced small, cup shaped 'apothecia'. Within these structures the tips of some of the dikaryon cells produce the the characteristic asci–elongate cells where karyogamy occurs to make the cell temporarily diploid. This is the only diploid cell produced by tar spot fungus or any ascomycete. The diploid nucleus undergoes meiosis followed by mitosis to produce a cell with eight haploid nuclei, each of which develops a cell wall to form ascospores. The ascospores of tar spot fungus are quite narrow and pointy.



A generalized apothecium, a cup shaped structure in which are born asci.

Sex and reproduction

Tar spot fungus can reproduce both sexually and asexually. Sexual reproduction, descibed above, is in a manner typical of Ascomycetes.

Matter and energy

Tar spot fungus is a herbivore, obtaining matter and energy from its host. Hyphae apparently can acquire nutrients from host cells without the presence of haustoria, evidently obtaining materials that 'leak' from cells. Because of the fungus's modest growth habits (it doesn't grow particular fast and does not grow extensively, i.e. it does not go through the entire leaf) there is minimal damage to its host.

Interactions

Recently some endophytes, like tar-spot fungus, have been recognized to benefit their host in a variety of ways: by producing toxins that deter other herbivores, by somehow making their host more able to fight off other diseases, by making their host better able to withstand harsh environmental conditions (e.g. drought).

Another endophytic interaction that you may have heard of is 'St. Anthony's fire', a human disease caused by the consumption of grain (e.g. wheat, rye) infected with another endophytic fungus. The fungus produces alkaloids related to LSD that can cause hallucinations and death if grain harvested from plants infected by the fungus are consumed.

Further Reading

- "*Rhytisma acerinum* and *Rhytisma punctatum*, two causes of Tar Spot of maple" by Heather Hallen Adams and Tom Volk for the Fungus of the Month for October 2007
    - http://botit.botany.wisc.edu/toms_fungi/oct2007.html
- "Endophytes: A Treasure House of Bioactive Compounds of Medicinal Importance" by Sushanto Gouda et al. Nice review article.

    - https://www.frontiersin.org/articles/10.3389/fmicb.2016.01538/full
- “Multifaceted Interactions Between Endophytes and Plant: Developments and Prospects” by Ekta Khare et al. Interactions between endophytes and plants.
    - https://www.frontiersin.org/articles/10.3389/fmicb.2018.02732/full

THERMUS AQUATICUS

A Yellowstone hot spring, comparable to the one where Thermus aquaticus was first discovered.

T. aquaticus is the organism that makes PCR (polymerase chain reaction) possible. It is an 'thermophile', capable of living in high temperatures, specifically at temperatures over 70 C (150 F). It was discovered in 1969, at a time when biologists assumed that no living thing could survive at temperatures over 55 C. While *Thermus* can 'only' withstand temperatures up to 80 C, other organisms can live at temperatures even closer to the boiling point of water.

Phylogeny

Unlike many thermophilic (heat-loving) prokaryotes *Thermus* is not in the Domain Archaea but is a genus in the Domain Bacteria. Along with one other genus *Thermus* forms a distinct and ancient lineage within the bacteria.

Structure

Thermus aquaticus cells are rod-shaped, non-flagellated gram negative bacteria often occurring as filaments. Gram negative bacteria have a peptidoglycan cell wall layer sandwiched between an inner and outer phospholipid membrane.

Sex and reproduction

Like all bacteria, *Thermus* are not sexual, but they are capable of exchanging genetic material by other means.

