



Topic
Science

Subtopic
Biology

Plant Science

An Introduction to Botany

Course Guidebook

Professor Catherine Kleier
Regis University



PUBLISHED BY:

**THE GREAT COURSES
Corporate Headquarters
4840 Westfields Boulevard, Suite 500
Chantilly, Virginia 20151-2299
Phone: 1-800-832-2412
Fax: 703-378-3819
www.thegreatcourses.com**

Copyright © The Teaching Company, 2017

Printed in the United States of America

This book is in copyright. All rights reserved.

Without limiting the rights under copyright reserved above,
no part of this publication may be reproduced, stored in
or introduced into a retrieval system, or transmitted,
in any form, or by any means
(electronic, mechanical, photocopying, recording, or otherwise),
without the prior written permission of
The Teaching Company.



CATHERINE KLEIER, PH.D.

PROFESSOR OF BIOLOGY
REGIS UNIVERSITY

Catherine Kleier is a Professor of Biology and former chair of the Department of Biology at Regis University in Denver, Colorado. She has also served as the associate director of the Regis College Honors Program. She teaches courses in plant physiology, ecology, and environmental science.

Professor Kleier holds a Ph.D. in Organismic Biology, Ecology, and Evolution from the University of California, Los Angeles (UCLA). While at UCLA, she received a Mildred E. Mathias Graduate Student Research Grant, a Dissertation Year Fellowship, and the Lasiewski Award for outstanding graduate research.

Professor Kleier also holds a B.A. in Ecology, Population, and Organismic Biology from the University of Colorado Boulder and an M.S. in General Science with an emphasis in Botany and Plant Pathology from Oregon State University.

Professor Kleier's current research interests include long-term restoration ecology on trails in the Colorado Rocky Mountains, plant impacts from skiing, and urban ecology. Her laboratory work has focused on the effect of magnesium chloride on the growth and reproduction of plants.

Professor Kleier was awarded a National Geographic Society/Waitt Grant in 2011 to travel to northern Chile to explore populations of a rare, giant alpine cushion plant, *Azorella compacta*. She has presented many conference papers and posters at numerous professional societies, including the Botanical Society of America, the Ecological Society of America, the Society for Conservation Biology, and the Association for Environmental Studies and Sciences.

In 2010, Professor Kleier was selected as a scholar for the Aspen Institute's Aspen Environment Forum. In 2013, she was a Visiting Fulbright Scholar in the Department of Botany at the University of Otago in New Zealand, where she investigated facilitation in the alpine cushion plant genus *Raoulia*.

In 2014, Professor Kleier was elected Faculty Lecturer of the Year at Regis University, and in 2015, she was named the Colorado Professor of the Year, sponsored by the Council for Advancement and Support of Education and the Carnegie Foundation for the Advancement of Teaching. She is on the board of the Colorado Native Plant Society, and she often leads field trips to the beautiful Colorado Rocky Mountain alpine zone. She is also the creator and director of the Certificate in Applied Craft Brewing at Regis University. ■

TABLE OF CONTENTS

INTRODUCTION

Professor Biography	i
Course Scope	1

LECTURE GUIDES

1 The Joy of Botany	4
2 Plants Are like People	12
3 Moss Sex and Peat's Engineered Habitat	20
4 Fern Spores and the Vascular Conquest of Land	29
5 Roots and Symbiosis with Non-Plants	37
6 Stems Are More Than Just the In-Between	46
7 The Leaf as a Biochemical Factory	54
8 Photosynthesis Everyone Should Understand	62
9 Days and Years in the Lives of Plants	71
10 Advent of Seeds: Cycads and Ginkgoes	77
11 Why Conifers Are Holiday Plants	85
12 Secrets of Flower Power	94

13	The Coevolution of Who Pollinates Whom.....	106
14	The Many Forms of Fruit: Tomatoes to Peanuts	115
15	Plant Seeds Get Around	123
16	Water Plants Came from Land	130
17	Why the Tropics Have So Many Plant Species.....	138
18	The Complexity of Grasses and Grasslands	145
19	Shrublands of Roses and Wine	154
20	The Desert Bonanza of Plant Shapes	161
21	How Temperate Trees Change Color and Grow	168
22	Alpine Cold Makes Plants Do Funny Things.....	176
23	Bad Plants Aren't So Bad	184
24	Modifying the Genes of Plants	193

SUPPLEMENTARY MATERIAL

Bibliography	200
Image Credits	205

PLANT SCIENCE

AN INTRODUCTION TO BOTANY

Although the world is full of plants and we see them every day, we are often blind to their presence. More than that, our knowledge of these plants may not extend much beyond the idea that they use sunlight and carbon dioxide to produce oxygen and sugars, the very things that sustain our life on Earth. This course will help you learn to see plants, begin a relationship with them, learn their stories, and appreciate their amazing diversity.

The course will take a chronological approach in terms of when certain plants and plant traits appeared on Earth. You will begin by considering the differences between plants and animals. Plants are certainly different, but there are some similarities, too, in the way that plants and animals sense the world. Because the first true plants to colonize the land were mosses, that's the first plant group you will consider in depth. What makes a moss a moss, and what's important about mosses? Next, you will consider the ferns, and you will determine why ferns were an important step in the evolution of seed plants, which will come next.

Because most plants have a basic anatomy of roots, stems, and leaves, you will consider each part in detail. These structures are intimately linked to function. Many roots have a symbiotic relationship with fungi that enable absorption from more of the soil. Stems come in many different sizes and shapes—as do leaves, from small needles to leaves that are more than a square meter. You will discover why this is the case.

Because all plants undergo the life-support process of photosynthesis, you will next take a detailed look at the biochemistry of photosynthesis, beginning with carbon dioxide entering the leaf. This process is a cycle that depends on 2 reactions, one of which captures light energy and the other of which uses that energy to turn carbon dioxide into sugars.

Because they are light-sensing organisms, plants have a well-developed circadian rhythm that determines when they flower and fruit, and you will examine these mechanisms.

The seed was a remarkable adaptation that allowed plants to colonize more types of environments. The conifers and related plants were the first to have seeds, and you will learn that even though these plants lack flowers, they are uniquely adapted to the environments in which they live. When and how the first flower appeared is still a bit of a mystery, but you will consider the latest evidence about the evolution of flowering plants. You will learn about some important adaptations of flowers and discover the intricate relationship between flowers and their pollinators.

The exchange of pollen is necessary for the development of the fruit, and there are many types of fruits, each with a unique dispersal mechanism to spread the seeds of the next generation. Fruits have interesting botanical names, and you will learn a few of these. For example, a strawberry is not a true berry, but a tomato is, and a peanut is not a nut, but a hazelnut is. Botanists categorize flowers and fruits to put plants in taxonomic groups, and you will explore some of the major plant groups.

At this point, the course will explore plants in various habitats and examine the science behind adaptations to different environments. This tour will begin with underwater plants. You will discover that there are not just seaweeds that live in the sea, and water lilies and other plants have unique tissues that can keep them afloat.

Then, you will uncover some of the amazing diversity of the tropical rain forests. You will also examine evidence that suggests why these areas are the most diverse habitats on land. You will explore unique life-forms and discuss why these types of plants were so successful in the tropics.

The next habitat is unique because the grasslands are not only a community type but a dominant group of plants. They have a different structure than non-grasses and a different way of growing that enables them to thrive

under pressure from grazing animals. Grasses are also the most economically dominant group of plant, because all of our major cereal crops are grasses, such as corn, rice, and wheat.

An often-overlooked community type is that of the shrubland, but shrubs are some of the oldest and hardiest woody plants on the planet. Shrubs also include important ornamentals, such as roses.

Shrublands generally give way to true deserts. Desert plants undergo a different type of photosynthesis that allows them to conserve water. Because water is the most limiting factor for most plants, deserts have a myriad of unique plant forms to cope with this stress.

Deciduous trees may look alike, but trees are different in their reproductive capacities and susceptibility to pathogens. You will encounter a number of interesting trees in the deciduous forest.

Next, you will discover the wonderful world of alpine plants. You will learn how these plants survive in such extreme environments.

Although plants make life on Earth for us possible, there are some plants that strike fear in our hearts, such as stinging nettle and poison ivy. Some plants also get introduced to a new area and become invasive, which is also unpleasant. You will consider the why and how of these plants, as well as the strange carnivorous plants.

Finally, you will explore genetic modification of plants and the future of this new technology and botany.

LECTURE
1

THE JOY OF BOTANY

Botany is the study of plants—everything from biochemical reactions to whole forests. At first glance, plants might seem boring; they may not ignite our compassion like animals do. But plants have a quieter way of igniting our passion, because we're dependent on them. The goal of this course is for you to understand the fascinating differences, and similarities, between plants and animals; to get better acquainted with the various parts of the plant and what they do; and to open your eyes to the science of botany that is all around you.

PLANT DIVERSITY

- ◇ There is incredible diversity within the more than 300,000 species of plants.
- ◇ The dodder plant is a parasitic plant, which means it gets all of its nutrition from other plants. Dodder is a common name, and it refers to an entire genus of plants called *Cuscuta*.



- ◇ Because this plant is parasitic, it will often have no chlorophyll of its own, leaves so tiny they're easily overlooked, and a bright orange color. It's found all over the United States. Research with the dodder plant shows that it doesn't attack a host randomly; it actually searches out a host it prefers.
- ◇ Research into chemical signaling in plants and animals by Dr. Consuelo De Moraes showed that dodder vines grow toward plants and don't grow toward empty pots. What's more, if the dodder plant is given a choice between a tomato plant or a wheat plant, it will always choose the tomato plant.
- ◇ Dr. De Moraes wanted to see just how strong the dodder's responses were to tomato plants. In fact, according to a 2012 article in *Scientific American*, she wanted to test the hypothesis that the dodder plants could smell the tomato. What if the definitive marker for a sense of smell was just a response to an olfactory cue? If that's the case, could the dodder plant respond to the smell, or chemical signal, from the tomato?
- ◇ To test this hypothesis, Dr. De Moraes made a tomato perfume concocted from the chemicals found on the tomato plant and soaked cotton swabs with the tomato perfume. The dodder plants grew toward the cotton swabs that smelled like tomatoes.

- ◇ Another example of a unique plant, or group of plants, is the living stone plants from South Africa, which look like small stones. These plants have windows, or transparent membranes, which are an adaptation for plants growing in lower-light environments. These plants are found in areas with lots of cloudy days; the windows let in more light on a cloudy day.

BENEFITS TO STUDYING PLANTS

- ◇ With scientific advances, there are practical benefits to studying plants. The following are examples of when a little knowledge about plants goes a long way.
- ◇ Trees consume carbon dioxide and produce oxygen. But some trees can actually contribute to climate change by emitting volatile organic carbons (VOCs). When VOCs meet nitrogen oxides produced by our cars in the presence of sunlight, they help the formation of tropospheric ozone.
- ◇ Tropospheric ozone occurs in the troposphere, where we are. The thinning of the ozone layer is occurring in the stratosphere, particularly over Antarctica, but potentially over the Arctic, as well. This ozone protects us from harmful ultraviolet radiation, which can cause skin cancer and cataracts. But the ozone in the troposphere, which also goes by the name of smog, triggers asthma in children and is the primary component of air pollution in cities.
- ◇ Not all trees produce the VOCs that contribute to smog, but some do, and in large amounts. According to a study done by the U.S. Forest Service, sycamores, locust trees, and oaks were among the greatest VOC contributors. A little botanical knowledge can help citizens make good decisions about which trees will help improve air quality.
- ◇ Another example where botanical knowledge comes in handy pertains to rubber. Henry Ford, who bought a rubber plantation in 1927, used rubber for his car's tires as well as many of the hoses and connections within the vehicle.

- ◇ The scientific name for the rubber tree is *Hevea brasiliensis*. As the name suggests, it's native to Brazil, where it grows sporadically in the rain forest. Ford bought his plantation in the Amazon, where this tree is found natively. But within a few years, the plantation failed.
- ◇ In nature, rubber trees never grow in clusters, but in the plantation, they were all planted close together—so close that a disease, known as South American leaf blight, or *Microcyclus ulei*, was able to spread through the entire plantation.
- ◇ Most rubber today is grown in Southeast Asia. The success of rubber there has to do with the fact that the climate of Southeast Asia is agreeable to rubber trees, but also that the South American leaf blight has not yet made its way to Southeast Asia. However, most botanists think it's just a matter of time before this blight makes it to Southeast Asia.
- ◇ Like Henry Ford's plantation, this could be disastrous for the plantations in Southeast Asia. There may be trees in Brazil that are naturally resistant to the blight, or scientists may be able to develop a variety of rubber tree that has resistance to the blight, but this isn't happening. When the blight hits Southeast Asia, the research on these fronts will most likely begin in full force.



- ◇ Another example where a knowledge of botany is useful is bananas. All bananas that are in the supermarket are not only the same variety, but they are exact clones of each other—genetically identical. Just as there are different varieties of apples, there are different varieties of bananas, but the one everyone eats is called Cavendish.
- ◇ The seeds inside are too immature to grow, so Cavendish bananas are effectively seedless and unable to mutate. When Tropical Race 4, a banana fungal disease called *Fusarium oxysporum* f. sp. *cubense*, reaches Latin America, the banana plantations will be susceptible to total failure.
- ◇ Tropical Race 1 overwhelmed a previous clone banana everyone was eating in the 1950s—that was what led to the more fungus-resistant Cavendish. A more colloquial name for these Tropical Race diseases is Panama disease, which attacked bananas in 1874 in Australia. By 1890, the earlier form had made its way to Panama, where it earned its nickname. So far, research has identified possible varieties of bananas that appear resistant to Tropical Race 4.



NAMING, CLASSIFICATION, AND IMPORTANCE OF PLANTS

- ◇ Like people, plants have a first name and a last name. Their first name is the genus name, so it represents a larger group, sort of like our last name. Their second name is called the specific epithet, and those 2 names—the genus name and the specific epithet—make up the scientific name of each species of plant.

- ◆ There are more than 300,000 different species of plants—with a few thousand more discovered every year—and even the best botanists in the world don't know the scientific names for all of the species. There are unknown plants, and there are different traits to consider when deciding how to define a species.
- ◆ Although this course is not strictly about plant identification, you will be introduced to many plants and the ways that they are classified. A field guide is simply a book to identify organisms in their natural habitat. There are field guides for birds, mammals, and plants. These guides are meant to be used in the field, and they are often organized by flower color, so you don't need to know a lot of botany to use them.
- ◆ Field guides to trees are often organized by leaf shape and bark appearance. It's like a matching game. Anyone with careful observation skills can identify a common plant or tree using a field guide, but it's helpful to find the most local field guide you can. Most states have their own field guides for common trees or common wildflowers. Larger states, such as California, will have guides for particular parts of the state.
- ◆ Field guides are great for common species, but they won't include everything. That's where a manual or flora comes in: These are books that will identify all plants of a region down to the species, using a dichotomous key. A manual might be for a particular group of plants—for example, the grasses; a flora is meant to be an exhaustive account of all the plant species in a specific geographic region.
- ◆ Plants form the majority of our economic system—either as food, medicine, perfume, raw material for building, fuels, paper, clothing, or furniture—and we don't even have to pay for plants' top contribution to our survival: oxygen. According to a 2015 estimate by Royal Botanic Gardens, Kew, 10% of the world's plant species already have documented uses.
- ◆ The number-2 traded commodity in the world is a plant: coffee. Because coffee is grown and consumed on such a wide basis, the way coffee is grown can be a boom or bust to an ecosystem.

- ◇ Although plants are important to our survival, there is a real, though avoidable, phenomenon known as plant blindness, a term first coined by Dr. James H. Wandersee and Dr. Elizabeth Schussler. We go about our business, but we don't really see or know about the plants around us.
- ◇ A hundred years ago, identifying what a plant is played a more widespread role in education and daily life, whereas only recently have plant scientists been developing a much deeper understanding of how plants do what they do.
- ◇ Not only is plant knowledge useful, necessary, and life-saving, but it's also a good way of life. Celebrating the secrets of nature provides joy and satisfaction.

READINGS

Mabey, *Cabaret of Plants*.

If you want to go deeper with plant identification, pick up a local field guide. The Sierra Club, the National Audubon Society, and Peterson Field Guides all have good series. If you're already familiar with local field guides, perhaps you're ready to move on to the local flora, or a book that will identify all plants of a region to species using a dichotomous key, which you can obtain from the Native Plant Society website for a particular state. The U.S. Forest Service explains this here:

<https://www.fs.fed.us/wildflowers/features/books/>

This site also has links to several parts of the country where more specific books are listed.

QUESTIONS

- 1 How much do you already know about botany? Do you know the names of 5 plants in your yard? Would you know the name of 5 native plants near your home?
- 2 What was most surprising about plants for you in this lecture?

LECTURE
2

PLANTS ARE LIKE PEOPLE

In 1975, Jerry Baker published a gardening book called *Plants Are like People* that compares people and plants. For example, plants like the same temperature of water that we like. They like about the same amount of light that we do; with individual variations, we enjoy a sunny day, and so do plants. Plants have a circadian rhythm of rest and activity, and so do we. We drink water; they need water, too. In this lecture, you will discover some of the ways that plants are like people.

PLANT INTELLIGENCE

- ◇ A very hot topic of research is plant intelligence. This topic is a bit controversial because there was a book called *The Secret Life of Plants*, first published in 1989, that claimed, among other things, that certain types of music encouraged plant growth. Even though this has never been confirmed in a repeatable lab study, the book has been a wild success.
- ◇ In some ways, the book created a rift in botany that persists to this day. Scientists interested in the ideas of plant communication or plant behavior tend to be labeled on the fringe by more mainstream botanists. But there are also attempts to rethink plant behavior from a more mainstream perspective.
- ◇ Monica Gagliano, an Italian botanist who studies plant communication, published a 2012 paper with colleagues entitled “Towards Understanding Plant Bioacoustics,” which investigates the perception of sound in plants. The authors argue that many animals lack eardrums yet can still hear, so perhaps plants can hear through some organ or mechanism we don’t yet understand.
- ◇ They make a good argument that there are constant sounds in substrates such as soil. Animals who live underground still hear, though their hearing is generally reduced. The authors outline an experiment where the roots of young corn are shown growing toward a sound emitted in water.
- ◇ Roots need water, so it makes sense that roots will grow toward sources of water. It’s even been reported that roots will grow toward pipes with water in them, even if the pipes are sealed and not leaking any water. This also suggests that the roots are somehow sensing the sound.
- ◇ Gagliano has also been experimenting with *Mimosa pudica*, also known as the sensitive plant, to test its memory. It’s a small shrub-like, or frutescent, herb that is native to the tropics of North and South America. There are about 430 species of *Mimosa*, but only a few species display the special trait that *Mimosa pudica* displays: When touched, its leaves collapse immediately.

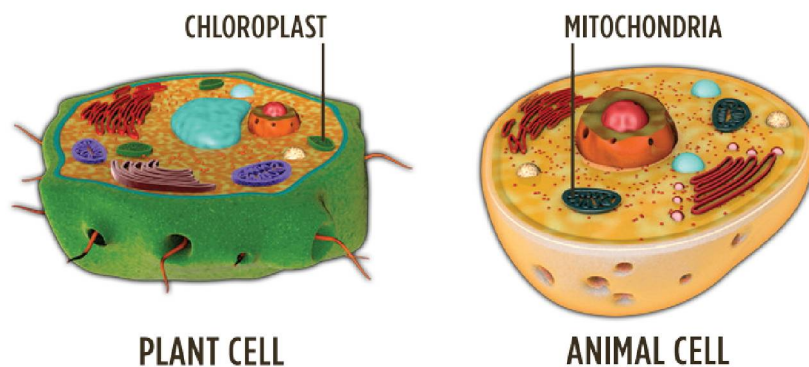


- ◇ The *Mimosa* plant itself doesn't move, but the movement of the leaves is rather instant. How do the leaves move so fast without muscles?
- ◇ The *Mimosa* also has a special thickening at the base of the leaf called a pulvinus. These cells are what control the drooping of the leaves.
- ◇ Consider that the leaf is fully turgid, a botanical term that means the opposite of wilting. The leaves are flat, but when you touch them, they droop or wilt immediately. When touched, the plant produces an electrical signal that causes potassium channels in the cell wall of the pulvinus to open.
- ◇ When all the potassium rushes out of the cell, the water will follow it by osmosis—the biologic principle by which water moves from an area of high water concentration to an area of low water concentration—thus causing the pulvini to wilt, or become flaccid, which makes the leaves droop. (The more general process of diffusion is the movement of anything from a high concentration to a low concentration.)

- ◇ A flaccid cell also causes plasmolysis, which is when the cell shrinks due to lack of water and the cell membrane pulls away from the cell wall. A flaccid cell doesn't always have plasmolysis, but if it remains flaccid long enough, plasmolysis will occur.
- ◇ In testing the memory of the plants, Dr. Gagliano would drop the *Mimosa* plants, and the leaves would collapse. She would repeat this several times until the *Mimosa* stopped collapsing their leaves. You could say that the potassium channels can't reboot or make some sort of physiological argument, but then she would drop the plants a week later, and the leaves would not collapse. To test them, she would give them some other stimulus, and the leaves would droop immediately because they had not been conditioned for a response.

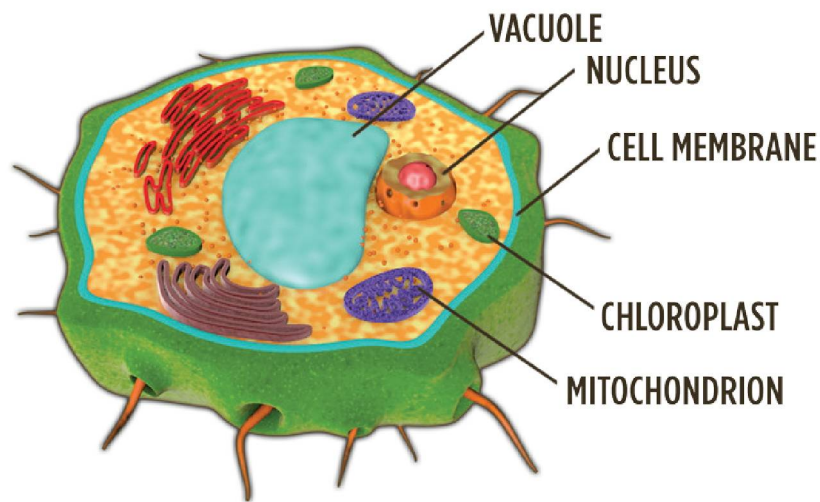
PLANTS VERSUS ANIMALS

- ◇ There are many ways that the cells of plants and animals are similar, but there are a few ways that they're different.
- ◇ Plant cells have 3 important structures that animal cells don't have: a cell wall, a vacuole, and chloroplasts.



- ◇ All cells, including animal cells, have some kind of boundary between the cell and everything else, the extracellular fluid or matrix. Both plants and animals have a cell membrane, but plants also have a cell wall. The cell wall is tougher, usually thicker, and has more structure than a cell membrane.
- ◇ In plants, the cell membrane is called the plasma membrane, and it is inside the cell wall. Put another way, on top of the plasma membrane is the primary cell wall. This cell wall is made up of polysaccharides, which is a fancy word for a lot of sugars stuck together.
- ◇ One of these polysaccharides is cellulose. We can't digest cellulose, even though it's just a chain of glucose molecules; instead, cellulose is a component of dietary fiber. Cellulose is also the most abundant macromolecule on Earth.
- ◇ These cellulose molecules are long strings of glucose that crisscross each other to add structure and strength. The cellulose molecules are called microfibrils, and embedded around these are pectin molecules. Pectin provides flexibility to the cell wall.
- ◇ Primarily, the cell wall keeps the cell from bursting under turgor pressure. Most plant cells are turgid, or full of water to maintain their shape. An animal cell membrane would burst under this pressure. Plants are able to get such high pressures in their cells because the cell wall holds in the water.
- ◇ Plant cell walls also have small pores in them, which allow for water, and a few small nutrients, to pass into the cell. Osmosis is the movement of water through a semipermeable membrane, and the cell wall is an example of a semipermeable membrane.
- ◇ Cell walls can be either primary cell walls, which are still growing and living, or secondary cell walls, which are mostly no longer alive but contain a substance called lignin to provide structure. In animal cells, the cell membrane is important because it receives many signals from the rest of the body.

- ◇ The cell membrane contains receptors on the surface of the cell membrane that receive signals from the rest of the body. If the cell needs some glucose, it has a glucose receptor on the cell membrane that is open and therefore receives glucose. The evidence that plant cell walls regulate responses in the same way is not that strong yet, and this is a big interest in botanical research.
- ◇ The second unique component, for nonwoody plant cells, is the vacuole. The vacuole is an organelle, or cellular organ, whose main purpose is to store water. The vacuole stores water, but this water is also the primary component that gives cells their structure.
- ◇ The third unique component that plants possess is the chloroplast. The chloroplast is an organelle that contains chlorophyll and is the main site of photosynthesis. In some ways, chloroplasts resemble the mitochondria of an animal cell, which is the main site of energy production.