Matter and energy

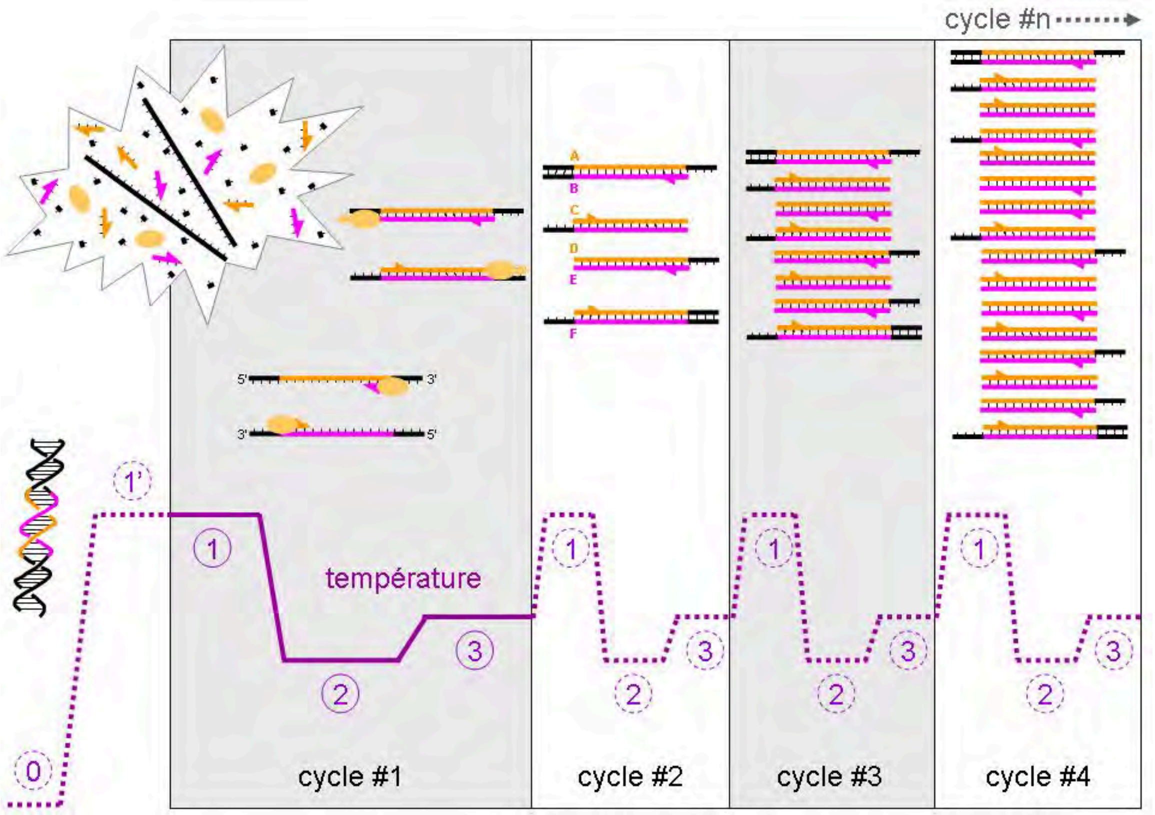
Thermus is a heterotroph and acquires matter and energy by absorbing organic compounds from its environment, organic compounds that that are derived from other living organisms either by excretion or degradation of the biomolecules that once was part of an organism.

Interactions

Thermus is found in sites with elevated temperatures, hot springs and near thermal vents in the oceans. It occasionally is found in hot water systems and in areas of thermal pollution (e.g. near power plants). It feeds off organic matter produced by other thermophiles including both members of the Domain Bacteria (including some photosynthetic cyanobacteria) as well as members of the Domain Archaea (see Halobacterium)

PCR

In the last 20 years the PCR technique has revolutionized biology research and plays a very significant role in 'applied biology' (e.g. testing for Wuhan flu, paternity testing, diagnosis of hereditary disease, forensic science, security). These are situations where having multiple copies of a certain portion of the DNA molecule are needed and PCR techniques allow the synthesis of multiple copies of a specific part (often a 'gene') of DNA.



PCR technique 1 = melting (T ~ 90°C, 2 = annealing (T ~ 55°C, 3 = extension (T~ 72°C. Note that there are two primers, one for each strand. In cycle 1 both before (center) and after (right side) extension are shown. After cycle #1 only the final products after that cycle are shown. Note that the DNA polymerase moves 3' to 5'.

Synthesizing DNA is accomplished by the DNA polymerase enzyme, an enzyme found in all cells. In the normal process carried out by all cells, two enzymes (topoisomerase, helicase) separate a portion of double strand DNA into two single-strands and DNA polymerase is then able to extend DNA strands complementary to each of the single strands that have been revealed. In PCR, heat is used to separate ('melt') the double stranded DNA into single strands. Then the mixture is cooled slightly to allow the two 'primers' to bind (anneal) to the single strands. The primers are two short sequences of single stranded DNA (one for each strand) complementary to each end of the gene that is to be copied. The annealing of the primers produces a two stranded 'starting point' from which DNA polymerase can add nucleotides, thereby extending a DNA molecule complementary to the existing single strand. The DNA polymerase from *Thermus aquaticus* (called 'Taq polymerase') is useful in this process because it can be heated to a temperature high enough to melt DNA yet is still able to function. The PCR machine (called a 'thermocycler') performs repeated cycles of high temperature, melting the double stranded DNA, then cooling slightly to allow primer sequences to bind 'anneal' to the single strand, and thereby allowing Taq polymerase to work to extend the primer strand in a manner complementary to the single strand. This process (a thermal cycle) is repeated multiple times to get multiple copies of the DNA under study. Although the technique is feasible using polymerases not from thermophilic bacteria, one would have to add additional enzyme after each heating because most enzymes are destroyed by the temperatures required to melt double stranded DNA. Taq polymerase can be added at the beginning and it remains stable through the multiple cycles (usually about 30) needed to produce enough (usually millions!) copies of the gene.

Further Reading

- "Life in Extreme Heat" by Yellowstone National Park Service
    - https://www.nps.gov/yell/learn/nature/life-in-extreme-heat.htm
- "Yellowstone Hot Springs" by Microbe Wiki
    - https://microbewiki.kenyon.edu/index.php/Yellowstone_Hot_Springs

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WHEAT

Wheat should be familiar to everyone although perhaps only as a food and not very much as an organism. Wheat is one of the oldest crop species, originating in Turkey probably close to 10,000 years ago, although some researchers place its origin older. As described below what we call 'wheat' is at least three different entities, differing in chromosome number, evolutionary history and also features related to harvesting and baking.

Phylogeny and taxonomy

Wheat is a flowering plant. Multicellular, terrestrial, photosynthetic organisms (" land plants") are generally put in the Plant Kingdom. The most important group within this kingdom, based on a number of different measures (number of species, economic importance, ecological importance) is a group that produces flowers, (flowering plants = angiosperms = the phylum Magnoliophyta). Within the angiosperms there are two main groups, monocots and dicots (now called eudicots). Wheat is in the monocot grouping, generally considered at the class level (Liliopsida), although modern treatments recognize the group but may not assign it a particular rank. In contrast to the dicots, monocots are considered monophyletic (originating from a single ancestor) and therefore a sound taxonomic entity. In contrast, the old dicot group is not considered monophyletic. This is why the grouping 'eudicot' came into being, it contains just those dicots (almost all of them) that are united by being monophyletic. Wheat is in the Poaceae, the grass family, one of the four most important families of flowering plants and the family that includes all our important 'cereal grains' (wheat, rice, corn, barley, oats). There are several different species called 'wheat' and these are related by polyploidy: one is diploid (eikorn wheat), two are tetraploid (emmer and durum wheat) and one is hexaploid (bread wheat).

Structure

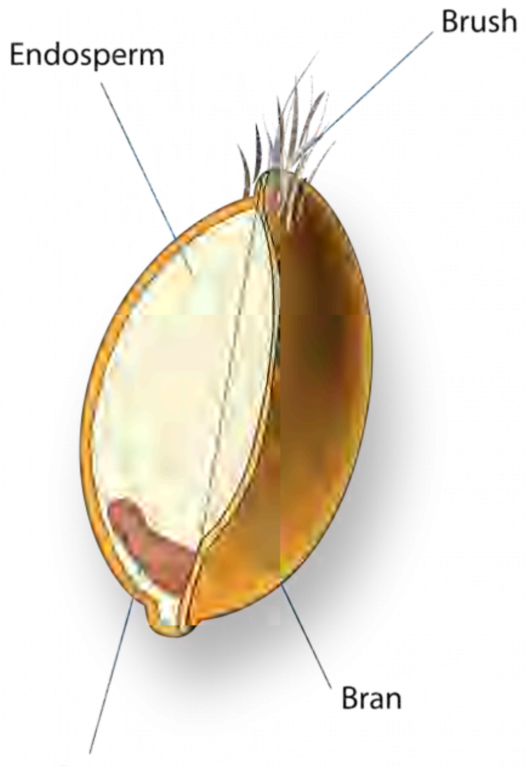
Wheat is a fairly typical 'herbaceous' (i.e. non-woody) plant. Like almost all organisms that are considered plants, wheat consists of cylindrical structures, shoots and roots. Both these structures have an embryonic region (apical meristem) at their tip that produces cells whose expansion elongates the cylinder. The shoot apical meristem also produces organs (leaves) that are typically broad and thin. The cellular organization of both roots and shoots shows a radial organization (i.e. a pattern from the inside to the outside) but the cells show few changes as you move up or down a root or shoot, except in the region close to the root or shoot tip where the cells are younger and have yet to develop some features. Given the proper stimulus, at least some of the shoots will develop into clusters of flowers (inflorescences) that will develop into fruits containing seeds. Grasses only exhibit primary growth, the growth resulting from the embryonic regions at the tips of roots and shoots, including branch shoots and branch roots. There is no secondary growth, growth that makes the roots and shoots of some plants wider and woody. Like most grasses, the wheat apical meristem does not elongate until the time of flowering and most leaves that the stem produces elongate before the main stem, producing what appears to be a stem but is actually a series of cylindrical leaf bases extending from the still unelongated stem.