- ◇ In fact, the chemical reactions are exactly opposite in the chloroplast and the mitochondrion. The chloroplast takes in sunlight, carbon dioxide, and water and creates glucose, oxygen, and energy. The mitochondrion takes in glucose and oxygen and creates carbon dioxide and water, a process known as cellular respiration.
- ◇ All plant cells also have mitochondria, just like animals, to break down the glucose produced during photosynthesis. But mitochondria are especially important for cells that don't photosynthesize, such as the roots.
- ◇ Both plant cells and animal cells contain a nucleus. The nucleus contains the deoxyribonucleic acid (DNA). The genetic information, or genes, are contained within the DNA. DNA works pretty much the same in plants as it does in animals. Plants and animals not only share the same DNA building blocks, but they also share many of the same DNA sequences, or genes.
- ◇ A group of cells together makes up a tissue. Because plants have such different cell types from animals, they also have different tissue types than animals.
- ◇ There are 3 main tissue types in plants, and these are categorized by the thickness of the cell wall. Tissue with the thinnest cell wall is called parenchyma, the tissue that makes up much of the internal structure of the leaves of plants.
- ◇ Collenchyma is tissue with irregularly thickened cell walls. These are structural cells, though they are not found in the roots. Typically, they are most common in stems of herbaceous (nonwoody) plants, such as celery.
- ◇ Sclerenchyma is tissue that contains cells with thickened secondary walls that may contain lignin, which is a substance that provides thickness. Sclerenchyma serves a protective or supportive function in the plant.
- ◇ Plants and people have some genes in common and use the same basic building blocks of DNA to make proteins. Plants also have tissues, but plant tissue types depend on the thickness of cell walls, which our animal tissue types don't have, so the form and function of plant tissues are different.

- ◇ Most important—and most surprising, given these differences—plants are able to sense their environments and respond. The open question is whether plant sensation is akin to sensation in animals and whether plant responses to their environment are akin to animal behavior and communication.

READINGS

Bock, et al, *Identifying Plant Food Cells in Gastric Contents for Use in Forensic Investigations*.

Chamovitz, *What a Plant Knows*.

Karban, *Plant Sensing and Communication*.

Trewavas, *Plant Behaviour and Intelligence*.

QUESTIONS

- 1 Do you think that plants can communicate like humans? Why do you think that botanists have been so slow to study plant behavior? Why would it be difficult to accept that plants are communicating?
- 2 What are cellular parts that plants have that animals don't have, and what are their functions?
- 3 Suppose that you had a red-flowered plant with dominant alleles for red, RR (one allele came from the mother and one came from the father). You are going to cross this red-flowered plant with a plant that has white flowers and is recessive with the alleles, rr. If color is completely dominant, what is the predicted outcome of the cross? How many flowers will be red, and how many will be white?

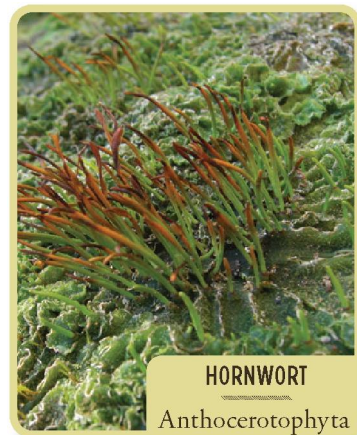
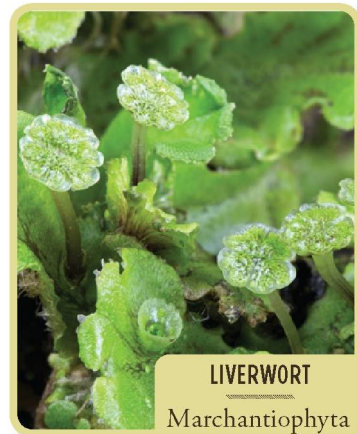
LECTURE
3

MOSS SEX AND PEAT'S ENGINEERED HABITAT

Mosses and the other bryophytes live in places that later plants on Earth have been less eager to inhabit. They can thrive in low light and nearly anaerobic conditions. And while they do need nearly constant water to thrive, many can bounce back from even a long dry spell within hours. They aren't large, but they offer sights—and insights—available nowhere else in the plant kingdom.

MOSS

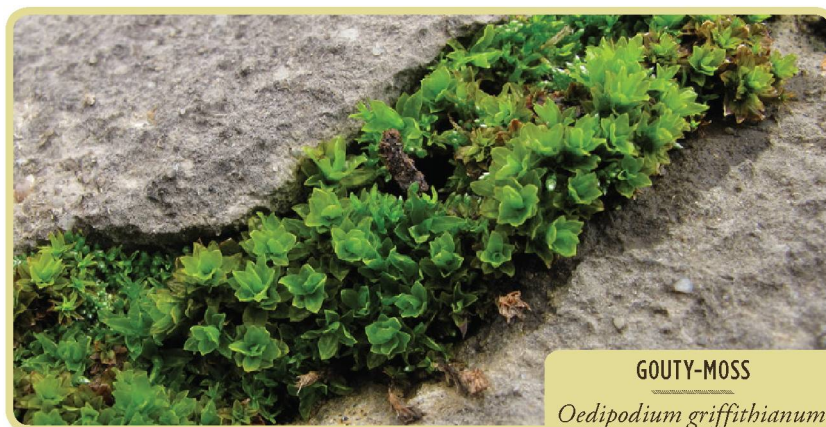
- ◇ The plant kingdom is divided into a dozen phyla, also known as divisions. The division that includes moss is known as Bryophyta. The bryophytes are thought to be one of the oldest groups of plants that first made it to land. This means that they developed new ways to breathe, preserve moisture, and reproduce. These 3 traits are what distinguish all plants from algae, even from algae that can do photosynthesis.
- ◇ A few smaller plant divisions were traditionally lumped in with the bryophytes: the liverworts (phylum Marchantiophyta), with upward of 6000 species; and the hornworts (phylum Anthocerotophyta), which have only a few hundred species.
- ◇ All 3 phyla of bryophytes, in this broader sense, were the first plants to colonize land. They also happen to be quite different, in shared ways, from all other plants. This is why they have all traditionally been grouped together and called bryophytes in a looser sense.





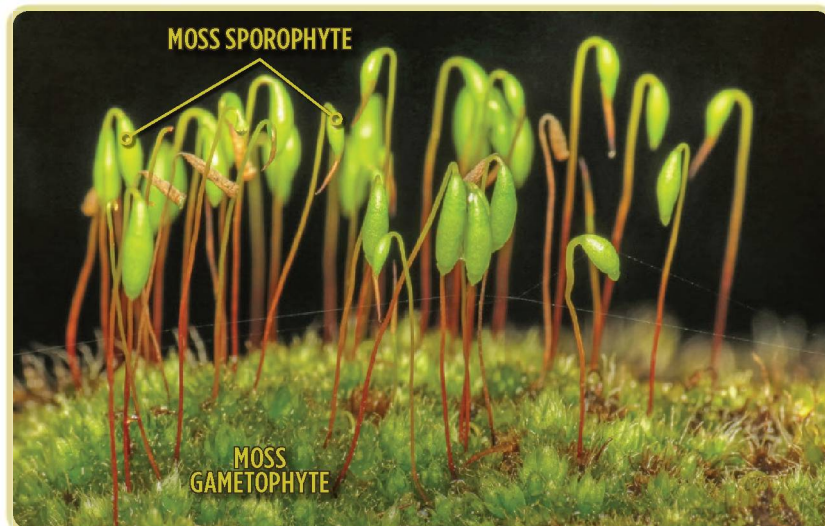
- ◇ They all lack true leaves and true roots; in fact, they lack vascular tissue altogether. This essentially means that they have no way to conduct sugars or water through the plant. It all basically happens by osmosis or diffusion. Without dedicated tissues to move water, minerals, and sugars through the plant, and without true roots to absorb water and minerals, bryophytes are restricted to being small.
- ◇ Just because mosses arrived early and aren't big doesn't mean that we have to consider them as evolutionary runts or remnants. They are still very well adapted to the habitats in which they live, such as the side of tall trees or on rocks in a stream. Mosses are necessary for many animals and form the basis of whole ecosystems, such as peat bogs. Mosses are also really good at being able to handle low-light conditions. Mosses do require habitats that are wet, at least some of the time, and this has to do with the way they reproduce.
- ◇ Across all 3 bryophyte phyla, there are only around 15,000 bryophytes, which is about 5% of all plant species, but they live in remarkable ways, in many habitats, and have a unique way of reproducing.

- ◇ How is a moss different from its ancestors? Green algae are a lot like bryophytes—they photosynthesize and need water to reproduce—but there are 2 important differences. The most important is that the mosses, like all other true plants, will have a protected place for the embryo to develop. By contrast, algae release their sperm and eggs directly into the water, where they fuse to form zygotes, which can then travel through the water to settle somewhere else as a developing embryo.
- ◇ A second partial distinction is that all algae can reproduce sexually or asexually, while only some plants can reproduce asexually, such as mosses. What separates mosses and other asexual plants more clearly from algae is that the asexual propagule in algae can be dispersed. But in plants, any asexual reproduction—when it's possible—is generally anchored to the parent plant.
- ◇ The other major difference between algae and bryophytes is that the bryophytes have a special waxy cuticle all over that keeps water in their cells. This cuticle is present in all plants. By contrast, only a few red algae have a cuticle. Because algae live in water, they don't need a cuticle. These 2 developments in the bryophytes—protection for the developing embryo and a waxy cuticle to protect the entire plant—were the most important adaptations to land.



MOSS SEX

- ◇ Both algae and mosses can reproduce sexually or asexually. They do something pretty unusual: They alternate between a haploid and diploid generation. Diploid means 2 copies of the chromosomes; haploid means 1 copy of the chromosomes. Algae also alternate generations. Animals don't have a haploid life stage. The only haploid thing in animals is the sperm and the egg, and these things are not free-living as whole generations for any animal.
- ◇ The production of the sperm and the egg is pretty straightforward—only in mosses, it's a whole gametophyte generation that produces sperm and egg, which means that the whole free-living plant is either male or female with only 1 copy of chromosomes (it's haploid).
- ◇ Then, the sperm swim to the egg, which is located in a special chamber, the archegonium. This swimming is why most mosses are found in areas that will have occasional water, so that the sperm can swim to the egg.



- ◆ When the egg and sperm fuse together, the fertilized egg, or zygote, develops in the archegonium. But that fertilized egg is now diploid, with 2 copies of the chromosomes—1 copy from the egg and 1 copy from the sperm. It is called the sporophyte, and it produces spores.
- ◆ Spores are another important characteristic of the bryophytes. Not only do bryophytes lack true leaves, true roots, and vascular tissue, they don't even have seeds. They have spores instead.
- ◆ A spore is haploid. In the sporophyte, a process called meiosis occurs, which changes the diploid cells to haploid. This is the same process that occurs in our bodies to make gametes, meaning our eggs or sperm.
- ◆ Seeds are diploid. They have all the information to make a diploid organism. But in plants that don't have seeds, spores will germinate to form new haploid plants, and this haploid plant is called the gametophyte.
- ◆ The gametophyte plant then produces egg and sperm, each of which are also haploid, and returning to the beginning of the life cycle. This process is called alternation of generations because the haploid and diploid generations are alternating. Even though they're alternating, they are still attached, because the sporophyte, the diploid generation, will grow out of the gametophyte.
- ◆ Although there are similarities in algal and bryophyte reproduction—in the alternation of haploid and diploid life stages—when bryophytes became successful on land, they had not only the waxy cuticle and a dedicated place for the fertilized egg to develop, but they also had a more sophisticated approach to alternation of generations.
- ◆ For algae, alternation of haploid and diploid generations produces no important change in the body of the organism. But for bryophytes, the haploid body is very different from the diploid body, with the haploid body being better adapted to independent life on land.

- ◇ In most mosses, the haploid body looks like a short, leafy structure that stays close to the ground. This is so that water can accumulate within the moss and the sperm can swim to the egg. The diploid part of the moss is a delicate stalk on which the spore-releasing capsule perches to disperse the spores.
- ◇ All the bryophytes have 2 unique adaptations that enabled them to live on land: a protected place for the embryo to develop and the waxy cuticle. The mosses have one more adaptation, the development of stomata. These are small pores in the leaf that allow for the exchange of gases, meaning that carbon dioxide goes in and oxygen goes out and thus the gases are exchanged. This greatly enhanced the ability of the mosses to live on land.

PEAT MOSS

- ◇ *Sphagnum* is a genus of a few hundred mosses that are commonly known as the peat mosses. This group of mosses is economically important because of their water-holding capacity, which comes from the fact that sphagnum includes many dead cells surrounded by live cells.



- ◇ Sphagnum grows in watery, treeless bogs. But it doesn't just live in bogs; it can actually create these bogs. Because sphagnum moss can hold so much water, it can basically flood out other plants. In fact, sphagnum moss can hold roughly 20 times its weight in water.
- ◇ This amazing water-holding capacity will make it very difficult for tree roots to access oxygen, because wetland soil is lower in oxygen. Tree roots need oxygen because the cells in the roots undergo respiration, and those roots will drown in too much water because they can't get oxygen. Over time, trees, shrubs, and many other plants will die out, but the sphagnum moss will remain, robust in its engineered habitat.
- ◇ The lack of oxygen also slows down the growth of bacteria, and without bacteria, decomposition is also slow. Because of slow decomposition, the dead sphagnum accumulates over time; this is the peat moss with which gardeners are familiar.
- ◇ This slow decomposition also means that there aren't as many minerals being released back to the soil, so bogs are limited in nutrients. The bog of sphagnum is also highly acidic; over time, the sphagnum moss changes the acidity by lowering the pH.
- ◇ The process of having some sphagnum in a pond or lake to a whole bog with roughly 2 meters of sphagnum and other bog plants takes time—hundreds or even thousands of years. Because a peat bog takes so long to accumulate, harvesting peat for burning isn't a sustainable resource, at least not on the timescale of trees. Burning peat, which holds a lot of carbon, isn't great for the atmosphere.
- ◇ The International Peatland Society is working on a sustainable practices certification and guidelines so that some peat harvesting can take place and gardeners can continue to use peat moss.
- ◇ Peatlands occupy only about 3% of Earth's surface, yet they store perhaps twice as much carbon as all the forests on Earth put together. So, preserving peatland may be an especially efficient way to keep carbon locked away, while degrading peatland may have especially serious effects.

READINGS

Gilbert, *The Signature of All Things*.

Kimmerer, *Gathering Moss*.

QUESTIONS

- 1 What is a distinguishing factor of a plant? For example, how are plants distinguished from algae?
- 2 How is sphagnum moss an ecosystem engineer?

LECTURE
4

FERN SPORES AND THE VASCULAR CONQUEST OF LAND

Even though ferns have been on the planet for a very long time, their ancestry is still a bit of a mystery, and they do a lot of unusual things. Even though we may not use them much economically, at least not yet, ferns still have a lot to tell us about themselves and the rest of the plant kingdom.

FERNS

- ◇ Our understanding of ferns isn't as deep as it is for other plants. We don't use ferns for much economically. They don't have seeds, flowers, or fruits, so there isn't much to eat, though there are some edible species and parts. We don't use ferns for much beyond horticultural beauty.
- ◇ Even botanists find it difficult to figure out their phylogeny, or ancestral tree. The names of the phyla, which is the second largest category after kingdom, have changed over time, and fern species often look alike, even to botanists, but they have different genes, which prevents cross-fertilization. Plus, ferns are among the oldest land plants, so they've had a long time to mutate back and forth.
- ◇ There are many gaps in our evolutionary understanding of ferns. As the phyla now stand, there are 4 different phyla of ferns that are extinct, which means that these phylogenies get figured out for whole groups of plants using only what can be seen in the fossil record.
- ◇ Ferns are very good at invading an area after a disturbance, which, in ecology, is anything out of the usual that will disrupt the growth of plants. Disturbances can be small, such as a herd of deer coming through to graze, or big, such as a volcanic eruption. Hawaii has had several volcanic eruptions in the last century. When lava flows over the existing plant life, everything underneath burns up. Eventually, the lava hardens. Even though there is nothing but hardened lava to begin with, eventually plants find their way onto this lava to colonize it.
- ◇ About 6 different types of plants can colonize these lava fields. How long it takes these ferns to move in depends on the amount of water. On the dry side of the islands, it takes much longer for colonization to occur. If it's wet enough, the National Park Service reports that sword ferns can appear on flows after about a year. Apparently, this fern is intolerant of shade but very tolerant of sun and areas of low soil quality.

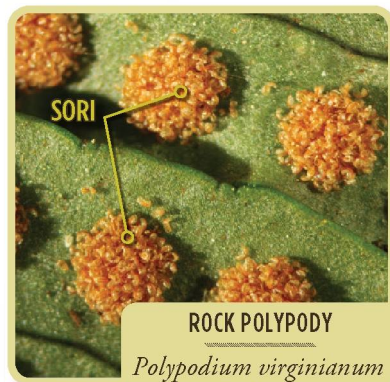
- ◇ In addition to needing water to grow, ferns, like mosses, need water to reproduce, because, like mosses, they still have swimming sperm. Like mosses, ferns need alternation of generations to reproduce, but ferns have a slightly different reproductive pattern. Still, there are some similarities with mosses, such as a free-living gametophyte stage.
- ◇ This haploid stage—meaning one copy of the chromosomes—is heart-shaped in ferns and is called the prothallus. This word is also used to describe the gametophyte of the mosses.
- ◇ This haploid prothallus contains both the archegonia, which will produce the egg, and the antheridia, which will produce the sperm. The prothallus also contains rudimentary rootlike structures called rhizoids, but it has no leaves. The prothallus grows flat on the ground, and it's small—about 2 to 5 millimeters wide.
- ◇ Then, as in mosses, the motile sperm must swim through at least a thin layer of water to the egg. The fertilized egg, or zygote, will then develop into the sporophyte, which grows right out of the archegonia to become the plant we recognize as a fern. In ferns, the gametophyte generation is still present, but it's much reduced. This trend will continue as we make our way to the seed plants.
- ◇ Like mosses, ferns produce spores instead of seeds. The spore is haploid and will produce the gametophyte. When we get to seed plants, there is no free-living gametophyte stage. Still, this way of life, with a free-living gametophyte stage, is very successful for ferns and mosses.
- ◇ Each fern plant can produce billions of spores, and each spore is about 20 times lighter than the lightest seed, and much smaller. This means that spores can travel massive distances on the wind. Fern colonization of the lava fields is probably more a result of getting there before seeds might be able to get there, rather than a specialized adaptation to germinating specifically on lava fields.



- ◇ This ease of dispersal is one reason why many ferns are invasive. Especially in the tropics, a field of ferns growing in full sunlight is an indication of a disturbance—usually, ground was cleared for gardening or grazing. These ferns form such dense thickets that trees cannot get established, and the forest cannot regrow without some assistance from people or another kind of disturbance, such as fire.
- ◇ Although ferns can travel anywhere, they can't survive everywhere. Unlike mosses, which thrive in the high latitudes, most ferns don't withstand cold very well, though both the Arctic and Antarctic possess several species.

DISTINGUISHING FEATURES

- ◇ Worldwide, there are anywhere from 10,000 to 15,000 species of ferns and what botanists call the fern allies, which are phyla other than the main phyla of ferns, which is Monilophyta. That name has changed over time to try to form a monophyletic group, which is a group that includes one ancestor and all of its descendants.
- ◇ Four other phyla generally included in the allies of ferns are all extinct. Those extinct phyla included the so-called seed ferns, which didn't so much die off as evolve into later seed plants. There are 2 phyla now that are extant, or still living: Lycopodiophyta, also known as the lycophytes or the club mosses, which are not actually mosses; and Monilophyta.
- ◇ Another phylogeny of ferns groups them into 4 classes, which is the next taxonomic level down from phyla. These classes seem to make the most sense. Plant phyla end in the suffix -phyta, classes end in -opsida, orders end in -ales, and families end in -aceae.
- ◇ Despite the difficulty in determining the fern phylogeny, all living ferns reproduce by spores. These spores are often the way you can determine if a plant is indeed a fern, or a fern ally.
- ◇ The spores are formed in organs called sporangia, and all the sporangia are typically grouped together in lines or small dots on the leaves of the fern. (Leaves for a fern are usually called fronds.) One of these small dots will contain numerous sporangia, and together these sporangia will form a sorus, which is one dot, or a group of sori, which is many dots.



- ◇ Another way to distinguish a fern is to determine where the leaves, or fronds, start. In ferns, all the fronds come from the base, and this is even true in tree ferns.
- ◇ Vascular tissue is the main adaptation that separates ferns from mosses. The development of this tissue cannot be overstated in its importance to life on land. Vascular tissue is equivalent to a circulatory system in animals. The difference between an animal that has to rely on diffusion for transport within the body versus an animal with a circulatory system is the same as the difference between mosses and ferns. All the other plants in this course have vascular tissue, and ferns got there first.
- ◇ All vascular plants have 2 main types of vascular tissue: the xylem and the phloem. The xylem transports water and minerals up from the ground, and the phloem transports sugars from photosynthesis in the leaves to the rest of the plant. The phloem typically travels along the inside of the bark in woody plants. Xylem and phloem are found in ferns, and no ferns are woody, not even tree ferns.
- ◇ Like other ferns, tree ferns don't have branches. All the fronds come from the top of the trunk-like stem. Also, like other living ferns and fern allies, tree ferns have lignin in the cell walls of the xylem. Lignin is a component of the cell wall in many vascular plants. Like cellulose, lignin is a polymer, but it is a polymer of phenyl propene basic units. Propene is a hydrocarbon, and phenyl signifies a 6-carbon ring with 5 hydrogens attached. This complex branching structure provides a lot of durability and strength to the cell wall.



- ◇ Together, vascular tissue and lignin provided the structure for all ferns to stand up and live on land, but tree ferns got even bigger. Tree ferns were very dominant growth forms, from about 200 million years ago, up until the extinction event that wiped out the dinosaurs. They were the quintessential dinosaur food. Most tree ferns living today are in the order Cyatheales.

LIVING IN THE UNDERSTORY

- ◇ While some tree ferns and the ferns that colonize lava fields can withstand full sunlight, many ferns are well adapted to living in the understory.
- ◇ Dr. Fay-Wei Li provided evidence about how ferns might have become adapted to living in the understory. It seems that many ferns that are adapted to full sun don't have a special photoreceptor called neochrome. A photoreceptor is a chemical within a plant that absorbs light.
- ◇ Most photoreceptors will only absorb light in a specific wavelength, but neochrome is special because it absorbs light in both the red and the blue. This means that ferns have a way to see in the dark understory. What's even more fascinating is that this trait wasn't just passed down from fern to fern in the 400 million years that ferns have been on the planet.
- ◇ Dr. Li showed that neochrome has only been present in ferns for about 179 million years. Dr. Li hypothesizes that genes were transferred between a hornwort and a fern about 179 million years ago and this is how some ferns are thriving in low-light levels. They borrowed the gene from a nonvascular plant, which perhaps got it from cyanobacteria.
- ◇ Fern dominance in low light is one reason why ferns make good houseplants. In fact, most of our common houseplants are understory forest plants that don't require a lot of light.

READINGS

Large and Braggins, *Tree Ferns*.

Mehlreter, Walker, and Sharpe, eds., *Fern Ecology*.

Moran, *A Natural History of Ferns*.

QUESTIONS

- 1 How are ferns different from mosses?
- 2 In what kinds of habitats would you expect to find ferns?



LECTURE 5

ROOTS AND SYMBIOSIS WITH NON-PLANTS

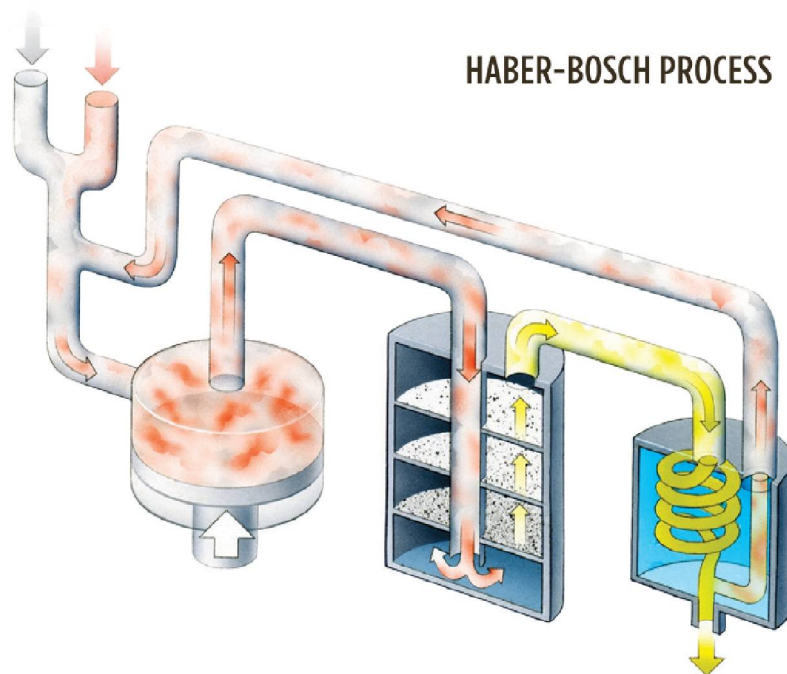
The biggest, tallest, heaviest, oldest living things depend on roots, even though we do not see most roots, because they are underground. Many people think of roots as going deep underground, but most roots are surprisingly shallow. Some plants are connected by a single system of roots and underground stems to form a single larger plant. All plants exchange friendly and unfriendly chemicals with each other through their roots, sometimes even across the species barrier, on a constant basis. Besides interacting with other plants, underground is also where most plants interact with bacteria to obtain nitrogen and where plants have symbiotic, often mutualistic, relations with fungi to increase the surface area of the plant root systems.