Reproduction and sex

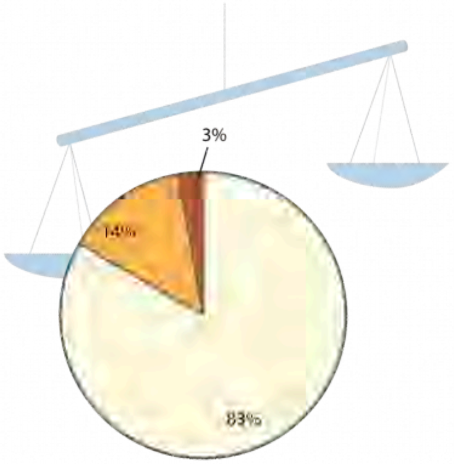
Wheat reproduces sexually in a manner typical of flowering plants. Seeds develop from the fertilized ovules present in the ovaries of flowers. All grasses produce flowers that have a single ovule per ovary and this develops into a one-seeded fruit with the fruit wall fused to the seed coat. A wheat seed consists of three parts: the embryo, stored food (endosperm) and a seed coat fused with with the fruit wall. These components are important to human nutrition. White flour is produced after milling the grains to remove: (1) the embryo, which is sold separately as wheat germ, (2) the seed coat / fruit coat, which is sold separately as wheat bran. The remaining endosperm is primarily starch but does contain roughly 10% protein, including two proteins that combine to form gluten as flour and water mixtures (dough) are massaged (i.e. kneaded). The germ represents only a small part of the fruit but it contains substantial amounts of protein, fats, minerals and vitamins. The bran is largely indigestible fiber but it does contain some protein and fat. This is what makes whole-wheat flour 'more nutritious', i.e. more protein, minerals, vitamins and fat than white flour. Unfortunately, 'more nutritious' also applies to fungi and bacteria; and whole wheat flour is considerably more likely to spoil than white flour, which is part of the reason white flour became favored. Other reasons were white flour's improved baking qualities and the ideal of 'purity'.

Matter and Energy

Wheat is a typical photosynthetic autotroph. Individual plants accumulate carbon dioxide from the atmosphere and use it to form carbohydrates that are both used to enlarge the plant (i.e. grow) and also to be 'burned' in cellular respiration to provide energy for the plant. Wheat is typical of seed plants, requiring 17 elements, carbon, hydrogen and oxygen (acquired as water and carbon dioxide) , plus an additional 14 'minerals' that are obtained from the soil solution by the root system.



A Wheat Kernel



Composition by weight

	Carb./g	Protein/g	Fat/g	Fiber/g	Iron (% daily req.)	Others
🟧 **Bran**	63	16	3	43	59	vitamin Bs
⬜ **Endosperm**	79	7	0	4	7	
🟥 **Germ**	52	23	10	14	35	vitamin Bs omega-3/6 lipids

Nutritional Value (per 100g)

Interactions

The most significant interactions of wheat are with humans who actively foster its growth by planting it and culturing it. Like many crop species (but not like most plants) it is an ‘annual’ species: it has a finite lifetime that is less than a year, resulting from the fact that the shoot apical meristem is converted into a flowering meristem within a year of planting. Once the conversion to a flowering meristem occurs, no further growth of the shoot is possible. Moreover, as flowers and fruits develop, the nutrients in the existing plant structure, especially leaves, are mobilized and delivered to the developing seeds, providing them with nutrients but eliminating the ability of leaves to photosynthesize. Wheat can be harvested in as little as 100 days after planting, and can be planted in late spring and harvested in late summer ('spring wheat') or can be planted in the fall and harvested in the late spring or summer ('winter wheat'). The inter wheat varieties need a cold treatment ('vernalization treatment') to induce flowering.

Important to the interaction between wheat and humans are interactions between wheat and:

1. climatic and soil conditions–wheat grows best in 'temperate' regions, i.e. not in the tropics or in arctic regions. It can tolerate relatively dry conditions but does not handle flooding well.
2. herbivores — a number of insect herbivores can drastically affect wheat growth and yield
3. diseases — a variety of diseases, caused by fungi, bacteria and other agents affect wheat growth. These diseases are trophic in nature and could be considered parasites, because the disease causing organism is eating the plant.

Watch

One or more interactive elements has been excluded from this version of the text. You can view them online here: https://milnepublishing.geneseo.edu/botany/?p=291#oembed-1

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WOOD FERNS

The wood ferns (genus *Dryopteris)* are a group of over 400 species and are commonly seen throughout temperate areas, especially in forests. Many are planted as ornamental plants and they are commonly used in landscaping and gardens. The group is known for hydridization, polyploidy and subsequent speciation which accounts for the large number of species (see discussion of speciation through polyploidy in Chapter 28).

Taxonomy and Phylogeny

Wood ferns are members of the Pterophyta, the fern group, which includes ferns, horsetails and wisk ferns. Most observers recognize ten orders within the group, the largest of these is the Polypodiales, which contains roughly 80% of the roughly 12,000 species put in the Pterophyta and is the order that contains the Dryopteridaceae, the family of roughly 1700 species that contains *Dryopteris.* Among other features that unite the Polypodiales is a sporangium with a band of cells, the annulus, that is interrupted by the stalk that attaches the sporangium to the fern leaf.

Structure

Fern fiddlehead, the early growth of fern leaves seen in the spring.

Wood ferns have an underground stem (rhizome) from which emerge the leaves. In most of the wood ferns the leaves are produced in clusters that produce an urn-like, circular groups of leaves. Leaves emerge in the spring as fiddleheads, exhibiting what is know as 'circinate vernation' i.e. they are coiled and unfurl from the base upwards. The leaves of most wood ferns are dissected 2-4 times. The petiole (stipe) of the leaf generally has large, scale-like outgrowths. Sporangia are produced on the underside of leaves in clusters called 'fruit dots'. There is a flap of tissue called an indusium that covers the cluster of sporangia.

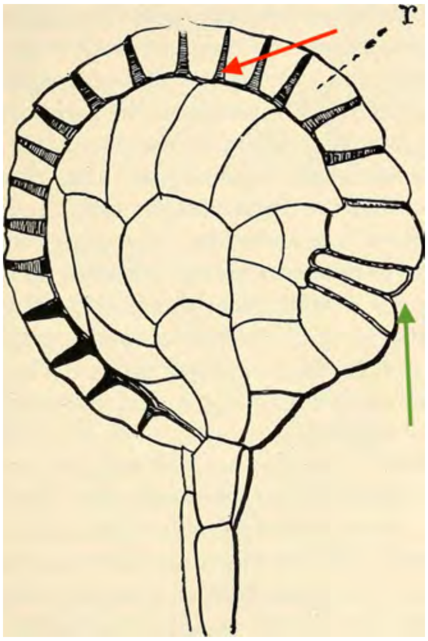
TRÄJON, DRYOPTERIS FILIX MAS (L.) SCHOTT.

Fronds and stipe of a Dryopteris fern, showing 'fruit dots' (clusters of sporangia) on the undersides of leaves. This fern leaf is dissected two-times (i.e. each leaflet has leaflets). Shown to the right of the fern leaves is a sporangium, the structure that produces and disperses fern spores; below is shown a group of sporangia covered by an indusium.

Reproduction

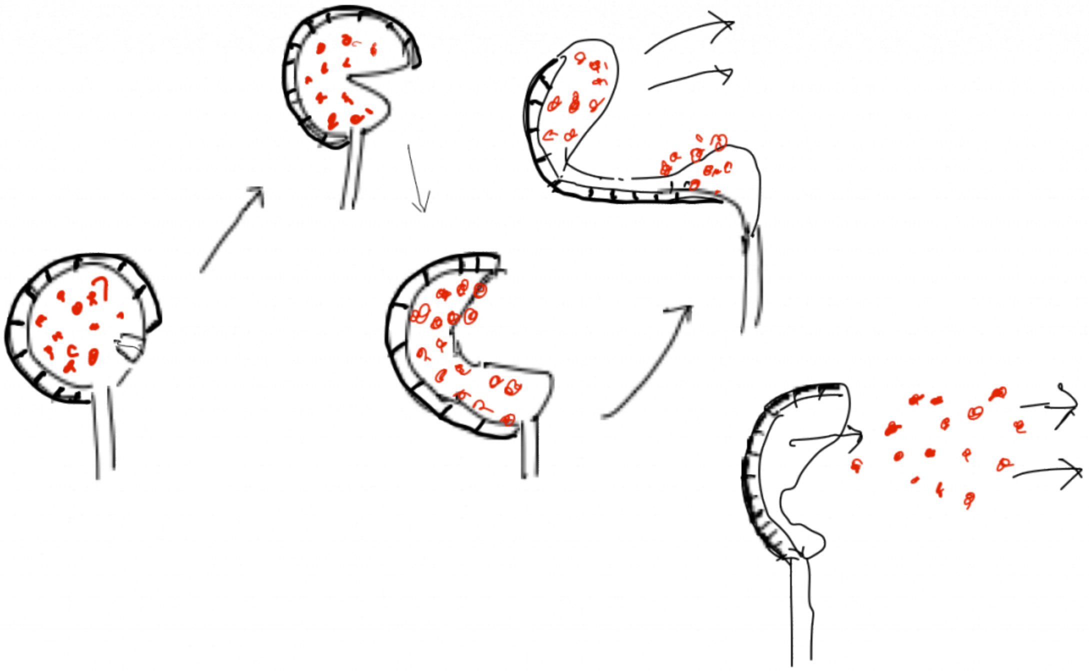
Like all plants, wood ferns exhibits alternation of generations with a visible sporophyte and hard-to-find bisexual gametophyte that is small, uncommonly seen, and quickly over grown by the sporophyte that grows out from the archegonia. Sperm are flagellated and swim to the egg.