THE IMPORTANCE OF ROOTS

- ◇ Roots are so important that they are the first evidence of germination in the seed. When a seed has germinated, it has sent out its new root, which is called a radicle. Roots are where plants absorb water, but what else do they do? And how does that water get all the way to the top of very tall trees?
- ◇ One redwood *Sequoia*, named Hyperion, was measured at approximately 379 feet tall. Roots for such a tall tree are surprisingly shallow, only a few feet deep, but they can spread horizontally for 100 feet in all directions.
- ◇ Although trees have root pressure, due to osmosis, root pressure is not enough to make water travel that high. Osmosis is the movement of water through a semipermeable membrane, and plant cells are semipermeable, especially to water. So, if a root has a lot of solutes in it, then the water will move from the soil, where the concentration of water is higher, into the root, where the concentration of water is lower. So, water flows down its concentration gradient into the root, but that's not enough pressure to send water up to the leaves.



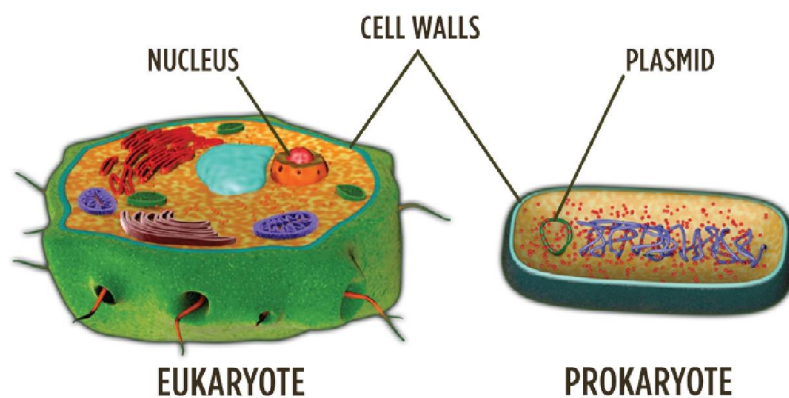
- ◇ For the water to get that high, it is drawn up by evaporation in the leaves. This means that the water concentration decreases as one goes up the tree. Because water is always moving from a greater concentration to a lesser concentration, it's moving up the tree to get to lesser concentration.
- ◇ The air outside the leaves will always have an even lower concentration of water than the leaves themselves, so evaporation is always occurring through the leaves. Moving water through the plant is called transpiration, so this particular process of water moving up and out of the plant is called evapotranspiration.
- ◇ But roots have much more to offer than just the uptake of water. Plants make their own sugars during photosynthesis, and for photosynthesis to occur, plants need other raw materials from the ground, including nitrogen, phosphorous, and potassium.
- ◇ The most important of these 3 elements is nitrogen, which is needed to make chlorophyll and DNA. Although the air we breathe is about 70% nitrogen, this is atmospheric nitrogen, or N_2 , which is a form that neither we nor plants can use. Plants need their nitrogen in a form where the nitrogen atoms can be removed and used, and N_2 is too energetically expensive for plants to break.
- ◇ The chemical process to make nitrogen fertilizer, the Haber-Bosch process, requires extreme heat and pressure to make ammonia, or NH_3 , which is a form of nitrogen that plants can use. Plants can also use NH_4^+ , which is the ammonium ion.
- ◇ Plants can also use nitrate, NO_3^- , which can be produced when lightning flashes through the sky, breaking N_2 bonds, and then rain brings the nitrate and other nitrogen oxides down to Earth. All of these molecules contain nitrogen, and because the bonds aren't as strong, plants can extract the nitrogen and use it.



NITROGEN

- ◇ All plants need a source of nitrogen, and most plants typically get it from bacteria.
- ◇ Bacteria don't have nuclei. They are in a group of organisms called prokaryotes, which means "before the nucleus." Plants and animals are eukaryotes, which means "true nucleus." Given that prokaryotes don't have a nucleus, they must have first evolved a long time ago, perhaps as early as 3.4 billion years ago, and some of these early bacteria were photosynthetic, though not exactly in the way that plants are today.
- ◇ Bacteria also have cell walls, though these are not like cell walls in plants. They have a completely different structure, and they are typically much smaller than a plant or animal cell.

- ◇ Bacteria do have chromosomes and genes, like plants and animals, but they are not contained in a nucleus. Bacterial genes are still on chromosomes, but they are free-floating in the cell.
- ◇ Bacteria also have extra pieces of DNA called plasmids, which are one reason why bacteria can change so quickly. Bacteria don't reproduce sexually; they simply divide. Mutation can occur and bacteria can exchange plasmids, but the genetic information of the bacteria can change quickly.
- ◇ Many people tend to think of bacteria only in pejorative terms. We call them germs and fight them with antibiotics. That's changing, and expressions like "probiotics" and "friendly bacteria" are more commonly understood. Plants have a lot to teach us about how bacteria can be very good, and the leading way bacteria are good is by providing usable nitrogen to plants.
- ◇ Bacteria can change atmospheric nitrogen into usable nitrogen in a process called nitrogen fixation. An organism that can fix nitrogen is called a diazotrope. Nitrogen in the atmosphere is pretty much inert because the 2 nitrogen atoms are joined together in a triple bond, which takes a lot of energy to break. Bacteria have special enzymes called nitrogenase that will break this bond and convert the nitrogen into ammonia. Other bacteria help decompose organic material to make nitrogen available to plants.



- ◇ There are about a dozen different bacterial phyla that can fix nitrogen. Some of these bacteria are free-living in the soil, using ammonia to make their own amino acids. Other bacteria are symbiotic with plant roots. The word “symbiotic” simply means living together. A symbiont doesn’t have to be beneficial. In the case of nitrogen fixing bacteria, these symbionts are beneficial. When both organisms of a symbiosis benefit, ecologists call this a mutualism.
- ◇ This mutualistic symbiosis occurs in the roots, and the process is best known in the legumes—the pea or bean family, called Fabaceae. This family has many species, and it has many species that we use for food, such as soybeans and peanuts. These beans and peas have the symbiotic bacteria rhizobia fixing nitrogen in their roots.
- ◇ Rhizobia infect the roots of the bean plant early on, so the seeds aren’t already inoculated with the bacteria when they germinate. In fact, the legume plant releases flavonoids, which are chemical want ads for rhizobia, into the soil. When the rhizobia sense the flavonoids, they release a chemical nodulation factor, which encourages the root to grow small nodules, which look like small peas attached to the roots.
- ◇ The bacteria form an infection thread to move in through the root hairs and fix nitrogen in their new home. The bacteria get a good habitat, and the plant gets a built-in source of nitrogen. The plant also feeds the bacteria sugars. Interestingly, although rhizobia can live in soil just fine, it can’t fix nitrogen when it’s free-living in the soil. It has to have a host.



- ◇ Not all legumes have associations with rhizobia. This leads to questions about how this mutualistic symbiosis came to be. It's possible that it evolved early on but then was lost by later descendants or that it evolved several times within the family. The mutualism is more common for legumes found in low-nitrogen environments. Rhizobia aren't the only bacteria that form symbiotic mutualisms with plants.
- ◇ Another genus of bacteria called *Frankia* form nitrogen-fixing root nodules with several types of woody plants. Even a few grasses get in on the action: Sugarcane, maize, and rice associate with different nitrogen-fixing bacteria that do not produce nodules. Bacteria have a variety of associations with plants. Some are very tight, forming nodules, and others are looser, with bacteria living in the area around the roots, called the rhizosphere.
- ◇ One exciting area of botany research involves seeing if other species can be coaxed into this bacteria mutualism. Because fertilizer is expensive to make and because plants only use about half of what gets applied, using bacteria to fix nitrogen across many kinds of crop species is an exciting idea.

OTHER MINERALS

- ◇ In addition to nitrogen, the other minerals that plants need are phosphorous and potassium. There is a host of macro- and micronutrients—including carbon, hydrogen, oxygen, phosphorous, potassium, nitrogen, sulfur, calcium, iron, and magnesium—that get into the plant the same way that water would, moving from a high concentration to a low concentration. Because it doesn't involve the movement of water, this process is called diffusion instead of osmosis.
- ◇ To pick up these minerals, plants need to have a lot of root area to exploit as much of the soil as possible. Overall, roots have 3 main functions: to support or anchor the plant, to absorb water and minerals, and to store carbohydrates. The first function of support can be met with the primary root system, which can be one big taproot or several fibrous roots. Most woody plants have a taproot first and then send out spreading roots.

- ◇ In addition to taproots and fibrous roots, there is another type of root called an adventitious root, which is derived from tissue other than root tissue. Adventitious roots often grow right out of the stem. A special example of adventitious roots are prop roots, which help prop up a plant, or provide extra support.



FUNGUS

- ◇ Another symbiotic mutualism that plants have to help increase the surface area of their roots occurs with fungus. Special types of fungus, called mycorrhizae, actually grow into the plant roots. The mycorrhizae are small threadlike structures of the fungus, called hyphae, that spread throughout the soil. The mycorrhizae increase surface area and therefore pick up extra nutrients, and the plant provides sugars to the mycorrhizae.

- ◇ Although they're special, mycorrhizae are very common; it's estimated that about 80% of all flowering plants and all of the gymnosperms have mycorrhizal associations.
- ◇ Scientists have found that the mycorrhizal associations beneath the forest soil connect trees of different species. Studies have also shown that trees can send chemical signals to each other via mycorrhizal connections.

READINGS

Capon, *Botany for Gardeners*.

Hodge, *Practical Botany for Gardeners*.

Kourik, *Understanding Roots*.

QUESTIONS

- 1 The beginning of the lecture talked about Pando, the giant clonal organism in southeastern Utah that might be the oldest and largest organism on Earth. Many plants are connected underground with underground stems or roots to form clones. What is a clone? What are the advantages to a clonal life-form? When would a clonal way of life not be so good?
- 2 What are mycorrhizae? Why are they so important for plants? What does the mycorrhizae get from growing with the plant?

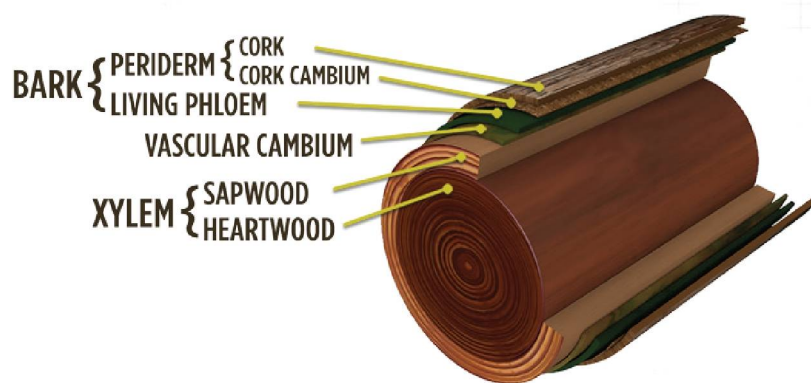
LECTURE
6

STEMS ARE MORE THAN JUST THE IN-BETWEEN

Stems—from the long stem of a rose to the amazing cork of *Quercus suber*—all seem to share 2 functions: gas exchange; and the transport of water up from the ground and the movement of sugars down to the roots. But there are exceptions. In early spring, the direction of movement is reversed, until leaves can be formed. Modified stem types exist that can store sugars. Stems can be rhizomes, below ground, where they look like roots. The stem is the vascular core of the plant, and arguably the overlooked heart of what it means to be a plant.

CORK

- ◇ Cork is the outermost layer of a stem. Many people would call this the bark, but the bark actually includes the cork. It also includes the phloem, which is the tissue that carries sugars from the leaves to the root. If all layers of the bark are removed, all the way around the tree—a process called girdling—then that will kill the tree.
- ◇ When cork is harvested, the inner bark is left intact. It's also important that the cork cambium is left intact. This is a layer just inside the cork and outside the phloem that will produce the new layer of cork. Any tissue called a cambium will produce other tissues.
- ◇ The cork is made up of cells that have cell walls that are filled with suberin. Sort of like lignin, the complex substance that provides toughness and allows ferns to stand tall, suberin is a complex substance that provides waterproofing. In fact, suberin is so complex that the molecule's exact structure is still being determined.



- ◇ All woody plants have cork. The *Quercus suber*, found throughout the Mediterranean coastlands, produces a lot of cork, which has a lot of suberin. Another oak, such as *Quercus rubra*, or red oak, doesn't produce nearly as much cork.

- ◇ The Mediterranean region, where cork grows, has hot, dry summers, perfect for fire. So, having a big cork means that the inside of the tree can be protected from the fire. Cork is fire resistant, so the fire, especially if it's a ground fire that doesn't get too hot or into the canopy of the tree, will just burn around the cork tree, leaving it unharmed.



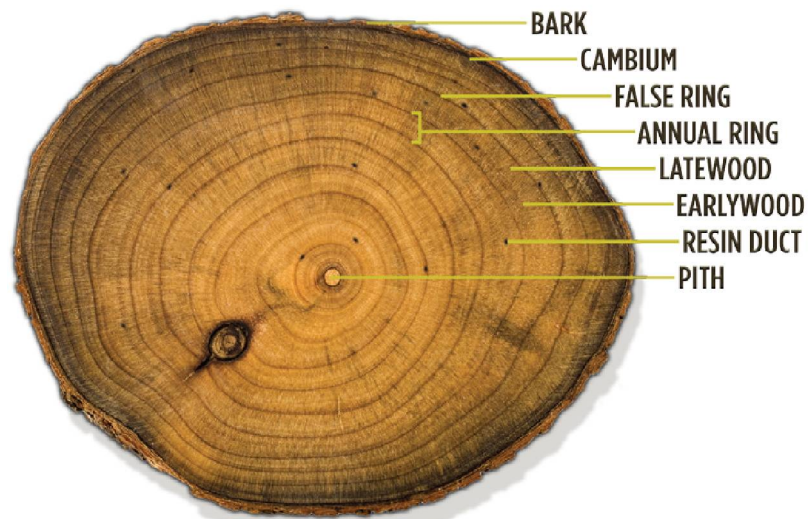
- ◇ On the outside, any woody stem has this structure: The cork is on the outside, and surrounding the cork is cambium (where new cork is made), which together are called the periderm. Inside the periderm is the phloem, which first appeared in ferns but is fundamentally the same for all vascular plants. The phloem transports the sugars from fronds or leaves down to the roots. There may be other parts of the plant that need sugars, too, such as developing fruits, and the phloem would transport sugars there.
- ◇ Interior to the phloem and xylem of the stem is the vascular cambium, which makes new vascular tissue. Cells within the vascular cambium differentiate to phloem on the side that is closest to the outside of the trunk, and cells nearest the inside become the xylem cells. The cells in the vascular cambium start off as undifferentiated stem cells, and as they move into the xylem or phloem, they develop traits of those tissue types. The accumulation of these xylem cells creates wood. Lignin is the substance responsible for toughness in the plant cell, and xylem cells are heavily ligninized.

- ◇ Both the phloem and the xylem don't contain just one type of cell. Like the blood of humans, numerous kinds of cells are involved. The cells are specialized in terms of their function. Many of the cells of the phloem are specialized to transport sugars. Likewise, many of the cells in the xylem are specialized for transporting water.
- ◇ The words “xylem” and “phloem” refer to all of the following: the tissue type, the cells that make up the tissue, and the fluids within the tissue. The 2 most important cells in the xylem are tracheids and vessel elements, both of which are lined with pits that open and close in very sophisticated ways to make sure that water gets to the parts of the plant where it's needed most.
- ◇ Like most other parts of the plant, stems also have 3 other basic tissue types: parenchyma, collenchyma, and sclerenchyma. Parenchyma are the cells with the thinnest walls, collenchyma has uneven walls, and sclerenchyma has the thickest walls.
- ◇ All of these cells are found throughout the xylem and phloem. Their function relates to their structure. The parenchyma cells usually act as storage cells because it's easy to get things in and out of a thin cell wall. Collenchyma cells typically provide fiber and a dynamic structure. Sclerenchyma cells provide even more structure.

TREE RINGS

- ◇ Trees can tell time. Tree rings are concentric rings in the tree as seen when the tree is in cross-section. The rings form because of the seasons. In the wintertime, the tree is growing very little if it's an evergreen, and not at all if it's a deciduous tree that has lost its leaves for the winter. Because the tree isn't taking up a lot of water and is making very few sugars to store in the wood, the cells are small, and therefore the cell walls are close together. This makes the rings darker in the winter.

- ◇ In the spring and summer, the trees are growing more quickly and the cells are larger, so the lighter wood between the dark rings is the wood that is laid down in the spring and summer. The dark rings put down in winter are called the latewood, and those laid down in the spring and early summer are called the earlywood.
- ◇ Tree rings can answer questions about climate change, fire history, and archaeology, so they are very useful. But not all trees have tree rings. Because the rings form due to the seasons, in climates that are not seasonal, trees will grow without obvious tree rings. Therefore, finding tree rings in tropical trees is very difficult. Many tropical climates have a wet season and a dry season, but for most species, the dry season is not long enough, or dry enough, to produce a visible ring.



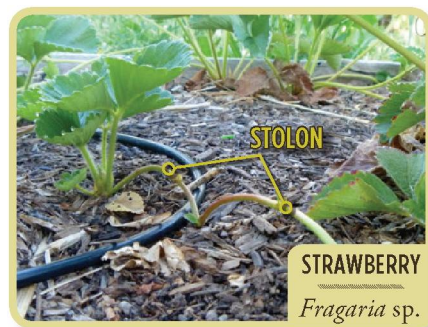
STEMS

- ◇ All stems start out as herbaceous stems, while only some become woody over time. When the stem first comes out of the seed, it's herbaceous material. The word “herbaceous” means anything that isn't woody, so this would include a grass, a buttercup, or a mint—any plant without woody growth.
- ◇ After the stem develops for a while and the cells start to differentiate, the cells in the xylem will get lignin deposited in their cell walls, and those cells will become wood. In this way, the development of the cork also comes later.
- ◇ Herbaceous stems don't have annual rings or wood, so the arrangement of the vascular tissue looks different. The arrangement of these tissues within the stem is an important clue to evolutionary relationships.
- ◇ The mosses didn't have vascular tissue, but the ferns did, so the arrangement of xylem and phloem within fern stems is considered the ancestral arrangement. The earliest vascular seedless plants have phloem that surrounds the xylem or columns of phloem dispersed within the xylem. Either of these arrangements is called a protostele.
- ◇ There are some unique types of stems. There is an important type of underground stem called a rhizome, also known as rootstock. You may wonder why a rhizome is a stem if it's growing underground, and the answer has to do with the arrangement of vascular bundles.



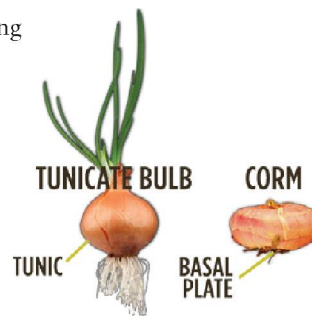
- ◆ The arrangement in a rhizome resembles the vascular arrangement in stems, not in roots. Rhizomes also lack root hair, so they are not absorbing water. The function of the rhizome is to spread the plant vegetatively. Many grasses are rhizomatous, as are many weeds that spread really well, such as bamboo. Rhizomatous trees include aspens and poplars.

- ◆ Another type of horizontal stem that grows on top of the ground, rather than underneath it, is a stolon, or runner. These are most familiar in strawberry. Although a stolon can have some rooting from the nodes of the stem, the main function of the stolon is the same as a rhizome, to allow the plant to spread clones.



- ◆ Other stem modifications are bulbs and corms. A bulb is often underground, but tulip bulbs and onions are both botanically stem tissue, rather than root tissue, for the same reason that rhizomes are stems.

- ◆ A corm is a bulb that is solid, meaning that it is swollen stem tissue that does not have leaves and has a basal plate, where roots will come from. Gladiola and crocus both have corms. A tuber, such as the potato, is another modified swollen stem that is underground, but it lacks the basal plate that corms and bulbs have.



- ◆ All of these modified stems are for storing sugars, but they can also give rise to new plants via vegetative propagation. “Vegetative” just means clonal, with the offspring identical to the parent plant.

- ◇ Although we typically don't think of stems as the site of photosynthesis, there are a number of stems that do photosynthesize. Basically, any stem that is green is photosynthesizing. Stem photosynthesis is especially prevalent in areas where leaf size might need to be reduced, such as climates that are hot or dry or maybe very windy.
- ◇ Stems also have gas exchange, which means that they exchange their waste (oxygen) for the gas they need (carbon dioxide). This gas exchange occurs through small, somewhat spongy openings in the stem called lenticels. Lenticels are visible to the naked eye, especially on the branches of woody plants. On trees like birch, with smooth bark, they're pretty obvious, but trees with thicker, rougher bark have lenticels, too.
- ◇ They look like small splits in the wood, but they are there on purpose to exchange gasses. If the stem isn't photosynthetic, then these lenticels can take in oxygen, because cells that don't photosynthesize will respire, just like the respiration in our cells.

READINGS

Capon, *Botany for Gardeners*.

MacAdam, *Structure and Function of Plants*.

Speer, *Fundamentals of Tree-Ring Research*.

QUESTIONS

- 1 Describe the difference between primary and secondary growth in stems.
- 2 What is dendrochronology? What kinds of applications can you think of that would use dendrochronology?

LECTURE
7

THE LEAF AS A BIOCHEMICAL FACTORY

Leaves can be surprising. We know that they are green and that they harvest light. We also know that we can eat some of them. But leaves showcase a myriad of sizes, shapes, and functions. For example, botanist Heather Whitney studies iridescence in the peacock begonia, whose leaves resemble a peacock feather—deep blue and green and shiny. There are even underground leaves. In Brazil, a species called *Philcoxia minenensis* has normal aboveground leaves, but it also has leaves that grow under the soil.

LEAVES

- ◆ Leaves from the coca plant are the raw ingredient for cocaine, but a lot of processing occurs to concentrate the cocaine from the coca leaf. Cocaine is an alkaloid, which means that it is a class of small molecules containing nitrogen. These alkaloids are alkaline, or basic.
- ◆ For humans, these compounds can act as psychotropic drugs that alter the brain, and this can happen in insect herbivores, too, causing disorientation. However, the alkaloids' main effect on other animals disrupts the digestive system.
- ◆ High alkaloid content will cause nausea in many animals, so a plant that produced these chemicals in high quantities would be less likely to be fed on and would therefore be more successful in producing successive generations.
- ◆ These compounds might even have a greater physiological effect on human digestion if our mouths and stomachs weren't so acidic. The acidity neutralizes the alkalinity of the alkaloid compounds. Without these defensive chemicals, the plants would be damaged much more by herbivores.
- ◆ Other than leaf protection, these chemicals aren't involved in photosynthesis. Because of this, these class of chemicals are called secondary compounds. It could be that these compounds are actually waste products. And unlike animals, plants store their waste products.
- ◆ Plant waste isn't so wasteful: The 2 products of photosynthesis are oxygen and glucose. Oxygen isn't stored at all; it's released to the atmosphere. The sugar glucose does get transformed into other products, such as cellulose, and then assimilated into many different storage products, such as wood and cell walls.
- ◆ There are chemicals in the leaf that the plant is using, and most of these involve photosynthesis. One of the major keys to photosynthesis is the plant pigment chlorophyll. A pigment is any chemical that can absorb light, and chlorophyll absorbs the wavelengths of light that are not green,

so the red and blue. When the chlorophyll goes away in the autumn, we see the other pigments that are in the leaf: the orange and yellow of beta carotenes and the red of anthocyanins.

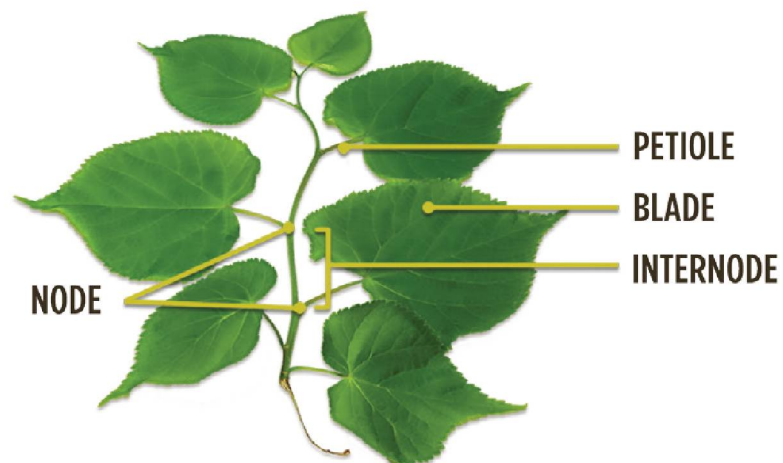
- ◇ How animals react to the red color in leaves is not so apparently advantageous to the plant. Red is often seen in developing leaves, and primates tend to prefer these leaves. Of course, this is not an advantage to the plant because all of its young leaves are eaten.
- ◇ But there are many hungry animals that depend on leaf eating. Although we broadly think of such animals as herbivores, an animal that has only a diet of leaves is called a folivore. There's been a lot of research into what kinds of leaves animals prefer, and this research provides clues as to the nutritional value of these leaves.
- ◇ Plants, however, don't make leaves to feed animals, or even to make them sick, or to provide brilliant fall colors for us. Leaves are to absorb light and power the photosynthetic machine. The structure of a leaf is tied to its function.
- ◇ Leaves are flat and thin, typically, but some leaves are more succulent than others, and some leaves, such as those of evergreen conifer trees, are needle-shaped and not flat at all.
- ◇ The thickness of the leaf depends on the amount of sunlight the leaf is trying to absorb. If the leaf is in full sun, it will likely be smaller and thicker because the leaf is not limited by light. If the leaf is growing in the shade, it is likely to be thinner and have more area, as it's trying to capture every bit of light it can get.



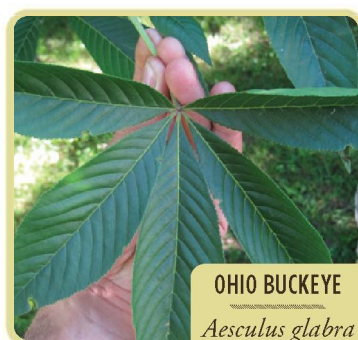
PARTS OF A LEAF

- ◆ Plants are typically arranged with nodes, where the leaves come out, and the stem space between the leaves, which is called the internode. The arrangement of leaves on the stem is also called phyllotaxy, and it's an important characteristic in identifying plants.
- ◆ Leaves can be opposite of each other on the stem, such as on dogwoods or maples; or leaves can be alternate, such as on elms; or they can be arranged in a whorl, which means a circular arrangement of leaves around the stem, such as on bedstraw.
- ◆ Overall, the leafy part is called the blade, and the stalk that attaches the blade of the leaf to the stem is called the petiole.
- ◆ The way botanists determine if something is a leaf or not is by the presence of an axillary bud in the junction where the petiole attaches to the leaf. If there is a small bud present, then the structure is a leaf. A petiole is just like a mini-stem to the leaf. The difference between a stem and a petiole is that the petiole attaches the leaves to the stem.





- ◆ If there is no bud, it's what botanists call a leaflet, attached to a vein. These are very similar to the veins of animals. The veins are where the vascular tissue, the xylem and phloem, come into the leaf, or leaflet.
- ◆ There are specialized terms that describe venation patterns: parallel, like in grasses; palmate, like a maple leaf; and pinnate, like elms.
- ◆ A leaf that is divided into many leaflets is called a compound leaf. Some are palmately compound, such as buckeye. Many are pinnately compound, such as hickory or walnut.



- ◇ This is how we can tell that the whole frond of a fern, even a large frond of a tree fern, is all one “leaf.” Other trees have simple leaves that are partially divided, such as lobed leaves.
- ◇ In addition to gathering light, leaves have to not blow off the plant and can’t overheat. Being a leaflet is a good solution to both of these problems. Smaller leaves, or leaflets, provide less resistance to the wind, so they would be less likely to blow off of the tree, and the wind going by them would cool them down. This is one reason many desert plants have leaflets.
- ◇ There are hundreds of terms that describe everything about a leaf—from the surface, to the number of hairs, to the overall shape, to the margin (the outside perimeter). The reason for this proliferation of terms is that leaves are often the easiest or most accurate way to identify a plant.
- ◇ There are even terms for the shapes of the hairs on the leaves. These hairs are called trichomes, and they are cool because they do more than help botanists tell plants apart.
- ◇ One function of these hairy trichomes is that they can be glandular. This is sort of like a hair follicle in people with a sweat gland at the base. Plants that have a lot of oils on their surfaces, such as basil, have a lot of trichomes where there are exudates of oil.
- ◇ Trichomes also serve as anti-herbivory structures. Just the presence of many trichomes can make the leaf unpalatable to an animal or gum up the mouthparts of an insect. Trichomes are also responsible for the sting in stinging nettle.



- ◇ Another very important function of trichomes is to increase the boundary layer around the leaf. This is the layer of air just next to the leaf. The hairs will help slow the air passing over the leaf, which decreases the amount of evaporation out of the leaf.
- ◇ This reduction of evaporation is important because water is lost through small openings in the leaves called stomata. Typically, leaves have more stomata on the underside to reduce water loss because the underside of the leaf is in the shade.
- ◇ The stomata are surrounded by 2 semicircle shapes, which are the guard cells. They open and close the stomata based on how drought-stressed the plant is, balanced with the need for carbon dioxide. So, the stomata are the sites where carbon dioxide diffuses into the leaf and where oxygen is released. At the same time, when the stomata are open, water is evaporating, and this is what makes possible evapotranspiration.
- ◇ Some transpirational loss is good because this is the process that pulls water up from the roots. But too much transpirational water loss will cause the cells to lose water and become flaccid, and the plant will wilt.
- ◇ Sometimes having leaves can be too costly in terms of water loss. Like so-called evergreens dropping their needles, most tropical trees gradually replace their leaves pretty quickly—anywhere from 2 months to 2 years.
- ◇ If the leaves don't last as long as the tree lives, what is the mechanism for the tree losing its leaves? Deciduous trees lose their leaves before winter. Some plants drop their leaves before a time of drought, and these plants are called drought-deciduous. These plants are common in deserts and arid lands. These may be the ultimate cues, but what is the mechanism in the plant?
- ◇ Plants have hormones that cause many of the developmental changes throughout a plant's life. Hormones tell the plant when to grow, which way to grow, and when to shut off certain parts, such as leaves.

- ◇ Nineteenth-century German botanist Julius von Sachs first proposed the idea that chemicals produced in one part of the plant would effect changes in another part of the plant. Much of the early knowledge of hormones was derived from similar studies occurring in animals.
- ◇ There are 5 main types of plant hormones. Of these, auxin was the first hormone to be discovered, and it's one of the first hormones to be expressed. Along with the hormone cytokinin, auxin is required for the plant to live. The ratio of these 2 hormones control many functions in the plant.
- ◇ Auxins are the longest-studied group of hormones, but there are other growth hormones, and botanists are discovering new chemical messengers and regulators all the time.

READINGS

Coombes, *The Book of Leaves*.

Farmer, *Leaf Defence*.

Lee, *Nature's Palette*.

Vogel, *The Life of a Leaf*.

QUESTIONS

- 1 How is a leaf botanically determined to be a leaf and not some other part of the plant or a leaflet?
- 2 Describe a tropism. Think about how differently plants and animals respond to their environments. Have you seen a plant tropism in action? What was it like?

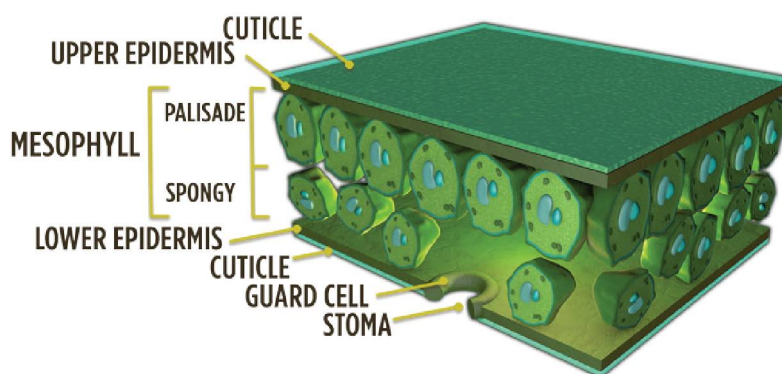
LECTURE
8

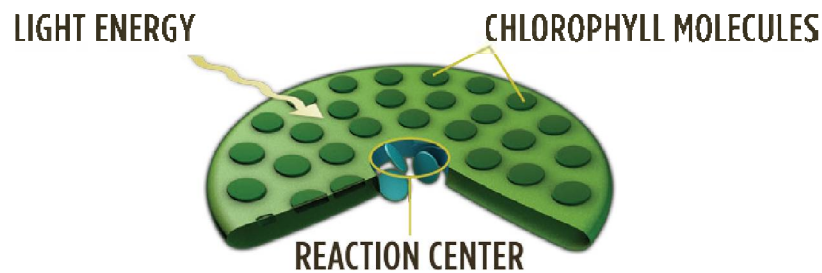
PHOTOSYNTHESIS EVERYONE SHOULD UNDERSTAND

Almost everything in our world depends on the biochemical process of photosynthesis. It is through this cycle that plants and trees are able to become so gigantic through molecules so small we can't even see them. The main difference between animals and plants is that animals have to consume mass to get energy, whereas plants are able to make their own energy from nothing other than sunlight, gas, and water.

THE ANATOMY OF A LEAF

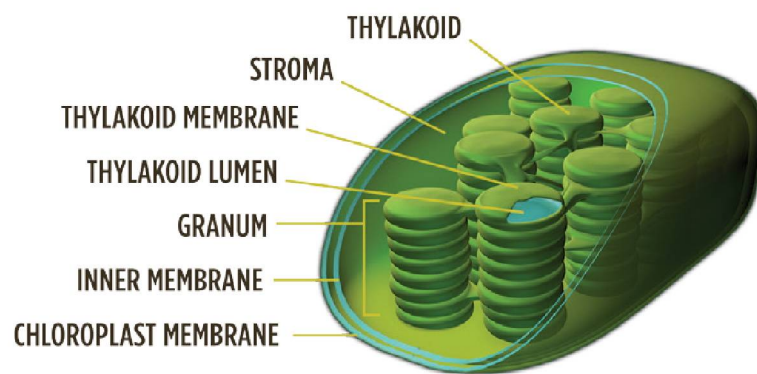
- ◇ Beginning on the top of the leaf, there is usually a layer of wax, called the cuticle. The waxy cuticle prevents water loss through the top tissue of the leaf. This is important, because the top is where most of the sunlight will fall, and this part of the leaf can heat up, and the evaporative loss could be quite great, but the cuticle will prevent most of this loss. The cuticle can also help reflect some sunlight as well, which is important in keeping the leaf from overheating.
- ◇ Next is a layer of epidermal cells. Like the epidermal cells in our own skin, these cells help protect the underlayer of cells in the leaf.
- ◇ After the epidermis, we get to the action site of the leaf, the parenchyma. This is typically where the majority of photosynthesis takes place. Parenchyma cells have thin walls, and these will be the majority of cells in the center of the leaf. These cells contain organelles called chloroplasts, which is where photosynthesis takes place. An organelle is to a cell what an organ is to a body. They are smaller subcellular structures that enable certain physiological processes.
- ◇ The chloroplast is so named because it contains chlorophyll, which is the green pigment that enables the process of photosynthesis.





- ◆ Plants have to be green to photosynthesize. Not all cells of the plant have chloroplasts; they are not in the roots, for example. However, because the leaf has chloroplasts, it has chlorophyll, and that is why the leaves appear green. Chlorophyll appears green because it absorbs most wavelengths of light, except green, which it reflects.
- ◆ There are other pigments in the leaf, and these are important for absorbing other wavelengths of light. Beta carotenes appear orange-yellow because they are reflecting those wavelengths and absorbing in the green-blue wavelengths. Anthocyanins reflect red and absorb mainly in the green wavelengths, where chlorophyll doesn't absorb at all.

CHLOROPLAST



- ◇ The chloroplast is shaped like an elongated jellybean. The outer part of the jellybean is called the chloroplast membrane. Inside the chloroplast jellybean are single layers and stacks of pancakes or pita bread, called thylakoids. The purpose of the shape of the pitas is to maximize surface area: The higher the surface-area-to-volume ratio is, the more efficient the structure can be.
- ◇ The outer part of thylakoids, the “skin” of the pita, is called the thylakoid membrane. The inner part, or the space inside the pita pancake, is called the thylakoid lumen.

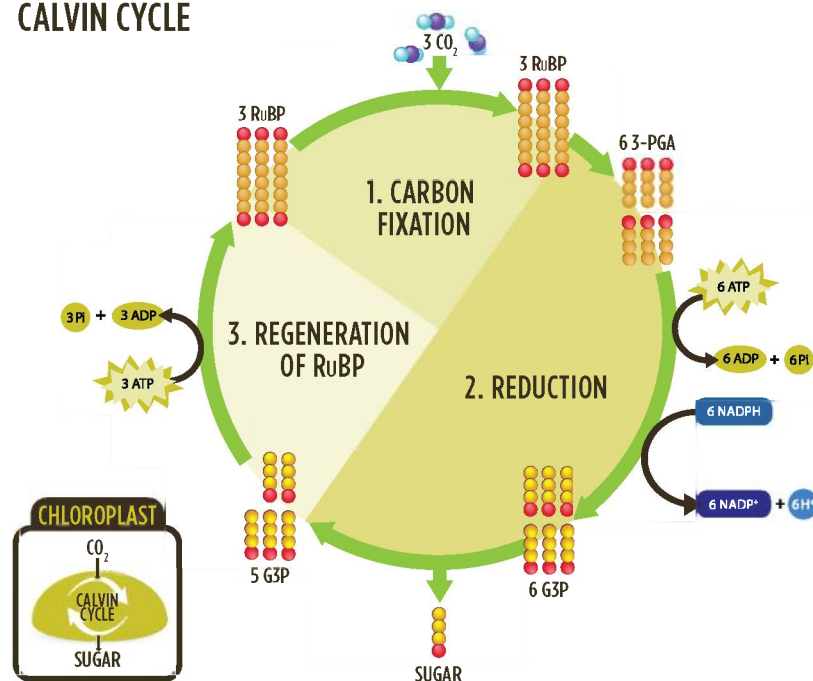
PHOTOSYNTHESIS

- ◇ There are 2 steps in photosynthesis: the light-dependent reaction (or light reaction), which occurs within and across the thylakoid membrane; and the light-independent reaction (or dark reaction), which occurs in the stroma, which is inside of the chloroplast but outside of the thylakoids.
- ◇ The light-dependent reaction harvests sunlight energy, and the light-independent reaction uses the energy from the light reaction to turn carbon dioxide into sugar. Both of these 2 reactions are necessary for the process of photosynthesis. It’s also important to understand that the light-independent, or dark, reaction doesn’t occur at night; the phrase “light-independent” means that this reaction isn’t actively harvesting light. The light-independent reaction also uses products from the light reaction to turn carbon dioxide into sugar—specifically, a 6-carbon sugar called glucose.
- ◇ The light-dependent reaction takes place on and through the surface of the thylakoid membrane, or the skin of the pita pancake. Embedded within the thylakoid membrane are many chlorophyll molecules. Chlorophyll is the green pigment that can absorb light (except green light, which it reflects).

- ◇ Many chlorophyll molecules are specially arranged together within the thylakoid membrane to make an antenna that intercepts photons, which are discrete packages of light. All the photons within several chlorophyll molecules get concentrated together, and this group of chlorophyll molecules is called a reaction center.
- ◇ All the photon energy within the reaction center then causes one particular chlorophyll molecule to have an electron that gets excited. This excited electron is unstable, meaning that it can be transferred to another molecule.
- ◇ In the reaction center of photosynthesis, phaeophytin will pass an electron down to plastoquinone. This is like the biochemical pathway of photon energy, only now the energy from the photons has been changed into the energy carried by one electron, so this electron is moved down the line, called the electron transport chain. This is how energy is transferred from molecule to molecule.
- ◇ Interestingly, the electron that gets excited was originally donated from the splitting of water to create an electron, a proton, and oxygen, so this is where and when plants produce oxygen.
- ◇ Together, the reaction center and the electron transport chain are called the photosystem, and there are actually 2 photosystems, but the first one to generate the excited electron from the splitting of water is called photosystem II. Photosystem I is where the excited electron goes to generate the products that will be necessary for the light-independent reactions.
- ◇ The whole point of photosystem II is to use the light energy to drive one proton, also called a hydrogen ion, across the thylakoid membrane and into the thylakoid lumen. As this process continues, we have a buildup of protons on one side of the thylakoid membrane.
- ◇ There are many protons on one side of the membrane and many fewer protons on the other side, and they all want to get through the membrane. The protons want to move down their concentration gradient—from the side with a lot of protons to the side with fewer protons.

- ◇ However, the only way the protons can get to the other side is through a turnstile called ATP synthase complex. ATP stands for adenosine triphosphate, and it is a molecule that can carry energy around in the cell. ATP synthase is an enzyme—a protein that can make reactions occur faster—that can make ATP, but it can only make ATP if it has the proper starting material, which is ADP, adenosine diphosphate, and the energy from protons moving down their gradient.
- ◇ In addition to creating the ATP from the ATP synthase, photosystem I also generates a molecule called nicotinamide adenine dinucleotide phosphate (NADPH). This molecule is important because it can carry protons and electrons around in the cell to do work. ATP and NADPH are both used in the light independent reactions.

CALVIN CYCLE



- ◇ The ATP and NADPH that were made from the light-dependent reaction now go to the light-independent reaction, which occurs outside of the pita pancake, and this space is the stroma. The light-independent reaction is also called the Calvin cycle, named after Melvin Calvin, who discovered it in 1950. It is also called the C3 cycle, because the cycle starts with 3 carbon dioxide molecules entering the cycle, one at a time.
- ◇ The light-independent reaction is a cycle, so we could start anywhere in the cycle and the cycle will just keep going. We're going to start with a 5-carbon sugar by convention, but this is the last product of the cycle. In an overview, this is the part of the cycle where carbon dioxide is taken up to create sugars. When carbon dioxide is added onto other sugars, this is called carbon fixation.
- ◇ The carbon dioxide is taken into the leaf through the small pores called stomata, which typically are on the underside of the leaf so as to be in the shade and reduce evaporation of water out of the leaf. These pores are surrounded by guard cells that regulate the opening and closing of the leaf based on the water status of the plant.
- ◇ When the plant has plenty of water, the stomata are open and carbon dioxide is diffusing into the leaf, but if the plant is drought-stressed, the guard cells will keep the stomata closed, and then the plant can't get carbon dioxide and can't undergo photosynthesis.
- ◇ Just as in the light reaction, the dark reaction is also catalyzed by an important enzyme. The enzyme in the dark reaction is called RuBisCO, which stands for ribulose-1,5-bisphosphate carboxylase/oxygenase. Ribulose bisphosphate is the 5-carbon sugar.
- ◇ Through the action of RuBisCO, a carbon atom from a carbon dioxide molecule is added to the 5-carbon sugar ribulose bisphosphate. Now we have a 6-carbon sugar, but it almost instantaneously splits into 2 3-carbon sugars called 3-phosphoglycerate.

- ◇ ATP from the light reaction will be used to put an extra phosphate atom onto the 3-carbon sugar, and it becomes 1,3-bisphosphoglycerate. Then, the other product from the light reaction, NADPH, breaks that phosphate off.
- ◇ This might seem curious, but it occurs because the phosphate bond to the sugar contains a lot of energy. When it's formed, it requires energy, using the ATP, and when it's broken, it releases energy that allows other reactions to occur. What really needs to occur in this process is that sugar must get made—and the cycle continues.
- ◇ The sugar that is formed then leaves the Calvin cycle. This sugar is called glyceraldehyde-3-phosphate (G3P), and it can make many different kinds of carbohydrates, such as cellulose or starch. In fact, 6 of these G3P sugars are made, and one of these molecules leaves the Calvin cycle to become sucrose or starch. The remaining 5 3-carbon sugars then get shuffled around with the help of ATP to form 3 5-carbon sugars. And each one of these 5-carbon sugars is the beginning of the cycle again: ribulose biphosphate.
- ◇ About 95% of the plants on Earth accomplish photosynthesis in the manner that was just described, but there are a few variations on this theme. The first variation is called the C₄ pathway (C₄). In this pathway, carbon dioxide is picked up by a different enzyme, called PEP carboxylase, and then the first product is a 4-carbon sugar called oxaloacetate.
- ◇ The benefit of the C₄ pathway is to avoid photorespiration. This can occur when there is light, but photosynthesis isn't happening—respiration is happening instead. The enzyme RuBisCO used in the Calvin cycle has an affinity to pick up carbon dioxide, but it will also pick up oxygen, and its probability of doing so increases with increasing temperatures.
- ◇ Plants that use the C₄ pathway pick up carbon dioxide using PEP carboxylase and then transfer the carbon as the sugar malate or aspartate to a whole different cell, called the bundle cell, where the normal Calvin cycle will take place. In this way, the carbon dioxide and RuBisCO, which is still present in the Calvin cycle, are spatially segregated so that RuBisCO doesn't encounter oxygen.

- ◇ A little less than half of the grasses use the C₄ pathway, and this group makes up the majority of plants that use it. Plants growing in warm conditions are most likely to use the C₄ pathway. Economically important species that use the C₄ pathway are sugarcane and corn.
- ◇ Another variation on this theme of photosynthesis is called crassulacean acid metabolism (CAM), which is commonly found in desert plants.

READINGS

Halle, *In Praise of Plants*.

King, *Reaching for the Sun*.

QUESTIONS

- 1 How does gas become mass in plants?
- 2 What are some environmental factors that would limit photosynthesis?
- 3 Farmers and growers aren't that interested in photosynthetic rates because these often don't correspond directly with yield. Why might this be?

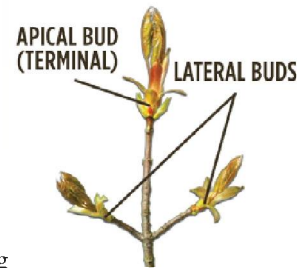
LECTURE
9

DAYS AND YEARS IN THE LIVES OF PLANTS

How does a plant know when to flower? And is climate change causing plants to flower earlier? This lecture will consider these questions by taking a 21st-century approach that will involve genes, which are recipes for proteins, and gene regulation, which determines which genes get activated. This determines which proteins get made, and those proteins, in turn, cause changes in the plant.

HOW DOES A PLANT KNOW WHEN TO FLOWER?

- ◇ Flowering is promoted by internal cues of hormones and the status of buds. If the bud is at the tip of a branch or plant, it's called the apical bud. This bud is also called the terminal bud, because it's at the terminal end of the branch or plant.



- ◇ Those buds that promote growth to the sides are called the lateral buds. Flowering can also be promoted by environmental cues. Two important cues are light and temperature. The light cue is called photoperiod, or the amount of light a plant sees during a certain time frame. With regard to the temperature cue, the amount of cold a plant experiences is just as important as the amount of heat it experiences.
- ◇ Phenology is the study of the timing of biological events. This timing can be seasonal or daily. A circadian rhythm is a pattern that exists over 24 hours, or 1 day.

- ◇ Plants are classified according to the length of photoperiod they need to flower. Short-day plants need a day that is less than 12 hours to flower, which would mean a short day, so they would flower in early spring or late fall. An example of a short-day plant is a Christmas cactus, which flowers in the late fall.



- ◇ A long-day plant would need a day longer than about 12 hours to flower, so these are plants that flower in the midsummer. Many of our midsummer vegetables are long-day plants, such as potatoes and spinach. In both cases, there is a critical length that must be met so that flowering occurs.

- ◇ Some plants are day-neutral plants, which don't flower in response to day length and instead flower in response to a different environmental cue. An example of a day-neutral plant is a tomato, which typically flowers in response to temperature. Many other day-neutral plants also respond to temperature, and this is why we see a proliferation of flowers after a particularly warm spring weekend.
- ◇ Although photoperiod is important for all plants, the degree of its importance is different for different species; that is, some plants use photoperiod as a cue, but they also respond to temperature—usually soil temperature, but also air temperature.
- ◇ How are plants sensing the length of the daylight, or the photoperiod? Plants sense the length of the night instead of the length of the day. Plants that flower early in the spring flower after long nights. Plants that flower in the middle of summer flower after short nights. And this effect is reversible because of a unique chemical in their leaves called phytochrome.
- ◇ If you interrupt a long night with light, then the plant “sees” a short night, and if it's a short-day plant, it won't flower. Likewise, if you break a long night up with a shot of light in the middle, the plant “sees” a short night and will flower, if it's a long-day, and thus short-night, plant. This interruption of flowering occurs inadvertently because of nighttime lighting.
- ◇ In the 1930s, Russian scientist Mikhail Chailakhyan conducted grafting experiments to determine how flowering was induced. A graft is when you take part of one plant—for example, the tip, which is also called the scion—and attach it to the base, or rootstalk, of another plant. When a plant is grafted, one plant can be connected to another by small pieces of tape.
- ◇ By conducting these experiments, Chailakhyan showed that the leaves were communicating the readiness of flowering. If Chailakhyan took a plant that was ready to flower and grafted it onto a plant that was not ready to flower, the plant would flower. And if a leaf was taken from a plant that was not ready to flower but was placed on a rootstalk that was ready to flower, the plant would not flower.

- ◇ So, it's been known for a long time that there is a substance produced in the leaves that signals to the rest of the plant that it is time to flower. Scientists also knew that this substance must travel through the phloem to get to the part of the plant where the flower buds would develop. This substance was named florigen by Chailakhyan. However, proving its existence was elusive.
- ◇ A paper by Jan Zeevaart in 2006 outlined the pathway of trying to find florigen over 70 years. This paper includes Chailakhyan's work. After this work, there wasn't much done in locating florigen and determining its exact role until the 1980s and the advent of molecular genetics.
- ◇ Most of these studies involved looking at mutant varieties of a rock cress plant called *Arabidopsis thaliana*, which is very useful in the lab because it has a very fast generation time from seed to mature plants with seeds—about 6 weeks. It also has a small genome, meaning the entire collection of its DNA, and it is fully mapped out, so scientists know where all the genes are on the chromosomes.
- ◇ Because it's such a good model organism, scientists were able to create various mutants of *Arabidopsis*. Some of these mutants flowered later than plants in nature, so scientists tried to determine the gene and/or proteins that these plants were missing.



- ◇ These experiments determined that 2 genes were important in flowering: CONSTANS (CO) and FLOWERING LOCUS T (FT). The way these genes interacted and the exact proteins they produced remained inconclusive until 2005. During that year, Tao Huang, and his colleagues in Sweden and France, conducted experiments to unify the CONSTANS gene and the FLOWERING LOCUS T gene.
- ◇ They knew that the day-length signal was phytochrome but then found that the plant's response to the day-length signal would switch on the FLOWERING LOCUS T gene. They knew that turning on just one of these genes in the leaf was enough to induce flowering. They also determined that it was the messenger RNA of this gene that traveled to the shoot apex, where it would induce flowering. Thus, the messenger RNA of this gene becomes the mystery florigen.
- ◇ Whether the same mechanism is true in all plants remains to be seen.
- ◇ Another environmental cue that many plants need to flower is a period of cold, called vernalization. To flower, many seeds must be given a cold treatment. Flowering can be promoted by a cold treatment given to a seed or a mature plant.