The sporangia of all ferns in the Polypodiales are small stalked structures less than a millimeter tall. They have a band of specialized cells, called an annulus (red arrow on the top), that run, starting at the stalk, around roughly 80% of the circumference of the sporangium. As the sporangium starts to dry the sporangium splits between two cells just below the annulus (green arrow, on the right). The cells of the annulus have specialized thickenings that can store energy as the sporangia dries and the annulus shortens to fully open the sporangium. The shrinkage generates a tension in the annulus that eventually overcomes the strength of water columns that are holding the annulus together. When the water columns break, the top of the sporangium rapidly snaps back, dispersing the spores into the air.



Matter and energy

Wood ferns (both the sporophyte and gametophyte) are a typical photoautotroph s, using the energy of sunlight to synthesize carbohydrates from carbon dioxide and then using the carbohydrates as an energy source in cellular respiration and as building materials to synthesize a variety of biomolecules. In addition to the water and carbon dioxide needed to make carbohydrates, plants require an additional 14 elements, absorbed from the soil where they are present in dilute amounts, requiring the roots to 'mine' the soil.



Interactions

Wood ferns contains a number of toxins and are rarely grazed by mammals but are eaten by some caterpillars. Wood ferns are found throughout the eastern U.S., generally in forested situations.

Further Reading

- “The fern sporangium catapult” by xavier noblin. Explanation and video of spore discharge.
    - https://www.youtube.com/watch?v=mDlHGrRlNPE
- *A Natural History of Ferns* by Robbin Moran, ISBN 1604690623. Great book on ferns.

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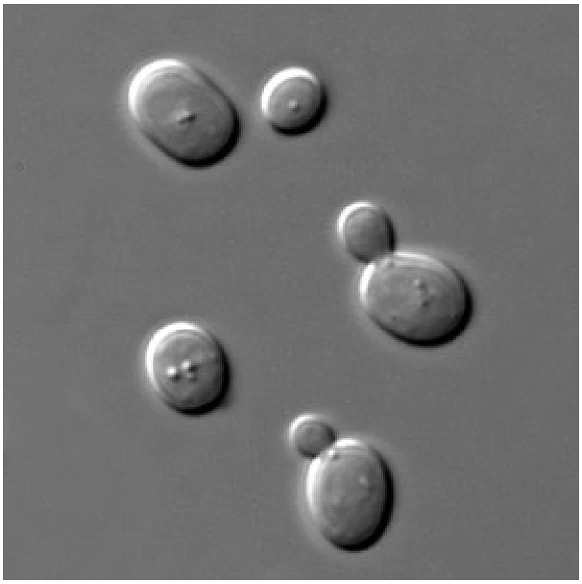
YEAST

Yeast—Saccharomyces cerevisiae



Brewer's (aka baker's yeast or commercial yeast), is the organism that is used to make bread rise and produce wine from the fruits of grape. It also is extremely important as a 'model organism' in biology. It was the first eukaryote to have its entire genome sequenced and studies using *S. cervisiae* have been highly significant in developing our understanding of meiosis, mitosis, cancer and a wide variety of cellular phenomena.