EFFECTS OF CLIMATE CHANGE

- ◇ Some of the sunlight that comes to Earth reflects back into space from the atmosphere, and some passes through our atmosphere and hits the Earth. As the light makes its way through the atmosphere and hits the Earth, it loses energy and slows down to become heat. This heat can't pass back out of our atmosphere.
- ◇ This is a natural phenomenon, and it's a good thing, because without our atmosphere trapping heat, we would all freeze to death. The problem comes from releasing carbon dioxide, methane, and other greenhouse gasses into the atmosphere. These gases trap the heat even more, thus warming the planet.

- ◇ Some plants are responding to climate change by flowering earlier. For example, Seth Munson and Anna Sher used herbarium records to determine how much earlier plants have been flowering in Colorado. Herbaria are collections of dried plants that have been collected in the field. The plants also contain information about the collection.
- ◇ Using herbarium records for 12 different rare plants in Colorado, they showed that the flowering date was on average 42 days earlier than in the late 1800s. That breaks down to 3.1 days per decade. On average, their flowering was about 1.5 days earlier per decade.
- ◇ There is a network called Nature's Notebook that is devoted to taking data about all kinds of plants in various areas of the world. On the organization's website, amateur naturalists can report the flowering of different plants in their area, and the data are available for anyone to analyze.
- ◇ In addition to species flowering earlier, another well-documented change is the movement of whole plant communities up mountainsides. A study done by Anne Kelly and Michael Goulden in 2008 documented observations of plants across a 2314-meter elevation gradient in 1977 and again in 2006–2007 in the Santa Rosa Mountains of southern California. They showed that the elevation of plant communities shifted about 65 meters upward.

READING

Glover, *Understanding Flowers and Flowering*.

QUESTIONS

- 1 What is phytochrome, and what does it sense?
- 2 How do you think plants would respond to 24-hour sunlight?

LECTURE
10

ADVENT OF SEEDS: CYCADS AND GINKGOES

Plants that have vascular tissue but lack flowers are called gymnosperms. Instead of flowers or fruits, these plants produce seeds. In flowering plants, the seed develops inside a fruit, but in gymnosperms, there are no fruits. The word “gymnosperm” is a morphologic rather than a taxonomic description. The gymnosperms include 4 major phyla. This lecture will address 3 of those phyla: Cycadophyta, Gnetophyta, and Ginkgophyta (with the fourth being Coniferophyta).

GYMNOSPERMS

- ◇ In the ferns and mosses, gametes were produced by a gametophyte generation. The gametes fused and gave rise to a sporophyte, which produced spores. Most of those plants just made one size of spore, so they were homosporous. However, some of the seedless vascular plants were heterosporous, meaning they had megaspores, which evolve into structures that produce the ovule, and microspores, which evolve into structures that produce the pollen grains. The whole gametophyte generation is reduced to the formation of the ovule or the spore.
- ◇ Gymnosperms have separate sexes. Male and female parts can be on the same plant or on different plants. If the sexes occur on different plants, the species is called dioecious; if there are male and female parts on the same plant, the species is monoecious.
- ◇ The seed was a big evolutionary move, because its success is much longer lived than a spore's. Even though spores are much smaller and can travel farther distances via wind, seeds have several advantages. Although spores are lightweight, they don't carry anything extra. The seed is heavier, but it has some reserves. The seed is basically an ovule that contains an embryo, so it's an embryonic plant with embryonic roots, stems, and leaves all ready to go in a package with food. A spore was one cell.
- ◇ Different seeds have different amounts of reserves. But all seeds have some, so that they can lie dormant for a while until conditions are right not only for germination, but also for the highest chance of survival. Seeds can remain in what is called a seed bank until conditions are best. Some seeds will only remain viable for a few months; others remain viable for years.
- ◇ The advantages of a seed plant can also be found in the pollen. Ferns and mosses are dependent on water for sperm to swim to the egg in the gametophyte generation; in seed plants, sperm and egg come together differently.

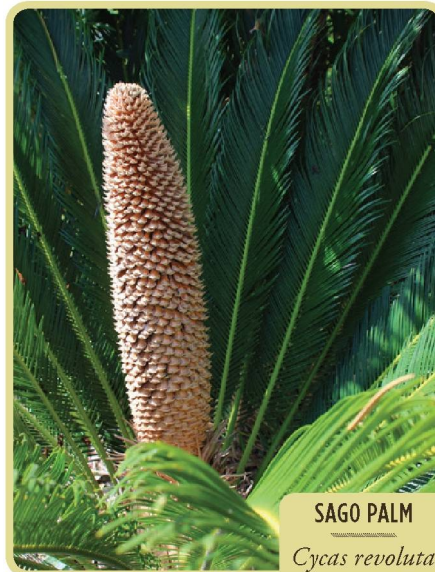
- ◆ The entire male gametophyte has been reduced to the pollen grain, which in seed plants contains a tube cell and a generative cell. When the pollen grain lands on an ovule via wind dispersal, the tube cell will grow a pollen tube through a special hole in the seed coat called the micropyle. The generative cell will eventually divide into 2 sperm cells, one of which will then fertilize the ovule. Only the cycads have retained a motile sperm.
- ◆ The seed is now ready to be dispersed. Seed dispersal can be done a variety of different ways, but pollination in the gymnosperms is entirely by wind, except for the cycads. Some members of the cycads are pollinated by beetles.

CYCADS

- ◆ Cycads flourished during the Triassic Period about 250 million years ago. Fossils of cycads have been found on every continent, suggesting a warmer world at that time. Now, there are only about 300 species in 11 different genera.

- ◆ Cycads superficially look like palm trees, but palm trees are flowering plants, and cycads have cones.

Some of the cycad cones get really big, too. Cycads and palm trees tend to occupy the same kind of habitat, but cycads actually prefer subtropical habitats—those just north or south of the true tropics. The cycads that do occur in the tropics grow at higher elevations, which have lower temperatures and lower humidity, according to Loren Whitelock, author of *The Cycads*.



SAGO PALM

Cycas revoluta

- ◇ Just to confuse nonbotanists, there is a plant called a sago palm, which is actually a cycad, *Cycas revoluta*. Even more confusing is that there is also an actual palm called a sago palm, where the pith is eaten and has many uses. Both are food sources. Although cycad ingestion is known from a number of cultures, these days most botanists understand that cycads are poisonous.
- ◇ Despite their poisonous toxins, cycads are heavily sought after and are in decline around the world. Part of the reason for their decline is that they poison livestock, so ranchers have removed cycads. Interestingly, only introduced animals seem to be effected. If animals are native to a region that has cycads, they either avoid the leaves or have developed some sort of immunity to the toxin.
- ◇ Another threat to cycads is the clearing of their habitat to make way for ranching and other kinds of settlement and development. Native forests don't provide the immediate economic benefit that ranching and farming do, so cycads need some kind of conservation strategy put into place if a cycad habitat is to survive.
- ◇ Cycads are also under threat from poachers. Due to their exotic good looks, cycads are removed from the native habitat to be placed as ornamentals in lawns and gardens. In fact, even though the country of South Africa has tried to establish preserves to protect cycads, there is still an active black market of cycads in that country. Like many black markets, when the product can be bought legally for a comparable price, the illicit market disappears, so governments must support nurseries and gardens that cultivate cycads for legal sale.

GINKGOES

- ◇ Ginkgophyta is another gymnosperm phylum that probably evolved around the same time as the cycads, around 200 million years ago. Although there is only one extant, or still-living, member of this phylum, it's an important member with much to set it apart.



- ◇ *Ginkgo biloba* is an oddity among this group of vascular plants with seeds but no flowers. All of the other gymnosperm plants have evergreen leaves. Even the conifers that shed their needles, such as the larch, have needles and not broad leaves.
- ◇ *Ginkgo biloba* is named for its characteristic leaf. It looks like a fan with a notch in the apex, thus giving the leaf 2 distinct lobes—biloba. Ginkgo leaves attach directly to the main branch with very little peripheral branching.
- ◇ Another curious feature of ginkgoes is that they all seem to lose their leaves overnight. No one knows why the synchronous leaf drop occurs, and the mechanism behind it is utterly befuddling.
- ◇ Many of the gymnosperms have male and female plants. Female ginkgoes produce seeds. The seeds of the female ginkgo have a peculiar scent—described as akin to vomit—that is due to butyric acid, which is found in the fleshy seed coat. Because of this, only male trees are planted these days.

- ◇ Ginkgo trees are native to Asia. Many Asian cultures eat ginkgo seeds in a variety of ways. They are purported to taste like chestnuts. Ginkgo also has some medicinal purposes. A chemical compound found in the leaves increases circulation and is said to reduce many of the effects of aging.
- ◇ The only way for reproduction to occur in the gymnosperms is for the pollen grains to land on the ovule within the strobilus, or cone. There are a few gymnosperms that are pollinated by insects, but for the most part, the gymnosperms have to rely on the wind. They must synchronize pollen formation with ovule ripeness.
- ◇ To increase the chance that the pollen will make it to the ovule, many gymnosperms have ovules that will secrete a special drop of fluid to hold the pollen grain above the opening to the ovule, which is called the micropyle. This bit of fluid is called a pollination drop. In ginkgoes, from formation to pollination to disappearance of the pollination drop takes about 10 days. As soon as the pollination drop receives pollen, it can completely disappear in 5 hours.

GNETOPHYTES

- ◇ Like the cycads and ginkgoes, the gnetophytes have some unique characteristics. For example, they have vascular tissue but lack fruits.
- ◇ Some molecular analyses place Gnetophyta as the closest gymnosperm group to the flowering plants. There are some similarities between the gnetophytes and flowering plants. There are flower-like structures on the strobili of *Welwitschia*, and many gnetophytes produce nectar on the tip of the cone. Also, the gnetophytes have special xylem cells called vessel elements that look like those found in the flowering plants.
- ◇ Gnetophyta is an even smaller phylum than the cycads, though not as small as the lonely ginkgo. There are 3 families that each contain 1 genus apiece: *Welwitschiaceae*, *Gnetaceae*, and *Ephedraceae*.

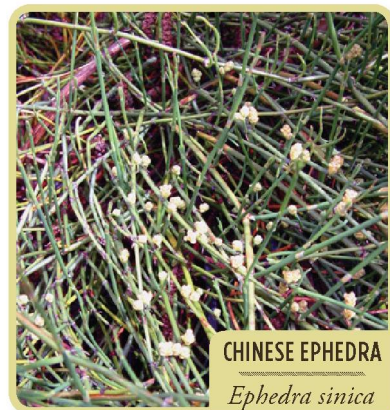
- ◆ Welwitschia is the only member of its genus and of its whole family: the Welwitschiaceae. It has a bizarre growth pattern: It only produces 2 leaves, but these leaves get really long and continue to grow throughout the life of the plant. Welwitschia also has giant strobili.



- ◆ The genus *Gnetum* has about 40 species. Most of these are vines that are restricted to rain forest habitats, and this may be due to the fact that this group is insect pollinated.



- ◆ The last genus of Gnetophyta is *Ephedra*, which contains about 67 plants, mostly shrubs, that are native to Asia, Europe, and North and South America. *Ephedra sinica*, which is native to China, gained some rather infamous notoriety during the 1990s as a popular weight-loss drug, because it is a stimulant. The plant's potent alkaloid, ephedrine, falls into the same category as caffeine and nicotine. However, with weight loss came heart problems and strokes, so the U.S. Food and Drug Administration banned the sale of dietary supplements containing ephedrine in 2004.



READINGS

Crane and von Knorring, *Ginkgo*.

Moore, *Medicinal Plants of the Mountain West*.

Whitelock, *The Cycads*.

QUESTIONS

- 1 What is the difference between a seed and a spore? What are the advantages and disadvantages of each?
- 2 Why is the ginkgo so unique?

LECTURE
11

WHY CONIFERS ARE HOLIDAY PLANTS

Although there are many species of trees that are used as Christmas trees, they are all conifers, which simply means cone-bearing. Although the cycads and Welwitschia also have cones, these are called strobili, and only the cones found in the conifers are true cones. This group used to be called Coniferophyta, but there isn't actually a conifer family, so now the name is Pinophyta, after the largest family found in the conifers, the pine family, or Pinaceae.

CONIFERS

- ◇ All Christmas trees have cones, and they all have a unique shape—a sort of conical shape, small and narrow at the top and expanding to the base. Not all conifers have this shape, though. For example, Monterey pine trees, which grow on the coast of California, look more like a rectangle.
- ◇ Although conifers grow all over the world, the ones people use as Christmas trees tend to be from places that have cold and snowy winters. A very popular Christmas tree species is the Norway spruce, from Norway. The shape of the Norway spruce, and all conical conifers, does 3 important things.
 - ◇ Having short branches at the top of the tree prevents snow loading on the top of the tree, which could damage the top or cause it to break off completely.
 - ◇ The tips being smaller reduces the wind loading on the tips of the trees, which could rip the tip off.
 - ◇ The conical shape allows greater light penetration to the bottom branches and leaves.
- ◇ Many spruces also have branches that tend to droop. This, too, is to prevent snow loading. Because the Monterey pines don't face a lot of snow, their shape isn't the same.
- ◇ Although we tend to think of conifers as growing in cold places, that isn't the only type of place they grow. Douglas fir and Ponderosa pine trees live near the West Coast of the United States, from California up through Washington. These trees are also found scattered throughout the intermountain West. There are also conifer forests in the Southeast. So, their conifers must be adapted to something other than just harsh winters to flourish in these different regions.



- ◆ Conifers are well adapted to a few different climates. They're adapted to the northern boreal forest because of their ability to thrive in snow and wind. This forest occurs at about 50° latitude, and it is the largest forest on Earth, covering 1/3 of Earth's forested land.
- ◆ The conifers' leaves, popularly known as needles, are also well adapted to not freezing in the wintertime. Many conifers have antifreeze proteins that they store in their apoplasts (area surrounding the cell) so that the tissue doesn't freeze. Sometimes, the apoplast will freeze, but this protects the cells inside from freezing. Also, photosynthesis slows down and will stop on very cold days, so the stomata are closed, and water is not moving through the leaf.
- ◆ Conifers are also well adapted to fires, and this may be one reason that they dominate in the Southeast, which has a lot of lightning. There are several different adaptations that make pines fire-resistant. Of course, no tree is going to be fire-proof, but many trees, especially the conifers, can survive mild to moderate fires.

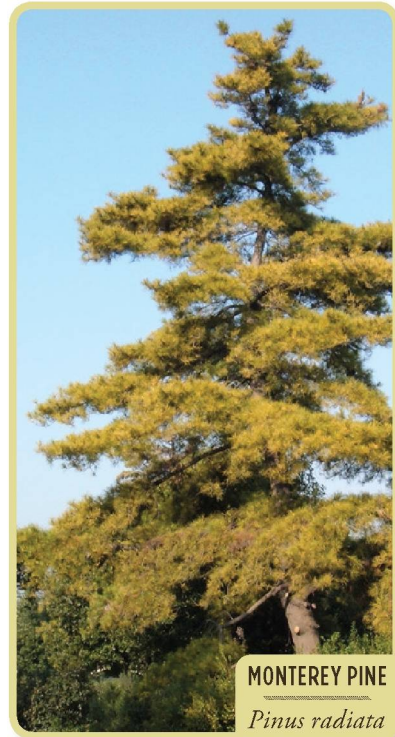
- ◇ A moderate fire typically doesn't get into the canopy of the forest, so it burns along the understory, which is the layer of vegetation under the main canopy. Conifers that are adapted to these understory fires usually have thick bark around the trunks. The bark may burn a bit, but then the fire will pass by, and the tree will survive. Fires like these will clear out the understory and ensure that there isn't a great buildup of dead wood and shrubs, which could then serve as fuel for another fire.
- ◇ Ponderosa pine has really thick bark that forms plates on the tree. This pine is adapted for small fires, and frequent small fires maintain a ponderosa pine forest. When we prevent these types of small fires from happening, the fuel in the understory can burn up and cause severe fires. Even fire-adapted conifers can't survive severe forest fires.
- ◇ Ponderosa pines also have an adaptation to fire by not having branches close to the ground. This is not true for spruces and other conifers that don't grow in fire-prone areas.
- ◇ Some conifers have cones called serotinous cones that will only open when exposed to the heat of fires. The degree of serotiny seems to depend on the fire regime of a particular area.
- ◇ Conifers are well adapted to soils that don't have a lot of nutrients, so we find conifer trees where flowering trees wouldn't thrive. Conifers have a lesser-developed root system than many other kinds of trees. That conifers don't have to put out a new bunch of needles every year is probably advantageous in a soil with fewer nutrients.

PINES, SPRUCES, AND FIRS

- ◇ Conifers include pines, spruces, firs, and other plants. Pines are the easiest group to identify. There are other families in the Coniferophyta, but Pinaceae, the pine family, is the largest both in terms of species and numbers of trees on the planet. The pine family contains pines, spruces, larches, cedars, firs, and hemlocks.

◇ All the pines, except for one, have the needles attached together before they are attached to the branch of the tree. This group of needles is called a fascicle. The number of needles within the fascicle is also a distinguishing trait to determine a particular species of pine tree.

◇ There are a little more than 100 species of pines, and they probably radiated out of Mexico. *Pinus* is the largest genus in the Pinaceae family, and there are native pines all over the Northern Hemisphere, but they are not native to the Southern Hemisphere. There are conifers in the Southern Hemisphere, but they are not members of the genus *Pinus*.



◇ The *Pinus* genus also gives us the oldest individual trees in the world. Generally, the Bristlecone pine, *Pinus longaeva*, which grows in the White Mountains of California, is thought to be the longest-lived tree on Earth.

◇ Pines are some of the fastest-growing and slowest-growing trees. Their adaptations to fire have shaped much of our more recent management policies as we understand that they are accustomed to mild or moderate frequent ground fires. Pines are one of the heaviest of all the conifer trees so they are used for furniture and construction.

- ◆ We often use the word “pine nut” to describe that tasty morsel that goes on salads or is used to make pesto, but a pine nut is not a nut—it’s a seed. Pine seeds have been fertilized, so there is an embryonic plant inside. In pines, these seeds are released by the female pinecone. The seeds of pinecones are an important food source for many animals.



- ◆ In addition to the pine family, there are many other families that are conifers. The spruces and firs are probably the next most well known in this group.



- ◆ Telling a spruce from a fir is almost as easy as distinguishing a pine. A fir is friendly—its needles are flat and not so prickly. A spruce does not have flat needles; it is decidedly unfriendly and prickly. A spruce also has the old needle scars apparent on the older parts of the branches. These will appear as bumps on the twigs.



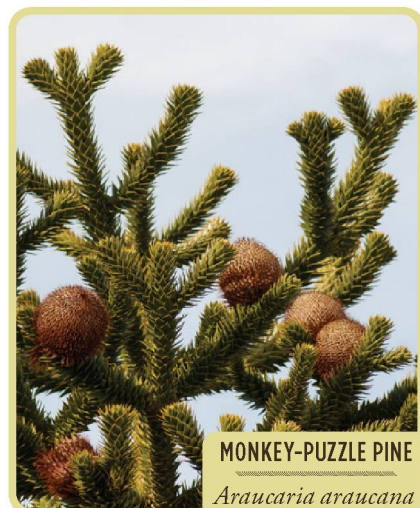
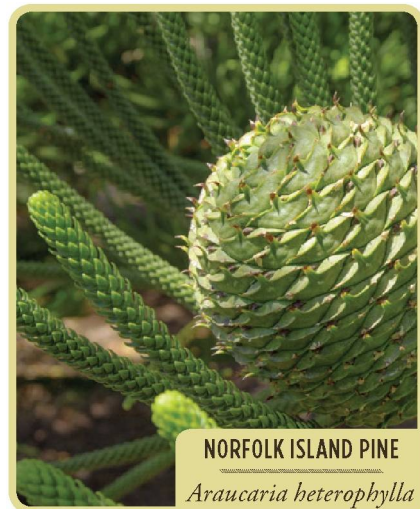
- ◆ Also in the pine family are the hemlocks. Their needles are also somewhat flattened but not like a fir. They are not as pointy as a spruce’s needles. The firs and hemlocks make friendlier Christmas trees.

- ◇ There is also another tree in the pine family called the Douglas fir (*Pseudotsuga menziesii*), which is not actually a fir. It isn't a hemlock either. It's sort of a cross between a fir and a spruce; its needles are not as stiff and pointy as a spruce's needles and are not as flat as a fir's needles.
- ◇ Douglas firs have extremely recognizable cones. Note that they are not called pinecones because Douglas firs are not pines. Their needles are not in fascicles. Douglas firs have a characteristic bract protruding between the scales of the cone.



- ◇ Douglas firs, along with all of the other conifers up to this point, have recognizable needles. The needles are the modified leaves of conifers. They are small and impregnated with a lot of lignin, which gives them their stiff texture. The small size means that they don't heat up too much in the summer, but also that there isn't a huge amount of water in the cells to freeze in the wintertime. The other families in the conifer group have needles that look much the same as the needles in the Pinaceae family.
- ◇ In addition to claiming the oldest tree with the Bristlecone pine, conifers also claim the tallest tree, with the giant sequoia, which commonly grows to more than 300 feet tall.
- ◇ The redwood, *Sequoia sempervirens*, is more susceptible to drought than other conifers. Also, its roots tend to spread wide rather than go very deep. Redwoods are also very disease resistant. This is one reason why their lumber is so sought after, especially for outdoor construction. Like other conifers, they are also resistant to fire. They also have an astonishingly fast growth rate, with some reports of up to 6 feet per year.

- ◆ One member of the conifer group is responsible for one of the most-prescribed cancer drugs on the market, Taxol. The Pacific yew tree is in the Taxaceae family and grows only on the Northwest coasts of the United States and Canada.
- ◆ Another family in the conifer group, Araucariaceae, does not exist in the Northern Hemisphere. This family contains a species called the Norfolk Island pine, which is a common house plant because it can tolerate low light levels as a juvenile. It's in the family Araucariaceae, so it's not actually a pine.
- ◆ One other interesting tree in this family is the monkey-puzzle pine, which is not a pine, but a very interesting-looking plant native to Chile, where it is the national tree, and Argentina. It's been successfully started in other places with mild climates and good rain, but it grows slowly and is somewhat endangered.



READINGS

Farjon, *A Natural History of Conifers*.

Richardson, *Ecology and Biogeography of Pinus*.

QUESTIONS

- 1 In what kinds of habitats do conifers thrive? What are some advantages of conifers over deciduous trees?
- 2 What is a cone, in botanical terms?

LECTURE
12

SECRETS OF FLOWER POWER

The first flower from the fossil record appeared 125 million years ago. Then, a mere 40 million years later, flowers were everywhere. This is a relatively short evolutionary time. Now, flowering plants are the dominant plant form on the planet in terms of species. Depending on how you count, there are anywhere from 330,000 to 400,000 species of flowering plants. How could natural selection, operating on a long timescale, explain the rapid evolution of flowering plants?

THE RISE OF FLOWERS

- ◇ We now have a pretty good idea of where flowers came from and how that evolution could have happened so quickly. We know about mechanisms for the creation of new species, and we also have a pretty good picture of the fossil record.
- ◇ It could be that flowers just don't fossilize very well, which they don't. It may also be that early flowers were just small. Additionally, the early flowers may not have been woody, and this would have limited their ability to form fossils.
- ◇ Interestingly, molecular evidence puts the advent of the flowering plants back to about 290 million years ago, in the Late Carboniferous Period. Why the fossil record and the molecular evidence don't match up probably has to do with early flowering plants not being the best at forming fossils.
- ◇ Whatever the exact origin of the flower, we do have some good evidence of what very early flowers may have looked like and how they might have evolved from conifers.
- ◇ Botanists also tend to agree that the flowers form a good group, also called a monophyletic group—that is, a group with one descendant and all of the offspring. Yet other botanists suggest that the flower may have evolved more than once.
- ◇ Still, conifers and ferns and mosses have been around much longer than flowering plants. How were there so many different species of flowering plants in such a short time?
- ◇ The answer may lie in the fact that many flowering plants are both pollinated and dispersed by animals. An animal moving pollen between plants could become more specialized and get pollen from only one type of plant. Now, the plants pollinated by that animal are reproductively isolated from other plants. This is the key to speciation, or the formation of new species.

- ◇ The other way animals can be key in speciation is through dispersal. If an animal disperses a seed to a new location where it can no longer breed with its old population, it becomes reproductively isolated and speciation occurs.
- ◇ Generally, field botanists, those interested in identifying plants, focus on the family level. Families are named after the type genus within that family, which is the genus that typifies the traits of the family. There are about 600 families of plants, and some of that number depends on the different ways molecular evidence might be used to define some of the families.
- ◇ It used to be thought that the earliest flowering plants were those like the Magnolia family—big, showy flowers, and you can almost imagine the center part of the flower looking like a cone. Next came a hypothesis that the earliest fossil flowers were quite small and looked more like those in the Piper family, or Piperaceae.
- ◇ Molecular evidence provides a bit of an alternative. In 2013, the entire genome of a small, weedy shrub native to New Caledonia, an island in the South Pacific, had been sequenced.
- ◇ For the decade before this full genome sequence was completed, botanists had used a variety of molecular techniques to determine that this shrub, *Amborella trichopoda*, was the oldest extant flowering plant. This shrub is the only member of Amborellaceae, and it probably had other relatives that were alive sometime in the past.
- ◇ It turns out that this shrub is the sister group to all the flowering plants, indicating that, indeed, it is a common ancestor to all flowering plants.
- ◇ This shrub gives us some clues about what the earliest flowering plants might have looked like. Because it is a shrub, botanists can confirm the hypothesis that the earliest flowering plants were woody. However, due to its weedy growth in the understory, likely the first flowering plants were not towering trees. Like many of the gymnosperms, this plant is dioecious—meaning that they have male plants and female plants—which is another clue about the early flowering plants.



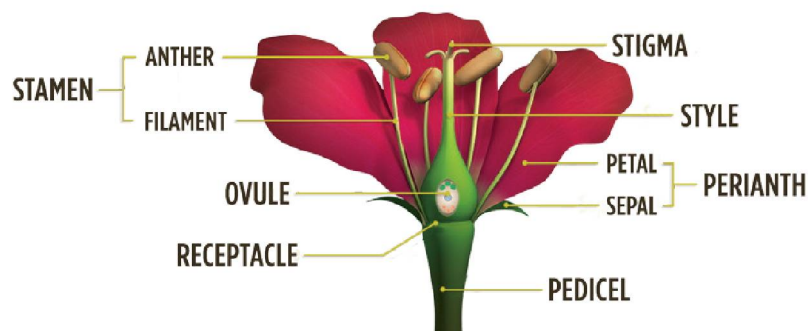
Amborella trichopoda

- ◆ There are several models for how a flower, even a rudimentary flower, might have developed. The best genetic techniques indicate that the same genes that are responsible for flower development in *Amborella* are the same genes that are responsible for the formation of the male cones of the gymnosperms. So, it seems that the flower developed from the male cone.

FLOWER PARTS

- ◆ All the flowering plants have an outer ring of male parts with an inner ring of female parts. In botany, when something forms a ring, it is called a whorl. So, the male parts of the flower whorl around the female parts. That this is the case for all flowers supports the idea that the flower only arose once in evolutionary history.

- ◇ Male parts are called stamens, which has an anther with pollen and a stalk called the filament.
- ◇ The female parts are a bit more complicated. There is a top part called the stigma, which is where the pollen will land. The stigma then becomes the style, which is usually long and thin and connects to the ovary at the base. The ovary is where the ovule is housed. Collectively, the female parts are called the carpel or the pistil.
- ◇ At a minimum, flowers have either male or female parts. The typical flower has both male and female parts, and they are called perfect flowers, but some flowers can be all male, called staminate flowers, and others can be all female, called pistillate or carpellate flowers. The petals and sepals are the perianth, and this part is optional: Some flowers have the perianth, which is the outer whorl of petals, which are usually colored, but other flowers do not have the perianth.
- ◇ Flowers don't have to have sepals, which are typically green. Sometimes, the petals and sepals can't be distinguished, so they are called tepals.
- ◇ The arrangement and number of stamens and carpels, and petals and sepals, varies with various families.



CLASSES OF FLOWERING PLANTS

- ◇ Flowering plants are called Anthophyta, or angiosperms. Instead of cones, which have open seeds, these plants will enclose the seed in an ovary that then swells to become the fruits.
- ◇ The phylum of flowering plants, the Anthophyta, is traditionally divided into 2 classes: dicots and monocots. However, the term “dicot” isn’t used anymore because it doesn’t represent a true evolutionary group. Instead of dicots, botanists use the term “eudicots.”
- ◇ The term “dicot” refers to dicotyledon. The cotyledon is the seed leaf, or the first leaf that emerges in the developing plant. In dicots, there are 2 cotyledons that emerge at the same time. In monocots, there is only 1 seed leaf. The difference between these 2 groups of plants can also be seen in several different physical aspects of the flowers, the veins in the leaf, and the arrangement of the vascular tissue in cross-section.
- ◇ Monocots have flower parts in groups of threes. They can have 3, 6, or even 9 stamens and 3 or 6 carpels. Monocots will also have 3 petals and 3 sepals or 6 petals and 6 sepals. Dicots have flower parts in fours or fives. The sepals, petals, stamens, and carpels are all in multiples of fours or fives.
- ◇ In monocots, the leaf veins—veins running through the leaf of xylem and phloem—are parallel. In dicots, the leaf veins are netted, or like a feather or a palm.
- ◇ The dicots have a tissue arrangement that is reminiscent of that which exists in woody plants. In fact, most trees are eudicots or belong to one of the groups that was removed from the dicots; all together those removed groups are the basal angiosperms.
- ◇ The eudicot vascular tissue arrangement has rings around the outside of the stem, with phloem on the outside and xylem on the inside, just like the woody stem, except there is no cork cambium and no bark. The monocots have vascular tissue arranged in bundles throughout the plant, and they consist of 2 large columns of xylem and phloem cells.

- ◇ There are a number of flowering plant families that don't really fit into either of these 2 categories, so botanists lumped them together into a group called the basal angiosperms, which make up less than 5% of all the flowering plants. Basal angiosperms often show combinations of the following traits: numerous flattened (laminar) stamens with wide filaments; numerous tepals; many separate carpels; and alternate, spirally arranged leaves.
- ◇ The old dicot name used to include many of the basal angiosperms. Once these plants were taken out of the dicots, the new name became the eudicots, or true dicots.

FLOWER IDENTIFICATION

- ◇ Flowers can be radially symmetrical or bilaterally symmetrical. There are a few descriptors for the shapes of flowers, such as tube-shaped and bell-shaped flowers, but other terms are reserved for specific flowers, and botanists don't use them broadly, probably because there are so many other ways to determine the family to which a plant belongs by looking at the flower.
- ◇ Most wildflower identification books use color; others use inflorescence types. An inflorescence describes how the flowers are arranged on the stem.
- ◇ There are quite a few descriptors of inflorescences. A single flower on a stem is called a solitary inflorescence, and flowers that alternate up the stems are an inflorescence called a raceme. If those flowers are tightly compressed on the tip of the stem, it is called a spike. An inflorescence that has numerous flowers forming a sort of umbrella shape is called an umbel.
- ◇ But the most influential factor in the determination of the species is the number and arrangement of the male and female parts.

THE EVOLUTIONARY TREE OF THE FLOWERING PLANTS

The oldest flower from the fossil record, *Archaeofructus*, was a simple shrubby plant with small flowers. Fast-forward about 125 million years, and we have the species *Amborella trichopoda*, which is the living sister group to all the remaining flowering plants. From there, the basal angiosperms were likely next on the scene, and from a common ancestor to the basal angiosperms, the monocots and eudicots appeared.

In terms of diversity, only about 5% of flowering plants are basal angiosperms. The monocots comprise about 25%, and all the rest are eudicots.

READINGS

Buchmann, *The Reason for Flowers*.

Essig, *Plant Life*.

Howell, *Flora Mirabilis*.

QUESTIONS

- 1 Why were flowers considered an abominable mystery for Darwin?
- 2 Do you think that flowers evolved more than once in evolutionary history? Why or why not?





TALL LARKSPUR
Delphinium barbeyi



MOUNTAIN AVENS
Dryas octopetala



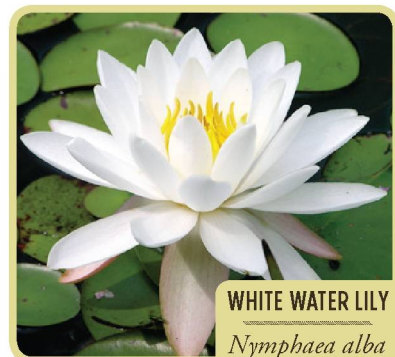
MEDITERRANEAN STORK'S BILL
Erodium malacoides



PURPLE DEAD-NETTLE
Lamium purpureum



LANTANA
Lantana camara





CORPSE FLOWER
Rafflesia arnoldii



CREEPING BUTTERCUP
Ranunculus repens



SPANISH OYSTER THISTLE
Scolymus hispanicus



WOOD LILY
Trillium grandiflorum



WAVY-LEAVED MULLEIN
Verbascum sinuatum

LECTURE
13

THE COEVOLUTION OF WHO POLLINATES WHOM

Pollen comes from plants—primarily from trees and grasses. Pollen delivers the male sperm to the top of the female part of the flower, the stigma, and this is the process of pollination. Of course, if you suffer from allergies, you're wondering, why there is so much pollen. Is it really necessary? It turns out that it is.

POLLEN

- ◇ Many plants are pollen limited, which means they could produce more fruits with seeds inside of them if there were more pollen. The pollen we see and breathe in the air is typically from wind-pollinated plants, especially grasses, trees, and weeds. Only wind-pollinated plants can produce so much pollen. Plants pollinated by animals can be more judicious in their pollen production because the delivery of that pollen is more direct. Wind pollination is called anemophily.
- ◇ Wind-pollinated flowers—such as those on birch trees, cedar, or alder—are usually inconspicuous, meaning they lack showy parts, because they don't need to advertise to any pollinators. In addition, showy petals might get in the way of the wind reaching the pollen, or the pollen reaching the stigma.
- ◇ Wind-pollinated flowers are also small, because they only need to attract wind. And flowers that are too big may get blown off, especially because wind-pollinated plants tend to live where it's windy.
- ◇ Wind-pollinated flowers typically lack any smell, because there are no pollinators to attract with fancy perfumes. The same goes for nectar. The wind needs no reward.
- ◇ A common inflorescence for wind-pollinated plants is a catkin, which is an arrangement of small flowers, usually unisexual, that hangs down in pendulous, small branchlets. Usually, the catkins on any one plant are of one sex because many of the plants that have this kind of pollination are dioecious, meaning that they have male plants and female plants. If wind-pollinated plants are bisexual, they are monoecious, meaning that they have separate male and female flowers on the same tree.
- ◇ The vast majority of flowering plants, though, have bisexual flowers with both male and female parts within them. Because they have both sexes, they can pollinate themselves, and this is called selfing. One advantage to selfing is that there is most definitely a source of pollen and an ovule. Also, because the plant formed gametes, the sperm and the egg, this is sexual reproduction, so a reordering of the genes will occur.

- ◇ The disadvantage is that the genes carried by that sperm and that egg are going to be pretty similar. They won't be identical, because during the formation of the sperm and the egg, only certain alleles, which are flavors of the gene, are passed on to the gametes.
- ◇ Even though selfing is still sexual reproduction, the genetic difference between the gametes within a plant wouldn't be as great as the genetic difference with another plant.
- ◇ In addition, many plants simply can't self. For those plants, when self-produced pollen lands on the stigma, the pollen tube simply won't grow. The pollen tube is that part of the pollen that will grow down into the ovule. The beginning of the growth of the pollen is called pollen germination because it begins by the pollen absorbing water and swelling, just like a seed germinating.
- ◇ This leads to an interesting dilemma: The stigma has to be able to recognize pollen that is self or not self and pollen that isn't even of the same species. There is a debate in botany as to what constitutes a species. With animals, the biological species concept is fairly well established. If 2 animals can mate and produce viable offspring, then they are the same species. If they can't, then they're not. Plants are a bit more promiscuous in terms of reproduction, which could account for so much variety and eventually speciation in plants.
- ◇ Some plants have developmental delays to prevent self-fertilization. For example, the pollen will mature and get blown away before the stigma is ready to accept pollen. Other plants will spatially segregate the pollen from the stigma. If the stigma protrudes far outside of the flower but the anthers are deeper inside the petals, then there is less chance that the pollen from the same flower will land on the stigma.
- ◇ Still, sometimes pollen from the same individual will land on the stigma. A group of genes is responsible for recognizing pollen as self or not self. When plants cannot self-fertilize, they are called self-incompatible, and about 50% of eudicot species fall into this category.

- ◇ The genes then provide a biochemical mechanism to prevent fertilization by pollen from the same individual. There are a number of different mechanisms to prevent self-fertilization.
- ◇ There are also mechanisms to promote outcrossing, or fertilization with non-self individuals. This is what pollination is all about.
- ◇ The majority of flowering plants are pollinated by insects. Insects get nectar or pollen, or both, and in exchange, the pollen they get on their body gets transferred to another flower when they visit it for more rewards.
- ◇ Flowers and insects can be so specialized as to have a monogamous relationship, in which one species of insect only visits one type of flower and no other flowers, and the flower, in turn, is only visited by one species of insect.
- ◇ In this relation, the flower should have to produce less nectar because the pollinator will only be visiting that flower. However, the flower runs the risk of that particular insect becoming scarce and not pollinating a significant amount of the plant's population; likewise, the insect will be out of luck if something bad happens to that particular species of flower.
- ◇ Alternatively, flowers can be pollinated by a variety of pollinators. The same is true for insects. A plant pollinated by many pollinators can increase its likelihood of successful pollination, but the stigma can get clogged up with foreign pollen. Also, the plant has to ensure a prodigious supply of nectar for any insect that comes to call, even if that insect next travels to an entirely unrelated species.
- ◇ Plants and insects can also choose an intermediate lifestyle, which is what most do. In other words, plants are pollinated by a group of insect types, such as beetles or flies. Likewise, insects tend to prefer plants that are suited to their needs, skills, preferences, and body types.

POLLINATORS

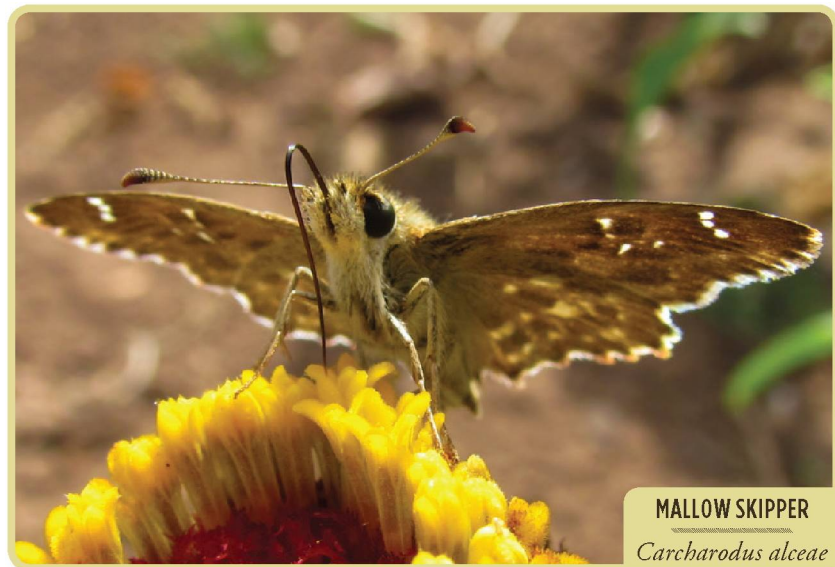
- ◇ Beetles are the oldest and most diverse group of insects. From the fossil record, we know that beetles were present long before flowering plants were, and we also know that some of the gymnosperms, particularly the cycads, are beetle pollinated.
- ◇ Most beetles are not great flyers because they are so heavy. Because they don't fly very well, a flower should provide them with a steady landing site. Also, beetles don't have very long tongues, so the nectar of a beetle-pollinated flower can't be buried too deep inside the flower. Furthermore, beetles don't have great vision, but they do have a good sense of smell, so we would expect a beetle-pollinated flower to be cream or white in color, because this would contrast best against a canopy of green. We would also expect beetle-pollinated flowers to have an attractive smell.
- ◇ Typical large flowers pollinated by beetles are magnolia and pond lilies, but smaller flowers that are clustered together are also pollinated by beetles, so the beetle doesn't have to travel too far, such as goldenrods.



- ◇ Although beetles may be the oldest pollinators, bees are some of the most important pollinators, especially because a good number of foods we eat are bee pollinated, including almonds, avocados, blackberries, blueberries, peaches, pears, cantaloupes, and watermelon.
- ◇ Bees, like beetles, are also fairly heavy insects. Additionally, because bees feed their young, they need a greater amount of nectar than some other pollinators. Bees also collect pollen as a protein source.
- ◇ Bees have long tongues, so bee-pollinated flowers can have spurs or nectar pockets. So, flowers pollinated by bees should still be large with a decent place for the bee to be while gathering nectar and pollen. But, unlike beetle-pollinated flowers, those pollinated by bees will be more colorful, but not as heavily scented.
- ◇ Flies are another common insect pollinator, but they are smaller and lighter in general than either bees or beetles. They also do not feed their young, so flowers pollinated by flies need not produce as much nectar or pollen as those pollinated by bees.
- ◇ Although flies can see a bit better than beetles, the flowers they pollinate still tend to be white, cream, or yellow and typically smaller than those pollinated by bees or beetles.
- ◇ Flies are important pollinators to plants that may be flowering at times of the year when there are not many bees or beetles. There tend to be more flies throughout the year, so if a flower is particularly early or late in its blooming, it may be fly pollinated.
- ◇ As such, we expect fly-pollinated flowers to be small, without much scent, and of a cream-colored hue. Members of the Apiaceae family are typically fly pollinated.



**FLY POLLINATING
AN UMBEL PLANT**



- ◇ The lepidopterans are insects that are moths and butterflies, and even though these 2 insects are in the same order and they look superficially alike, they pollinate different types of flowers.
- ◇ Butterflies are typically active during the day and hold their wings up when at rest, and their antennae are thinner and have a small club at the end. Butterflies also have good color vision, so they tend to prefer flowers that are yellow, red, or orange. Because butterflies don't have much sense of smell, flowers they pollinate don't have much scent.
- ◇ Moths are generally active at night, hold their wings out or folded on their backs, and have thicker antennae that lack a club at the end. Because moths are active at night, they tend to pollinate white or cream-colored flowers. However, moths have a good sense of smell, and a strong scent can help them find flowers at night, so moth-pollinated flowers have a strong scent, usually at night.

- ◇ Both moths and butterflies have long proboscises, which are the tubular structures through which they suck up nectar. As such, flowers that are pollinated by moths and butterflies have long nectar spurs, which are elongated parts of the flower that have nectar in the bottom. Moths have even longer proboscises than butterflies.
- ◇ Because butterflies are smaller than moths, they have lower energy requirements, so there is generally less nectar produced in butterfly-pollinated flowers. Despite their larger body size, moths prefer to hover while gathering nectar, which means that moth-pollinated flowers must produce even more nectar. Because of the hovering, moth pollinated flowers tend to be bilateral in shape and have a corolla and nectar spur that are easily accessed by a hovering moth.
- ◇ Insects aren't the only animals to pollinate flowers. Like butterflies, birds also have good vision but lack a well-developed sense of smell. Bird-pollinated flowers are larger than butterfly-pollinated flowers, and because birds are larger and have more energy requirements than butterflies, bird-pollinated flowers produce a lot of nectar. The shape of the flower depends on the type of bird performing the pollination.
- ◇ Bats, like moths, are major nocturnal pollinators. Vision is not very important to bat pollinators, but like many mammals, bats have a well-developed sense of smell. So, like moths, bats pollinate white or cream-colored flowers that have a strong scent.
- ◇ There are also nonflying mammal pollinators. About 50 other species of mammal, usually rodent-type animals, pollinate flowers. Typically, flowers pollinated by nonflying mammals have flowers close to the ground with a strong odor. These flowers also have to be sturdy to hold up to the mammals.
- ◇ Many times, the animal receives either nectar or pollen as a reward for its services. Sometimes, however, there is no reward. This is called deceit pollination.
- ◇ We use pollination generally for many crops. A huge variety of fruits depend on pollinators to reproduce.

READINGS

Fenner, *Seeds*.

Harder and Barrett, *Ecology and Evolution of Flowers*.

QUESTIONS

- 1 What, botanically, is pollen, and why do plants produce so much of it?
- 2 Can you draw a typical pea flower?
- 3 Think about your favorite flower. Describe its color, scent, and shape, and then postulate what kind of animal pollinates it.

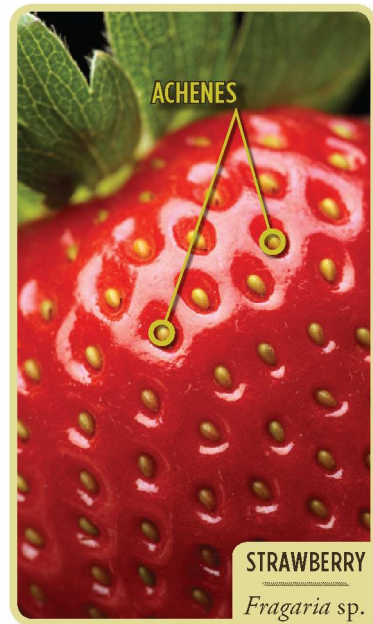
LECTURE
14

THE MANY FORMS OF FRUIT: TOMATOES TO PEANUTS

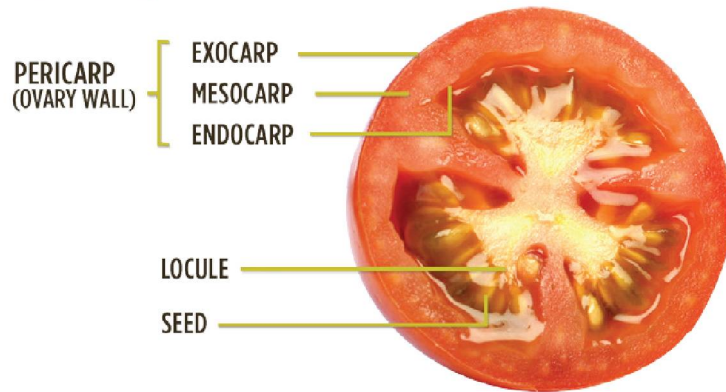
Fruits are how plants move—at least how they move their progeny. You probably know that plants have a myriad of fruit types, but what you may not realize is that they are all based on how the carpels were organized in the flower. Of course, botanists have names for all of these fruit types.

FRUITS

- ◇ Some fruits that we think are fruits are actually not fruits. For example, a strawberry is botanically not a berry. In fact, it's not really a fruit because it's not the swollen ovary of the plant. But there are fruits on a strawberry.
- ◇ What might appear to be seeds on the outside of the strawberry are actually the fruits. They are a small type of fruit called an achene, which is a simple fruit, meaning that it is derived from one carpel, within a flower that has a superior ovary. All of the other flower parts will insert into the receptacle below the ovary in a flower with a superior ovary.
- ◇ What one might call the actual berry of the plant is not botanically a berry; it is a receptacle, which in most plants is simply where the petals, sepals, and other flower parts insert into the stem. In the strawberry, this receptacle becomes red and swollen when ripe, exposing the tiny fruits on the outside. This type of fruit, where the actual fruit part isn't an ovary, is called an accessory fruit. The swollen receptacle is an accessory to the actual fruit, the achenes on the surface.
- ◇ What many people might call a vegetable—the tomato—is a fruit, and it's botanically a berry. Botanically, a berry is a fruit with several carpels, each of which has many seeds. Blueberries and cranberries fit this definition, as do grapes, although many grapes in stores are now seedless.



FRUIT (A BERRY OF TOMATO)



- ◇ Inside a tomato, there's the gooey part with tiny seeds, and there's the wall part. There's a fruit wall on the outside, and this is called the pericarp generally. In a tomato, the outermost part of the pericarp is the exocarp, the middle is the mesocarp, and the inside is the endocarp. The endocarp is pretty difficult to distinguish in a tomato, but the exocarp is clearly the skin, and the mesocarp makes up most of the fruit wall.
- ◇ The runny parts are called locules, but usually each locule started off as a carpel, so there are several different carpels within the ovary. There are also several seeds within each carpel.
- ◇ A true berry has a fleshy inner fruit wall. A tomato is a true berry because the whole fruit wall is fleshy in a tomato.
- ◇ There are 2 other variations of berries. If a berry has a leathery rind, it's called a hesperidium. An example of this is an orange. There are many carpels: Each of the sections of the orange, the orange slices, is a carpel. There are typically many seeds inside, and there is a leathery fruit wall instead of a fleshy wall.

- ◇ The watermelon is a second type of berry. Although it's difficult to see the carpels when looking at the cross-section of a watermelon, they are there. It's easier to see them in a related plant, the cucumber. Both of these plants are in the Cucurbitaceae family. Other members of this family are cantaloupe, squashes, and pumpkins. The fruits of this family are called pepos. A pepo is a berry with a hard outer fruit wall.
- ◇ Blackberries and raspberries aren't botanically berries. They are what botanists call aggregate fruits, which have several carpels aggregated together in one flower, so that the carpels are separate but still together in one fruit.
- ◇ A blackberry is an aggregate of many small balls, each with a seed inside. Each of those small round balls with a seed inside came from a carpel. Those small balls are a fruit type that botanists call a drupe, which is any fruit that has one to several carpels but only a single seed. Each one of those blackberry or raspberry fruits has one seed inside. Blackberries and raspberries are called an aggregate of drupes.