In both scientific experimentation and bread/beer making what makes yeast particularly useful is the fact that it is easily cultured—it can be readily grown (i.e. it is not fussy about growth conditions) and is easy to keep alive/viable (i.e. it is tough to kill) and actually can be kept viable under what is often considered harsh conditions — cooling, freezing, drying. In bread making what is needed is an organism to make carbon dioxide gas which 'leavens' dough, releasing carbon dioxide gas into a matrix of hydrated starch and protein molecules (bread dough), thereby producing a product with a light, aerated texture. Leavening can be accomplished chemically using baking powder or by adding an organism that generates carbon dioxide. Nearly any organism does this but yeast does it rapidly and predictably. Moreover it is relatively easy to keep yeast around even when not baking.

Yeast's role in beer making requires specific abilities that not all organisms possess. The translation of the scientific name is: saccharo = sugar, myces = fungus, cerevisiae = beer, reflecting its ability to make beer (an alcoholic beverage) out of sugar water. It accomplishes this feat by carrying out a processes termed fermentation, an anaerobic respiration process that releases carbon dioxide while converting six-carbon sugars (glucose and/or fructose) into ethanol. While a number of organisms can do this, yeast is easy to culture, can grow rapidly, and its behavior is predictable

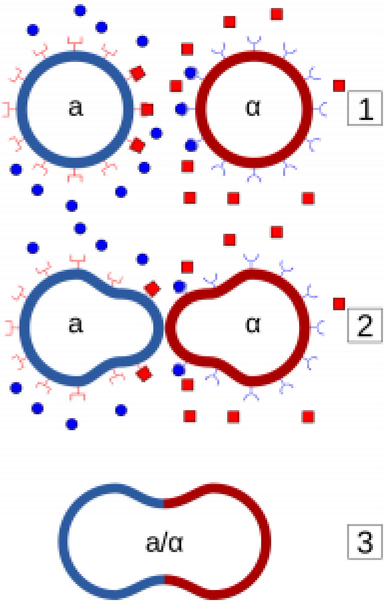
Phylogeny and taxonomy

The name yeast is a morphological term referring to unicellular fungi. Used in this context it does not relate at all to phylogeny. Convergent evolution has resulted in unicellular fungi in several different groups including Zygomycetes (bread molds), Basidiomycetes (club fungi) and Ascomycetes (cup fungi). Most unicellular fungi (yeasts) are ascomycetes but even within this phylum there are yeasts that are not closely related. Commercial yeast (*Saccaromyces cervisiae*) is an ascomycete, as is fission yeast (*Schizosaccharomyces pombe*), another yeast used in brewing and also an important model organism with its entire genome sequenced. Although fission yeast and baker's yeast have a similar ecology and are in the same phylum they are not closely related, having diverged from each other over 300 – 1000 million years ago.

Structure

Yeasts in general are unicellular fungi and in form and size very similar to bacteria. Like all fungi, they have a cell wall composed of chitin and possess a nucleus and other organelles, in particular, mitochondria. In many ways they represent fungi that have evolved to become 'bacteria-like' in their form and ecology. Baker's yeast is typical of yeasts in generally — they typically are roughly spherical and around 5 um in diameter.