- ◆ Drupes also include all of the stone fruits, such as peaches, plums, apricots, and cherries, which are in the Rosaceae family. Drupes also include avocados and mangoes. Botanists have not been able to develop a seedless stone fruit, but they're getting closest with plums.
- ◆ A coconut is another drupe. When the coconut is on the tree, the brown round ball is encased in a big husk, which helps protect the coconut that has the seed on its journey through the world's oceans. The husk is generally removed before being shipped to temperate countries.
- ◆ Despite their common name, coconuts aren't nuts. For that matter, neither are almonds, walnuts, or pecans. Like the coconut, all of these are drupes—specifically the hard, stony seeds of a drupe. For botanists, true nuts are fruits, whereas a lot of what the grocery store calls nuts are really seeds.
- ◆ A peanut is a legume, which is a dry—as opposed to fleshy—fruit that splits along both sides at maturity. A legume is the botanical name given to all the plants of the Fabaceae, or pea, family: The fruit of a bean plant is the pod, and the seeds are inside the pod.
- ◆ To make matters more confusing, there is also a peanut butter fruit from the peanut butter tree, *Bunchosia argentea*, that produces cherry tomato-sized fruits, which are berries that are somewhere between a date and a peanut.
- ◆ Botanically, a nut is a fruit with a hard shell surrounding the seed. Hazelnuts, acorns, and chestnuts are true nuts. A true nut cannot be encased in any other kind of fruit. The almonds we eat are seeds inside a hard-fruit shell. Walnuts are seeds encased inside an even bigger fruit.



- ◇ An oddity among the would-be nuts is the cashew, which is in the same family as mango, which is a drupe. The infamous poison ivy also belongs to this family, Anacardiaceae. What we call the cashew is actually produced on the bottom end of a larger fleshy receptacle (the base of the flower) called the cashew apple. The cashew nut, which is a nut because it's in a hard shell, attaches to the bottom of the cashew apple. For this reason, some botanists call it a drupaceous nut.
- ◇ A cashew apple is not an apple because it is the swollen receptacle and doesn't have seeds. A real apple is botanically called a pome. The only fruits that are pomes are apples and pears.
- ◇ The pome develops from a compound ovary that is inferior, which means that the sepals and petals attach above the ovary instead of below it. The part of the apple we eat is actually the receptacle. The ovary begins where we stop eating, at the exocarp, or the papery membrane that surrounds the core.



- ◇ The pome is interesting in terms of ripeness. Apples are a long-lasting fruit because they stay ripe for a long time. A pear, on the other hand, has a narrower window of ripeness, and unlike apples, many people enjoy pears when they're soft.
- ◇ While opinions of the perfect ripeness of fruit may vary, figuring out cues to ripeness is a big business. A fruit that will stay unripe during transport and then become ripe just when it goes for sale at the grocery store is probably the best kind of fruit from a grower's perspective.

FRUITING BODIES

- ◇ Although not a fruit at all, a mushroom is a kind of fruiting body. The mushroom we see above the ground is the reproductive organ of the fungus that lives mostly underground. Because it's difficult to transport spores underground, when conditions are right, the strands of fungus, called hyphae, all come together to form the structure we recognize as a mushroom.
- ◇ This is why the mushroom is called a fruiting body. It doesn't produce fruits with seeds, but it is a structure that forms to produce spores, which are a form of reproduction. The spores in mushrooms are much like those of mosses and ferns. They are single-celled, very light, and very easy to disperse via wind.
- ◇ Fungi are more closely related to animals than plants; however, unlike animals, they have cell walls, like plants, but unlike plants, they don't photosynthesize. They are not plants, but they are not animals, and because of that, they have traditionally been grouped with the plants—not taxonomically, but informally.
- ◇ Most mushrooms are formed by one particular fungal group, the Basidiomycota. But there are some delicious notable exceptions. The morel mushroom happens to belong to another group, the Ascomycota. Because the morel can't be cultivated, the gathering of morels is a big business.

- ◇ The same is not true for the truffle, which is also an Ascomycota. Truffle farms have been appearing all over, but it takes a while for them to be productive. One must first inoculate a tree with the fungus and then wait. In France, however, 80% of truffles come from truffle orchards.
- ◇ Truffles are mycorrhizal fungus, which means that they form a symbiotic mutualism with the roots of trees. The fungus increases the plant's ability to absorb minerals and water because it greatly increases available surface area of the roots. The plants provide the mushrooms with sugars.
- ◇ Like ferns and mosses, mushrooms reproduce by spores, which are microscopic and haploid. The fungal life cycle is fairly complicated, but suffice it to say that these spores are released from the gills under the cap of the mushroom. Once the mushroom begins to grow, it can double in size in 24 hours.

READINGS

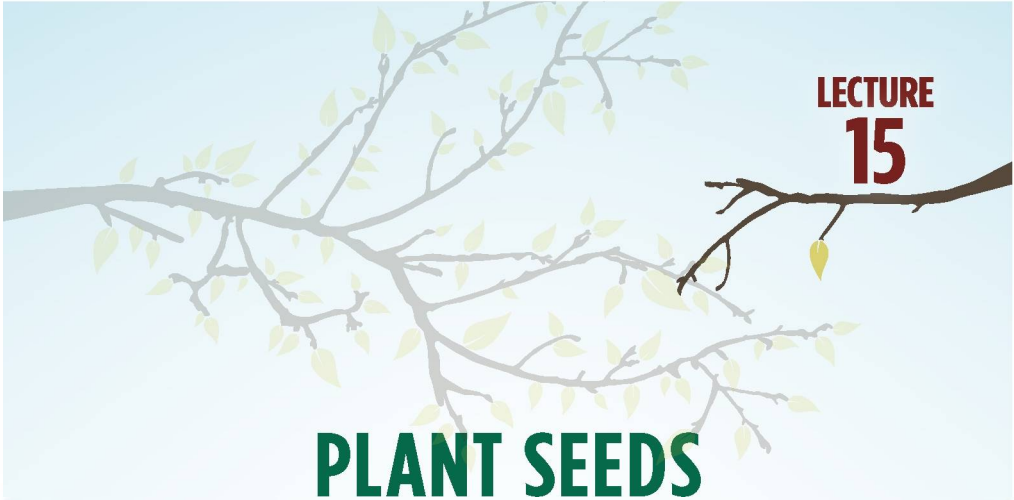
Blackburne-Maze, *Fruit*.

Chase and Llewellyn, *Seeing Seeds*.

Stuppy, *Fruit*.

QUESTIONS

- 1 When you think of your favorite fruit, can you locate the exocarp, mesocarp, and endocarp? What is its botanical name?
- 2 How are mushrooms like fruits?



LECTURE 15

PLANT SEEDS GET AROUND

The evolution of the seed was a major advantage for land plants. But unlike gymnosperms, which had a naked seed, the flowering plants produce a fruit around that seed, which aids in germination or dispersal—or both. The seed includes an entire embryonic plant, complete with an immature leaf, the cotyledon, which also stores starch so that the embryonic leaves can grow. Some flowering plants, the eudicots, have 2 of these immature leaves. The embryonic plant also has an immature root, called the radicle. A seed has germinated when the radicle first emerges from the seed. But before germination, the seed is dispersed. Like pollination, there are many ways that fruits, with the seed or seeds inside of them, can be dispersed.

EXPLODING SEEDS

- ◆ Fruits come in many forms. If fruits are fleshy, then they are botanically called fleshy fruits. However, not all fruits are fleshy. Many fruits are dry at maturity. When they are completely ripe, dry fruits either split open or don't. Dry fruits that split apart at maturity are called dehiscent, and only dry fruits will split, as fleshy fruits will simply decay. Dry fruits that never split are called indehiscent.
- ◆ Launching the fruits a far distance ensures that the seeds won't try to germinate right beneath the parent tree and then compete with it.
- ◆ *Hura crepitans* is a tree that is native to the American tropics and produces a fruit that is botanically classified as a capsule, which means that at maturity, it's a dry dehiscent fruit that develops from 2 or more carpels, which are divisions of the ovary. A capsule also has many seeds and splits along or between the carpels. There are also capsules that have pores at the top, where the seeds come out, and these are called poricidal capsules.
- ◆ The fruits look innocuous enough, but as they dry, they begin to split along the carpels, and the cells become smaller and smaller because the water has left. The seeds will split from the wall of the fruit, and if harvested at this time, the fruit will sound like a rattle with the loose seeds inside. Eventually, the cells will break, and the seeds will shoot out of the fruit. The seeds are discoid shaped, which reduces their wind drag and helps them go even farther. These ballistic seeds could do some damage if you, or other plants, got in their way.



SANDBOX TREE
Hura crepitans

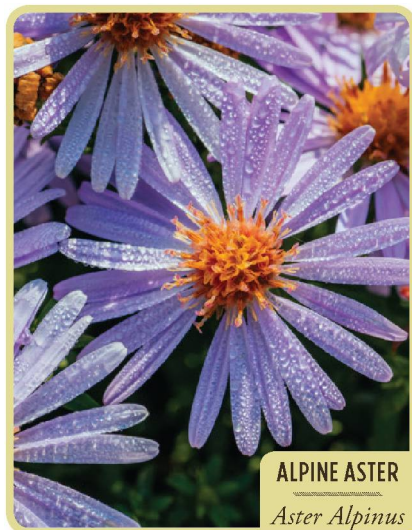
- ◇ There is also a plant called the touch-me-not that, when disturbed by a breeze or a touch from an animal, will also explode its seeds. However, these seeds are much smaller and pose no threat of injury. In fact, a number of plants employ this drying-out mechanism, called xerochasy, for ejecting their seeds.



- ◇ Plants can also explode by using hygrochasy, which is opening by water. This mechanism still involves the loss of water. It occurs when enlarged cell walls shrink with water loss and then expand with its uptake. Then, these increases in the swelling tissue create pressure because this swelling tissue is attached to lignified, non-swelling resistance tissue. When the pressure becomes too great, the fruit explodes.
- ◇ Hygrochasy doesn't just occur in dry fruits. There can also be fleshy fruits that explode, and even different fruit types in the same family can explode.
- ◇ This is just one of the many ways that plants disperse the seeds. There are negatives and positives for each type of seed dispersal. If the seed doesn't go too far, as in the case of exploding seeds, then chances are that where it lands is a pretty good place to germinate, because it's not too far from the favorable habitat where its parent germinated. This is why we sometimes see clumps of a certain type of plant in nature.
- ◇ On the other hand, too many individuals in one spot can lead to competition in that spot. Plus, maybe the parent plant is in a spot that might be good for an adult but not so great for germination. In this case, the seeds might be better off if they are dispersed a greater distance. For these greater distances, plants can't rely on fruit explosions alone, and there are a myriad of ways that plants disperse their seeds.

DISPERSAL BY WIND AND WATER

- ◇ In addition to explosions, the other abiotic, or nonliving, dispersal methods are wind and water.
- ◇ Many fruits have very small seeds that are dispersed by wind. In addition, a plant that has an animal pollinator might also have a different dispersal method. For example, the orchid family, Orchidaceae, is animal pollinated but wind dispersed.
- ◇ A dandelion is a wind-dispersed fruit. One reason a dandelion can produce so many seeds is that it can produce seeds without pollination, a process called apomixis. This form of reproduction is asexual, but the cloned seeds are derived from ovules that would have given way to sexual reproduction had they not skipped pollination and gone straight to seed development.
- ◇ Dandelions are part of the sunflower family, Asteraceae. The name of the family comes from the genus *Aster*, which means star, because these flowers look like stars. The main fruit type of the sunflowers is called a cypsela, and they are perfect for riding on the wind with their own miniature parachutes. A cypsela is basically like an achene—a fruit that is derived from one carpel, within a flower that has a superior ovary—except that it is derived from an inferior ovary.
- ◇ A parachute is just one way to use the wind. A plant could also produce cottony seeds that are easily blown around. Cotton is a great example of this dispersal method, and so is the Kapok tree, which produces so much cottony fiber that it was used as mattress filling.



- ◇ Another dispersal method is the winged fruit. A maple tree produces a winged fruit called a double samara. The botanical description of a samara is an achene with a wing on it.
- ◇ Another means of wind dispersal is found in the tumbleweeds. This dispersal mechanism is convergent, meaning that it's found in a number of different plant families. About a dozen families have plants that employ this method of moving the seeds around as the bush-like plant gets blown across the landscape. Baby's breath forms a tumbleweed as a dispersal mechanism.
- ◇ After wind, the other abiotic disperser is water. Plants don't have to grow in water to be dispersed by water. Plants that grow near water often use water as their dispersal agent. These plants will often produce fruits that are buoyant because of their small size or because of their structure. The coconut has an outer seed coat that is impermeable to water, so the coconut fruit can travel across oceans.
- ◇ Sea beans is a common name that refers to seeds and fruits that are produced in one place and ride the ocean currents to end up somewhere entirely new. They are also called drifter seeds. There are more than 200 species of plants that are dispersed in this way. Most times, these fruits are produced by trees in the tropics. Many people enjoy collecting these fruits and using them for art; they have also been used by oceanologists to map out currents.



COCONUT TREE
Cocos nucifera

DISPERSAL BY ANIMAL

- ◇ Perhaps the most complex mode of dispersal involves animals. There are 2 major strategies for plants: Be a delicious, irresistible fruit that animals can't wait to eat, or fashion yourself into some kind of hook or barb to attach to animal hair and hitch a ride.
- ◇ Even though insects do the lion's share of the work in pollination, vertebrates, especially birds and mammals, do the majority of the dispersal effort carried out by animals.
- ◇ The seeds produced by many fleshy fruits will pass through the digestive tract of the bird or other vertebrate without being harmed. Some plants with fleshy fruits actually have seeds that must pass through an animal's digestive tract to weaken the seed coat.
- ◇ This is the process that will start germination. As the seed coat weakens, it becomes permeable to water, and this will cause the cells inside to swell and grow, and the radicle will emerge, and germination has occurred.
- ◇ An example of a seed that must pass through an animal is a blackberry or a raspberry. The fruits are each individual spheres, and inside each one is a tiny seed, which needs to be roughed up in a bird's gizzard before they can germinate. In fact, gardeners who grow these plants from seed have to scratch these seeds in some way, usually using sandpaper, to weaken the seed coat and ensure germination.
- ◇ Plants that hitch a ride often have barbs or hooks to ensure that they hold for a little while. In fact, it was burdock, a biennial aster plant, that was the inspiration for Velcro.
- ◇ Birds and mammals seem likely fruit dispersers, but other vertebrates, such as tortoises and iguanas—and even some fish—eat fruits and disperse seeds, too.

- ◇ Even though vertebrates do most of the fruit dispersal by animals, a good number of plants also employ ants for this purpose. Plants that have ant-dispersed fruits have a special growth on the outside of their seeds called an elaiosome. This small, but visible, fleshy appendage contains proteins, sugars, fats, and vitamins.
- ◇ The ants carry the seed and elaiosome back to their nests and use the elaiosome to feed other workers, or their developing larvae. While the elaiosome gets eaten, the seed is generally unharmed, and the seed will germinate in the waste pile of the ants' nest, where the seed is protected from predators and already has a source of nutrients surrounding it. Common examples of plants dispersed by ants in North America include many violets and hyacinths.

READINGS

Fenner and Thompson, *The Ecology of Seeds*.

Hanson, *The Triumph of Seeds*.

Kessler and Stuppy, *Seeds*.

QUESTIONS

- 1 How does a seed know when to germinate?
- 2 Find some seeds in your neighborhood. Can you think of how they are dispersed? If it's wintertime, look on the Internet for pictures of seeds of local plants and determine their dispersal method.

LECTURE
16

WATER PLANTS CAME FROM LAND

Plants started in shallow water, like a freshwater algae, and then eventually moved to land, where flowering plants dominated—but then a few came back to the water. The approximately 70 species of seagrasses are distributed in 4 different families of flowering plants. Most likely, these groups diverged from a single monocot flowering plant around 100 million years ago.

SEAGRASSES

- ◇ Despite being in different families with growth forms that vary from grasslike to very leafy, all seagrasses grow in similar habitats. They grow in sandy or muddy bottoms of shallow coastal waters. They all deal with the same stresses, including low light levels, sediments that are anaerobic and nutrient poor, and the difficulty of getting carbon dioxide into the leaves and stems.
- ◇ Part of the reason that seagrasses face low light levels even though they're in shallow water is because areas just off the coast usually receive a fair amount of sediment, which diffuses light as soon as it enters the water. Some of the sediment will land on the seagrass and limit light levels even further.
- ◇ Light levels are also low because there are small algae growing on the seagrasses. Algae that grow on seagrasses will also grow on almost anything else, living or dead, within the ocean. This type of algae is called periphyton, and it absorbs sunlight, further reducing the amount of light that makes it to the seagrass.



PERIPHYTON GROWING ON SEAGRASS

- ◇ Seagrasses deal with these low light levels by putting their chloroplasts, which is where photosynthesis occurs, in the epidermis, the outermost layer, whereas most plants have their chloroplasts internal to the epidermis. Seagrasses have chloroplasts in their stems, too, not just their leaves.
- ◇ As a further adaptation to low light levels, seagrasses are rhizomatous, like many terrestrial grasses. The advantage of the rhizome, an underground stem, is that it can store sugars for times when light levels are so low that photosynthesis can't take place. In fact, seagrass roots undergo fermentation, just like yeast, after they've been in the dark for a few hours. And, like brewer's yeast, they release alcohol, ethanol, as a waste product into the water around them.
- ◇ Another issue that seagrasses have to face is an anaerobic substrate. It's not actually soil because it's underwater. The substrate around the roots is anaerobic—it has no oxygen. This is a problem because roots don't photosynthesize. The cells in the roots have mitochondria, just like human cells do, and these mitochondria need oxygen, just like humans do. If roots become waterlogged and can't get oxygen, they die, and the plant dies.
- ◇ Seagrasses have an amazing adaptation to deal with this. The leaves and stems of seagrasses are photosynthesizing during the day, and photosynthesis produces oxygen as a waste product. Seagrasses release this oxygen back into their own tissues, which are cavernous and full of small spaces. The oxygen then diffuses down to the roots because the roots don't have any oxygen, so there's a lower concentration of oxygen there. This transport ceases at night, though, because photosynthesis doesn't work in the dark, which is why the roots undergo fermentation after a while.
- ◇ Not only is the substrate devoid of water, but it also lacks nutrients. Marine phytoplankton tend to absorb nutrients in the seawater. As plankton die and fall to the seafloor, their decomposition provides some nutrients in the substrate, but these are often consumed by bacteria. To maximize nutrient uptake, seagrasses absorb minerals from ocean water and the substrate. Seagrasses also have bacteria that live in their roots that can break down nitrogen into a usable form.

- ◇ There is yet another hurdle that seagrasses have to jump to live underwater. Seawater doesn't have much dissolved carbon dioxide. Most of the carbon dioxide that is in seawater is in the form of the bicarbonate ion, so seagrasses use active transport to get the bicarbonate ions into the tissues, where an enzyme called carbonic anhydrase converts it into carbon dioxide so that it can be run through the Calvin cycle to make sugars as part of photosynthesis.
- ◇ Seagrasses, like all plants living in a marine environment, also have to deal with copious amounts of salt. Seagrasses cope with high salt levels by increasing the solute concentration in their tissues. By concentrating salts in their tissues, it can be even saltier than the ocean water, which ensures that it doesn't lose water to the surrounding environment.
- ◇ Seagrasses are mostly dioecious, with separate male and female plants, so pollen has to travel through the water column to get to a flower on a female plant.
- ◇ One genus of seagrass, *Amphibolis*, has some of the largest pollen among the flowering plants. This long pollen can travel to the female plant in 1 of 3 ways.
 - ◇ Pollen can float to the surface of the water when tides are their lowest and drop pollen from there onto (hopefully) female plants below.
 - ◇ Pollen can conglomerate on the top of the substrate, whether it is sand or mud, and form a collective tower, which can reach a meter in length. Because many seagrasses grow in colonies, a meter is enough distance to ensure meeting a female flower and completing pollination—again, hopefully.
 - ◇ A third method, which is the same mechanism used by many marine animals, involves broadcasting sperm into the ocean water and, again, hoping for the best. This is called hydrophilous pollination.

- ◇ Once pollination has occurred, fruits develop and then need to be dispersed. In the seagrasses, dispersal entails floating fruits, mainly achenes or capsules, being carried in water currents. Oddly, none of the seeds float, so once the fruit settles, or is eaten, the seed will attempt germination where it lands. Germination can happen within a few hours or a few years.

MANGROVES

- ◇ Another flowering plant that lives in the ocean—but isn't submerged and is a tree—is the mangrove. There are about 55 different species of trees and shrubs that grow as mangroves do, in the ocean, and don't occur elsewhere.
- ◇ As with seagrasses, the condition of being a mangrove appears to be convergent; that is, the character to live this way is found in 16 different families. Because these families are unrelated, the traits enabling a tree to be a mangrove arose in evolution multiple times as an adaptation for living in seawater.
- ◇ Mangroves have a more restricted range than seagrasses. They are limited to tropical and subtropical coasts, whereas seagrasses can extend into the temperate ocean as far as the southern coasts of Greenland and Norway.
- ◇ Mangroves also live in shallow water because their crowns are exposed to air. Even though they can do normal gas exchange like terrestrial plants, they still have a suite of unique features to live in the ocean.
- ◇ Like seagrasses, mangroves have to deal with anaerobic substrates and roots. Some species have the advantage of living in tidal areas that are periodically free of water, and in these habitats, mangroves produce growths from their roots that go straight up. Most roots grow down, but these special structures in mangroves are negatively geotropic, so they grow upward. The growths are pneumatophores, and they carry oxygen to the rest of the root system.

- ◇ The pneumatophores are covered with small openings called lenticels. Because there is a lower concentration of oxygen inside the root than outside, the oxygen diffuses into the pneumatophore. This only works when the tide is out and the pneumatophores aren't covered with water.
- ◇ Mangroves have other root adaptations besides pneumatophores. They have prop roots and drop roots. Prop roots grow from the trunk and look like they are propping up the tree, and they are helpful for support, but these roots also transport oxygen to the submerged roots, like the pneumatophores do. Drop roots drop down from the branches of the tree and serve the same function as prop roots—to anchor the tree and increase oxygen to the submerged roots.
- ◇ Like seagrasses, mangroves also have much aerenchyma tissue, which means that the internal tissue contains many spaces for holding air, both in the roots and in the stem. In addition, many mangroves have rather spread out and shallow root systems so as to avoid very anoxic, deeper substrates.



- ◇ Also like seagrasses, mangroves have ways of coping with the salinity of ocean water. Mangroves are facultative halophytes, which means that they can grow in either freshwater or ocean water. However, because of their unique abilities to live in saltwater, there is less competition there, and saltwater is where they are mostly found.
- ◇ Facultative halophytes, including mangroves, can either be salt excluders, which don't take salt into their roots, or salt secretors, which do take in the salt but then excrete it, usually on the leaves. To exclude salt from entering the roots, mangroves concentrate other ions in their root tissues that will enable the water to enter the root, but not the salt. The excretion of salt may be one reason why mangroves don't keep their leaves very long.
- ◇ Perhaps the most interesting adaptation of mangroves is that they are viviparous, which means that the fruits of mangroves have a seedling that is already developed. In this way, they don't disperse fruits or seeds—they disperse seedlings.
- ◇ Mangroves do this because of the harsh conditions of germination. A mangrove seed would have to land in an appropriate substrate and anchor in by the time the tide came back in or it would float away. Seedlings can grow as much as 70 centimeters before they drop off the parent plant. By that time, they are ready to hit the substrate and root. In some species, these seedlings are contained in a long cylindrical casing that can float, and they can root and be upright in the substrate before the next tide.
- ◇ The seagrasses and the mangroves make up the only 2 groups of truly marine vascular plants. Interestingly, the ferns and gymnosperms don't have members that live in the ocean. They are confined to the land or freshwater. Many angiosperms live in freshwater systems and are usually called aquatic plants or water plants.

ALGAE

- ◇ All of the other plantlike organisms in the ocean are not true plants. They are algae, which are in the protist kingdom. Algae are not considered as part of the plant kingdom, primarily because the zygote, also known as the fertilized egg, does not develop in a special chamber. That said, algae are often grouped with plants because they both photosynthesize.
- ◇ Algae come in different colors—green, brown, and red—and this is one way that they are grouped taxonomically. Red algae are an important food source in Asia and have a high protein content. Giant kelp is a brown algae, and next to coral reefs, kelp forests make up the second most diverse and productive ocean community.
- ◇ As interesting as these marine organisms are, in terms of vascular plants, there are many more species that live in freshwater. Though some families are dominated by aquatics, there are many more aquatics scattered throughout other groups of ferns and flowering plants.

READINGS

Hogarth, *The Biology of Mangroves and Seagrasses*.

Mabey, *Cabaret of Plants*.

QUESTIONS

- 1 Why do seagrass and mangroves have different global distributions?
- 2 Why do you think there aren't more flowering plants, or any conifers at all, living in the ocean?

LECTURE
17

WHY THE TROPICS HAVE SO MANY PLANT SPECIES

Tropical regions are the most diverse ecosystems on land. Rapoport's rule, named after Eduardo Rapoport, who provided some of the first evidence for this trend, states that diversity increases toward the tropics, which is with decreasing latitude. The tropics are defined as any geographic region between the Tropic of Cancer, at 23.5 degrees north, and the Tropic of Capricorn, at 23.5 degrees south.

BIODIVERSITY IN TROPICAL REGIONS

- ◇ There are several reasons for the rich biodiversity that is found in tropical regions. For example, biodiversity can also refer to genetic diversity within a population. Like any population, there is generally variety among the individuals. And genetic diversity within a population is also important. But, at its simplest definition, biodiversity refers to the number of species within a given area, and ecologists refer to this as species richness.
- ◇ Although the tropics include seasonally dry forests and grasslands, and even mountains, the amazing diversity occurs in tropical rain forests, which are the most diverse terrestrial ecosystems on the planet. Typically, tropical rain forests are very wet and pretty warm. Ironically, it's this narrow temperature range that may have led to such high biodiversity.
- ◇ In the temperate zone, a plant must tolerate freezing cold temperature, either by being dormant, or an annual, or simply toughing it out. Tropical plants don't have to do this, but this might mean they have a very narrow temperature range in which they can operate. This would lead to species only being able to occupy a small range, so as soon as one travels up a mountain within a tropical rainforest, the temperature will become slightly cooler, and new species will be there.
- ◇ Warm and wet could also affect biodiversity through many parasites and diseases that thrive under warm and wet conditions. If a parasite can only infect one particular species of host, then it would be called a specialist. If neighboring seedlings had slight mutations that prevented infection from the parasite, they might thrive and eventually become their own species—increasing the amount of biodiversity.