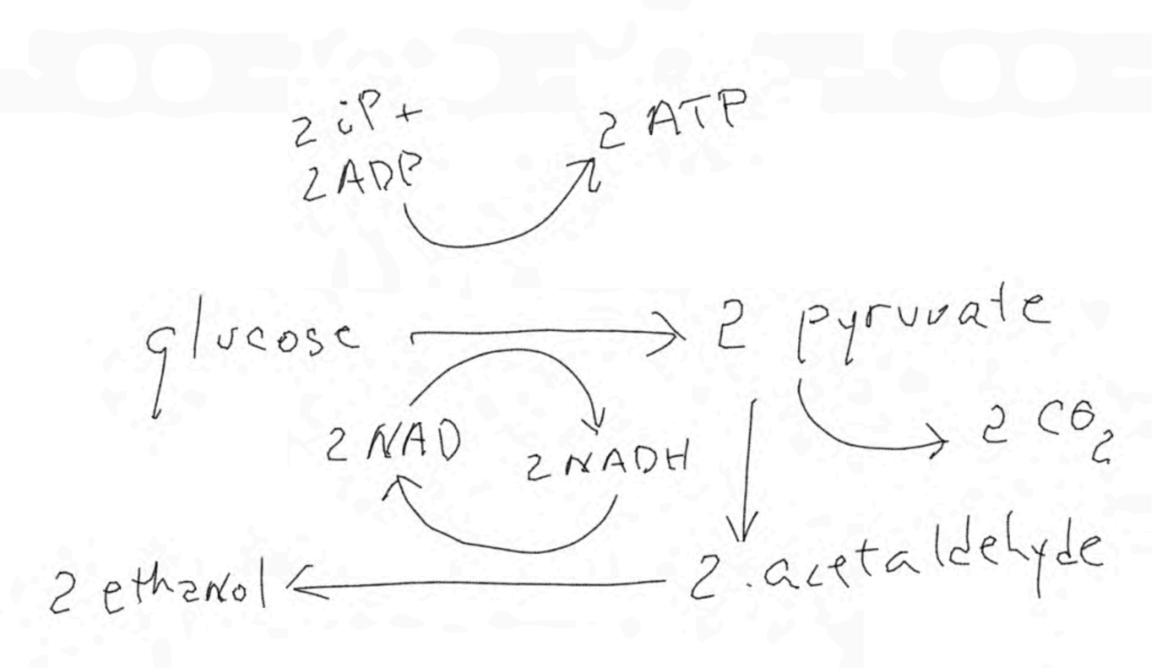
Sex and reproduction



Brewer's yeast primarily reproduces asexually, by 'budding', which is basically cell division but where the daughter cell starts as an outgrowth (bud) of the parent cell and eventually separates. Brewer's (and fission) yeast are capable of sex when the diploid cells undergo meiosis, forming cells that can fuse with each other (i.e. serve as gametes) to restore the diploid condition. Both fission yeast and commercial yeast can occur as haploid or diploid cultures. Haploid cultures can be maintained by not bringing together different mating strains, while diploid cultures can be maintained because specific culture conditions (nitrogen starvation) are needed to bring about meiosis. When haploid cells of different mating strains encounter each other, chemical communication (pheromones) trigger the production of extensions ('Shmoo's') that allow cells to fuse with each other (plasmogamy). In the diagram above the blue 'a' strain produces a mobile chemical (pheromone) designated by the blue circles and has receptors (red 'football goalposts') that can bind the pheromone (red squares) produced by red 'alpha' strain. Similarly, the red alpha strain has receptors for the pheromone produced by the blue 'a' strain. In both strains the binding of pheromones produced by compatible strains induces the production of a schmoo and the eventual creation of a diploid cell.

Matter and energy

Saccharomyces is a heterotroph with a sweet tooth — it prefers living off of simple sugars, although some strains can breakdown sugar polymers, e.g. starch, into simple sugars, thereby broadening its diet. Its mineral needs are obtained by absorbing small organic molecules (amino acids) and minerals like phosphate. Various strains differ in their ability to breakdown organic matter and absorb and metabolize nutrients; these features may be useful in genetic/cell biology experiments.



Alcoholic fermentation: Two molecules of NAD+ are reduced to two NADH while a glucose is converted to two molecules of pyruvate. Each loses a carbon dioxide to form two acetaldehydes and then the acetaldehype is reduced to ethanol while NADH is oxidized back to NAD+, allowing the process to continue.

Interactions

Obviously yeast have significant interactions with humans in providing food products and beverages. The 'native habitat' of both brewer's yeast and fission yeast is the skins of sugar containing fruits such as grapes, apples and pears, making the 'invention' of wine-making relatively easy. In addition to ethanol, genetically engineered yeast are used to produce a variety of compounds including insulin. While brewer's yeast is non-pathogenetic some yeast species can cause disease in humans and other organisms.

Further Reading

- "You had me at hello: Frisky yeast know who to 'shmoo' after 2 minutes" on Brightsurf. An i nteresting article on sexual reproduction in yeast.
    - https://www.brightsurf.com/news/article/041810243765/you-had-me-

    - at-hello-frisky-yeast-know-who-to-shmoo-after-2-minutes.html
- "Sour Microbes: Yeast and Bacteria Explained" by American Homebrewers Association. Yeast and bacteria used in beer making.
    - https://www.homebrewersassociation.org/how-to-brew/sour-microbes-yeast-and-bacteria-explained/

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CHANGE LOG

Version 2.0, Summer 2022

- Numerous links added to interesting and helpful material. Most of these are listed at the end of chapters.
- All chapters: minor rewordings and some paragraphs of information added
- Chapter 22: added figures on the nitrogen cycle
- Chapter 28: section on Brassica crops added
- A Sampling of Inanimate Life: rewritten and expanded
- New organisms added:
  - Chara
  - Methanogens
  - Nitrifying bacteria