AMAZON RAINFOREST

- ◇ Another hypothesis for the diversity has to do with insect herbivores. Many plants in the tropics have leaves with various chemical compounds that are unpalatable to certain insects, or even poisonous. An insect couldn't possibly adapt to all the chemical compounds that exist in leaves in the tropics, so most insects specialize their feeding on one species, or perhaps one genus, of plants. But the plants need to stay ahead of the insects, and one way to do this is through mutations that lead to different chemical structures in the leaves.
- ◇ Another feature of speciation, which isn't restricted to the tropics, is the spatial separation of species. If there was one species—for example, a small terrestrial herb that is dispersed by ants—and this species has a population that gets separated by a river, now there are 2 different populations of the herb. Over time, these populations might become different enough so as to be different species. Perhaps there are very different soil types on either side, or perhaps the ant that used to perform dispersal didn't make it to the other side, so now a different type of insect does the dispersal.
- ◇ This type of speciation caused by a population being physically separated is called allopatric speciation, and it may have occurred a lot in the tropics because of past climate changes. The example of the river may have happened a few times, but river separation isn't thought to have spurred much diversification in the Amazon, which has many rivers.
- ◇ Although the tropics were never fully glaciated, we can suppose that some glaciers came down and retreated from mountains, which would cause separation of populations on either side of a glacier or mountain range.
- ◇ Changes in sea levels and lake levels could cause physical separation, too. If the sea level goes down, land bridges can form between islands and mainlands and between islands of archipelagos. As ocean levels rise, populations become isolated and speciation can occur. Rising and falling lake levels can act the same way.
- ◇ Being near the equator means that there is a lot of sun energy hitting the tropics, and this is another hypothesis for why these latitudes are so diverse. More energy means that more plants can use this energy.

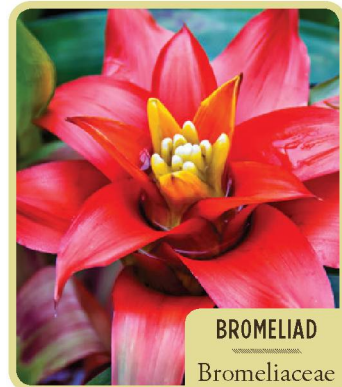
- ◇ Another idea about why the tropics are so diverse has to do with available habitat. The tropics are certainly expansive in space, but the boreal forest region just below the North Pole takes up much more area than the tropical forests. Rain forests have several layers of vegetation, and this is probably possible in the rain forests because of the intense sunlight, which shines for about 12 hours a day. Because of this energy input, sunlight can penetrate through the layers, and a small amount can reach the forest floor.
- ◇ Getting sunlight is a major theme in the tropics. With so many plants around, it's a cutthroat game to get to the top or deal with the shade, so many tropical plants are shade-adapted plants. This is why so many houseplants are tropical plants—because they thrive in low light levels.
- ◇ Tropical rain forests are shady, not too hot, and pretty moist—even when it's not raining. The ground is covered with plants of all shapes and sizes. If there is a very thick middle layer, there will be fewer plants, and it won't be quite so dense on the forest floor, but there are still many plants thriving in those low light levels.

TROPICAL PLANTS

- ◇ The understory of the canopy is where many animals—particularly arboreal, or tree-dwelling, animals—live. The canopy in general in rain forests has many more species than temperate forests do; by some estimates, about 40% of all plants are in the canopy of rainforests.
- ◇ The plants that live in the canopy on the trees are called epiphytes. Temperate latitude forests have epiphytes, too, many of them mosses, but the tropics have a greater diversity and a larger quantity of epiphytes.
- ◇ One temperate epiphyte that is pretty common is mistletoe, which is parasitic. It grows rootlike structures into its host tree and uses the host's sugars. But most epiphytes are not parasitic; they just use the tree for real estate.

- ◆ There are 3 major types of epiphytes common in the tropics, and they are all pretty much absent from temperate canopies. The major epiphytes are bromeliads, orchids, and lianas.

- ◆ Bromeliads are often called tank plants, because their overlapping leaf bases form a small tank where water can collect. These type of plants, including the pineapple, are all in the Bromeliaceae, or bromeliad, family. The tanks of bromeliads form their own microecosystems of algae, insects, and amphibians. Bromeliads aren't limited exclusively to the tropics.



- ◆ Today, orchids, in the Orchidaceae family, are arguably the most diverse plant family on Earth. Orchids are famous in the botanical world for having unique relationships with pollinators; that is, there are many orchids that are pollinated by a single species of insect. Not all orchids are epiphytic, and not all orchids are tropical, but many orchids in the tropics are epiphytic. Many people think of orchids as fragile flowers, but epiphytic orchids are able to survive on little water and no soil in the canopy.
- ◆ The liana is a woody vine. There are many different types of lianas found in different families, so it's a convergent form. A familiar liana is the rattan. There are several genera of rattan, and they are all in the palm family, Arecaceae. Palms, including rattans, don't have true wood. The rattan, as a palm, doesn't produce wood like an oak, but the stems are very woody nonetheless, and they can be woven into furniture.
- ◆ Rattan is a fairly sustainable forest product where it grows in Southeast Asia. Because it's a liana, it grows faster and can be harvested easier than trees. But if it's overharvested, then there won't be any left.

- ◇ The palm family is very large and mostly restricted to the tropics. It also provides the coconut palm; the date palm, which grows in deserts; and the oil palm. Unlike the sustainable rattan liana, there is some controversy over the sustainability of the oil palm, because large parts of tropical rainforests are being destroyed to make way for palm oil plantations. Palm oil and palm kernel oil are used for all kinds of things, from cosmetics to food to lubrication for machinery.
- ◇ The most exported tropical crop, and the second most traded commodity in the world after oil, is coffee. This is a shrub that is native to the Ethiopian highlands, which aren't tropical rainforests, but this area falls geographically within the tropics. Coffee can be somewhat sustainable because the best kinds of coffee are shade grown. This is good because forests in the tropics have many layers, especially the canopy and the understory. If the canopy is left intact, and coffee is grown in the understory, then there is still some habitat left.
- ◇ An even better tropical crop for sustainability is chocolate, *Theobroma cacao*, which is in the same family as common hibiscus and cotton, Malvaceae. Chocolate flowers are produced on the trunk of the tree, and despite all the flavor and smells of chocolate, the flowers have very little scent. Chocolate trees are understory trees that are native to South America and are adapted to shade, and as of yet, there isn't a full-sun variety, so by definition, chocolate is shade grown.



READINGS

Attenborough and Graham, *The Private Life of Plants*.

Bernhardt, *Wily Violets and Underground Orchids*.

Royte, *The Tapir's Morning Bath*.

QUESTIONS

- 1 Why are there more plant species in the tropics than anywhere else on Earth?
- 2 Why are the orchids, in particular, so diverse?

LECTURE
18

THE COMPLEXITY OF GRASSES AND GRASSLANDS

Grasses are not only the basis of human diets today, but they have also played a major role in the development of human society. In addition, botanically, grasses are very interesting, and they are very easy to recognize. Even though the orchids, sunflowers, and peas might have more species, the grass family is the most important plant family in terms of crops for energy, forage for animals, building material, and even delicious seasonings.

GRASSES

- ◇ Grasses are interesting in that they are defined ecologically, functionally, and taxonomically. This means that a grass isn't in any other family, but the grass family and grasses are pretty unique in terms of their botany.
- ◇ Grasses are all nonwoody, except for the bamboos. They are monocots, which means that they have parallel veins in their leaves, which are long and slender. These plants are visibly different from broadleaf plants, which have netted or palmate venation in the leaves. Grasses have a very unique, small, but highly complex, flower morphology. Most grasses are wind pollinated.
- ◇ Grass botany is difficult because of the complexity and scale of how to identify grasses. Identifying a plant in this family is pretty easy, but identifying it down to species is much more difficult.
- ◇ There are 2 other families that can sometimes be mistaken for grasses. One family is the sedges, known botanically as the Cyperaceae family, after the most characteristic genus, *Cyperus*. A fairly notable member of this genus is *Cyperus papyrus*, which is the source of papyrus. The other family is the Juncaceae family, which are the rushes. A common rush is bulrush, which is the common name for many aquatic rushes in the *Scirpus* genus.

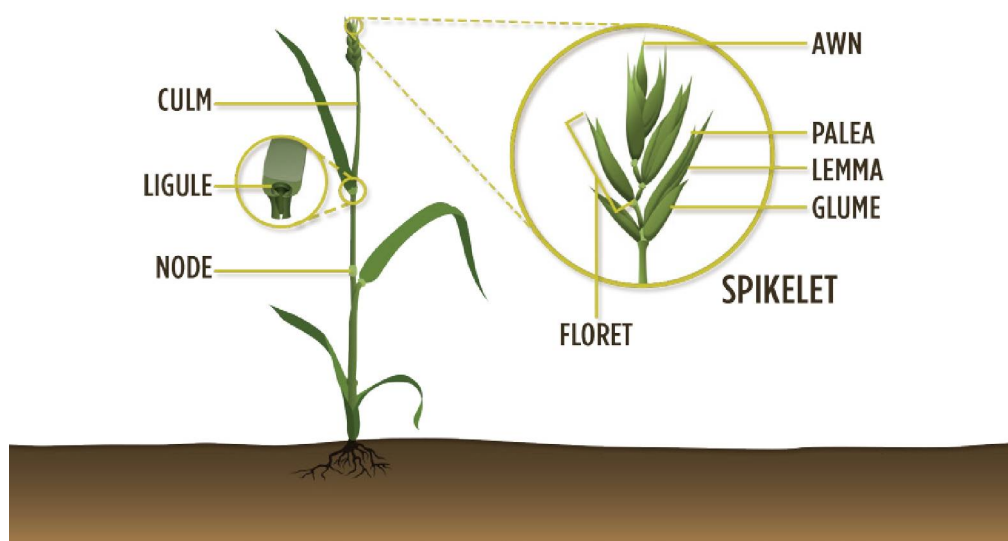


GIANT TIMBER BAMBOO
Bambusa oldhamii



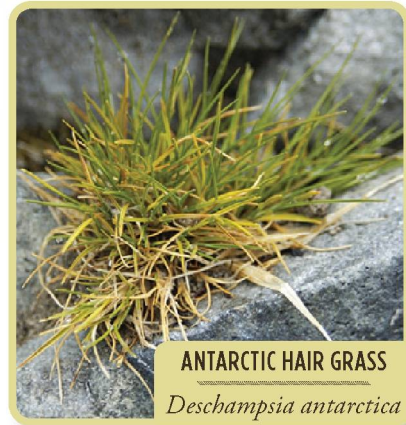
- ◇ Sedges, like papyrus, often have triangular stems. Rushes have round stems and often have stems that are solid. Grass stems are typically hollow.
- ◇ Grasses typically have leaves coming off of the main stem at several junctions. The node is where a leaf comes off the stem. Often at this junction there will be a small membrane called the ligule, which is just one of the structures that are unique to grasses.
- ◇ It's hypothesized that the ligule's function may be either physical or physiological. The hypothesis that refers to the ligule's physical function is called the passive hypothesis. This idea suggests that the ligule prevents dirt, water, and pathogens from getting to the vulnerable parts of the culm, which is a special name for the stem of a grass. The physiological hypothesis about the ligule, called the active hypothesis, suggests that the ligule may play a role in the storage of starch produced in the blades.

- ◇ There is a special vocabulary just for the grasses; the blade, culm, and ligule are vegetative vocabulary. The grass flowers have their own vocabulary, too. In grasses, the flowers are called florets because they are small. A few florets make up a spikelet, but the exact number of florets in a spikelet depends on the species. Each flower is subtended by 1 or 2 modified leaves called palea, and above the flower is another modified leaf called a lemma.
- ◇ Several spikelets make up a spike, which has a different arrangement on the stem based on the species type. Typically, spikes are solitary or arranged on a panicle. These floral spikelets have special structures above and below them. Each spikelet is subtended by a certain number of modified leaves called glumes.
- ◇ There are suppositions that these structures might provide certain adaptations to drought or heat, but they're certainly not to attract animals. The grasses are almost exclusively pollinated by wind and dispersed by wind. There is no need for the flower to invest in showy flowers that would cost a lot of carbon, or in beautiful scents, to attract animals. The flowers of the grasses have a utilitarian beauty.



ADAPTATIONS OF GRASSES

- ◇ The grassland ecosystem is on every continent except Antarctica; though, interestingly, there are only 2 vascular plants on Antarctica, and one of them is a grass. A small bunch grass called *Deschampsia antarctica* grows on the western peninsula of Antarctica, but this growth isn't prolific enough to be called a grassland.



- ◇ Grasslands are estimated to make up about $\frac{1}{3}$ of the terrestrial land area of the planet. Grasslands are broad in that they can be cold or hot, wet or dry. Typically, though, they are drier than forests. Rainfall may be seasonal, falling at one time during the year. Some areas that are dominated by grasses may not be what we commonly think of as grasslands. Habitats such as tundra, which is too cold for trees, and wetlands, which are too wet for trees, come to mind.
- ◇ Grazers are typically animals that eat grass. A browser is an animal that browses on leaves of shrubs or trees. The grasslands have evolved with grazers. There are several adaptations that grasses have employed to exist in landscapes full of hungry grazers.
- ◇ One of the most interesting adaptations of grasses is that they grow from the base. Trees and most other plants, by contrast, have their growing tissue at the top of the tree and the tips of the branches.
- ◇ In all plants, the growing tissue is called the meristem. If the plant has determinate growth, it will grow until the plant reaches the size that it has genetically defined and then stop. In plants that have indeterminate growth, the plant will continue to grow until the plant dies.

- ◇ The meristem is a region of cells that are constantly dividing. The meristem of the grasses is found at the base of the blades, so it's called a basal meristem—which in grasses is a great adaptation to grazers. The grazer comes along to eat the top of the grass, but that doesn't kill it; in fact, most times, it will actually promote growth of the plant.
- ◇ This is the same principle behind mowing our grasses. When we mow, we promote the grasses to reproduce vegetatively, which means that the grass will produce more rhizomes, which are underground stems. The promotion of more of these underground stems will eventually send up more shoots, and the grass will look fuller.
- ◇ Another unique and adaptive feature of grasses is the presence of very small bits of silica, called phytoliths, in the epidermal cells, which are the outermost cells of the blades. There are 2 hypotheses about the presence of phytoliths in grasses: that grasses developed these phytoliths to inhibit grazing and that grazers developed teeth that could withstand silica in the blades.
- ◇ Grass leaf blades are not only adapted to grazers, but they are also adapted to the climate in which they live. Grasses from humid environments typically have larger, wider leaf blades, while those from drier regions have blades that are more linear. Grasses in the most arid environments have blades that can roll up during extreme sunlight and heat or leaves that are almost needlelike.
- ◇ Although grasses are now found in a variety of habitats, they most likely evolved in hot places.
- ◇ Many grasses have another unique adaptation to a hot environment: a special kind of photosynthesis called C4 photosynthesis, which was described in Lecture 8.

TYPES OF GRASSES

- ◇ Even though grasses probably evolved in warm regions, there are grasses that are accustomed to growing in cool climates. We tend to think about grasses as being warm-season or cool-season grasses. Warm-season grasses will become green and flower when it's warm. They will continue their life cycle through the warmest part of the summer. A cool-season grass is one that will become green and flower early in the spring, and by midsummer, these grasses will start to turn brown and finish their growing season.
- ◇ Examples of warm-season grasses are Bermuda grass and zoysia grass. Common cool-season grasses are Kentucky bluegrass and perennial ryegrass.
- ◇ This isn't the only way that grasses are classified. They are also grouped as bunch grasses versus turf grasses. A bunch grass will confine its growth to a small clump, or bunch, while a turf grass will spread out.
- ◇ Almost all grasses will send stolons or rhizomes out to promote vegetative growth, but the rhizomes in turf grasses will typically be longer, so that the individual culms of the grass can spread out. In this way, a whole field of grasses might be genetically the same, what botanists would call one genet, while each individual culm of grass would be a ramet.
- ◇ Grasses typically have much deeper roots than we might expect from just looking at the above-ground growth. Grass roots are not only very deep, but they are also very dense; that is, they are fibrous and have many root hairs that go in between the major roots. In grasses, these root hairs arise from trichoblasts, which are specialized cells in the roots.
- ◇ Grasses also have many more root hairs than other kinds of plants, which is one reason why grassland soils are so rich. Not only is there sparse rainfall, so nutrients don't dissolve away in the rainwater, but the grasses, with their deep roots and grass hairs, prevent erosion and soil runoff when it does rain.

- ◇ Because many grasslands have been used for crops, grasslands are declining. Not all of the grasses grown for crops are used for food; many grasses are grown for use as biofuels. Anything that was alive contains carbon, and when it dies, it can be burned for fuel. This is true of wood, paper, and even manure.



- ◇ Corn is a common biofuel that is used to make ethanol, which is most commonly used as an additive to gasoline. In addition to corn, sugarcane is another popular grass that is used to make biofuels, but now native prairie grasses are also being used.
- ◇ Despite looking monotonous to the untrained eye, grasslands are actually very diverse. Most grasslands have a number of other species, most notably members of the sunflower family, Asteraceae.



READINGS

Bone, *Steppes*.

Cooke, *Grasses and Bamboos*.

Darke, *The Encyclopedia of Grasses for Livable Landscapes*.

Gibson, *Grasses and Grassland Ecology*.

QUESTIONS

- 1 Some botanists are working on changing rice, a C₃ plant, to a C₄ plant so that it could be more efficient. Why aren't all grasses C₄? Why would plants that grow in hot climates still maintain the C₃ photosynthesis pathway?
- 2 How are some herbicides able only to kill eudicot, or broadleaved, species? Would it be useful to have an herbicide that only killed grasses? Why or why not?

LECTURE
19

SHRUBLANDS OF ROSES AND WINE

A shrub is a somewhat overlooked plant growth form. Shrubs don't quite have the majesty and presence of a tree, and they also lack the economic importance of the grasses. Few people grow a shrub lawn, yet shrubs are important types of plants, and shrublands are an interesting ecosystem. Plus, there are economically important shrubs.

SHRUBS AND SHRUBLANDS

- ◇ The common definition of a shrub is a lignified (woody) plant that has more than one main stem (underground or above ground). It's difficult to judge a shrub by its height because some plants might be small trees that are grown and pruned to form a hedge, so they look like a shrub. The Leyland cypress is an example.



- ◇ Although shrubs might look like trees and might only be distinguished from herbs by the presence of a woody stem, their in-between status gives them advantages. For example, a shrub's woodiness means that it doesn't need to reestablish its entire above-ground shoot as herbaceous plants must do every spring. This continuous growth season after season means that most shrubs can grow larger than most herbs, which offers them a competitive advantage for sunlight.
- ◇ Also, if it's a particularly stressful season, a shrub can forego reproduction and wait for better times in the future. An herb doesn't have this advantage. If an annual herb doesn't reproduce, it doesn't get another chance. Perennial herbs, too, might try to flower during lean times and then not have enough storage to make it through the winter.
- ◇ Shrubs have some advantages over trees, too. Because shrubs don't have as many leaves as trees do, there is less water loss through evaporation in the shrub's canopy. This means that shrubs are generally more drought tolerant than trees. Shrubs also have an advantage in their shortness. A shorter plant can avoid greater wind stress. And shorter plants with branches closer to the ground are more likely to trap snow, which is a huge advantage in arid climates.

- ◇ Given that there are so many advantages to the shrub life-form, there are shrubs virtually everywhere. Shrubs are found in grasslands, in the understory of temperate or tropical forests, above the tree line in alpine regions, and in the desert landscape.
- ◇ There are whole ecosystems that are comprised of shrubs. These special, shrub-dominated ecosystems are referred to as Mediterranean-type ecosystems (MTEs), named after the landscapes that border the Mediterranean Sea. This region is known for its hot, dry summers and cool, wet winters. This type of climate is found around the world.
- ◇ MTEs are just to the north (in the Northern Hemisphere) or to the south (in the Southern Hemisphere) of deserts. Above the Sonoran Desert of Arizona and California is the chaparral region of California. Just below the Atacama Desert of Chile is the *matorral* (which means “shrubland”) region of Chile. In South Africa, the fynbos (a word from Afrikaans that means “fine bush” and refers to the slender leaves found on the plants there) is located south of the Namib and Kalahari Deserts. In Australia, the range around Perth is just to the south and west of the Great Victoria Desert.
- ◇ Coincidentally, the 5 MTEs are also the great wine-making regions of the world: the Mediterranean region, including France, Spain, and Italy; Chile; California; South Africa; and Australia.
- ◇ Just as these landscapes are dominated by shrubs, they are also dominated by fire. This is in large part because of the shrubs themselves. The shrubs in these regions are evergreen, so most of them don’t drop their leaves during the winter. That’s good because that’s when the rain falls.
- ◇ However, because of the long, hot, and dry summer, the leaves have to be tough. The leaves of many chaparral shrubs are called sclerophyllous. The sclerophyll is from lignin, that same substance that makes up wood. There’s not as much of it in these leaves as in wood, but there’s enough to make the leaves tough. This helps the leaf keep its structure without retaining a lot of water.

- ◇ A leaf with a lot of water in it would be a plant that is losing a lot of water through transpiration. Plants that live in MTEs can't afford to lose a lot of water, especially in those hot, dry summers.
- ◇ Many chaparral shrubs contain volatile organic compounds. This is one reason why so many of our kitchen herbs, such as sage, rosemary, bay leaves, and thyme, come from MTEs. All of these plants contain volatile oils that we can smell, and thus we add them to our food for flavor.
- ◇ These volatile oils also deter insect predators, and plants will readily vary the amount of oils in their leaves based on how much sunlight they receive and how much herbivory they are facing. Their water status can also determine how many oils are present. And these oils are flammable.
- ◇ These shrubs grow very close together, adding to the possibility of spreading fire. But the fire isn't meant to consume everything. These areas are adapted to fire, and plants typically have a way of coming back after the fire through various means, usually by resprouting or reseeding. The fire is meant to come in hot and fast and burn out the competition and promote this resprouting or reseeding.
- ◇ For plants that are resprouters, the soil protects the base of the shrub, which has a thick, woody, underground burl. After a fire, the shrub will resprout from this burl.



- ◇ In plants that are reseederers, the adult plants die in the fire. The seeds left in the soil from previous years respond to cues from either heat or chemicals leached from the charred organic matter in the soil. The seeds that accumulate in the soil are collectively referred to as the seed bank. Plants make deposits of seeds over the years, and then when a fire occurs, there is a withdrawal as the seeds begin to germinate.
- ◇ The traits of small, dry leaves and volatile oils are adaptations to frequent fires. These fire-adapted MTEs are fairly biodiverse. Although the 5 MTE regions make up only 2% of Earth's land, they are responsible for 20% of the named plant species.
- ◇ One reason that these regions are so diverse probably has to do with fire. When an ecosystem is very stable, the plants don't need to change much to adapt to new conditions because conditions are staying the same. Alternatively, if there is a lot of change occurring frequently, there are opportunities for new species to develop.
- ◇ Many areas where shrubs dominate experience regular disturbance, such as fires in the MTEs. Other areas are somewhat new in an evolutionary sense. One example of recent change is the intermountain West. This is the region west of the Rocky Mountains but east of the Sierra Nevadas. It's also called the Great Basin. Much of this vast region is dominated by shrubs.

EXAMPLES OF SHRUBS

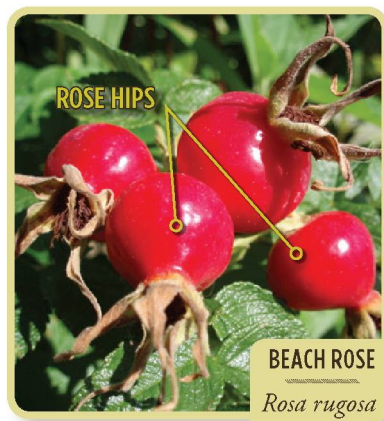
- ◇ One of the major shrubs of the Great Basin is the sagebrush. There are actually a few dozen different plants that go by the name of sagebrush. They are all in the *Artemisia* genus in the Aster family, or Asteraceae, which is the sunflower family. There are about 300 more species in this genus, but those other species aren't known as sagebrushes.
- ◇ Although sagebrushes make up a large portion of the Great Basin, they are currently in decline because of invasive species such as cheatgrass, which outcompetes the slower-growing shrubs. Another factor in the sagebrush



decline is overgrazing. Cows don't eat sagebrush, so ranchers destroyed sagebrush habitats to make way for grasses that cows would eat. This matters because a large number of species depend on sagebrush.

- ◆ Shrubs provide a lot of food to animals. Blackberry, raspberry, and thimbleberry are all shrubs that are economically important. Another shrub from the Great Basin that produces something people call a berry is the juniper. Although the small bluish balls on this plant are called berries, they're not technically berries. Juniper is a conifer, and what is commonly called a berry is actually a cone with fleshy cone scales.
- ◆ Unlike sagebrush, which is a common name for a number of North American shrubs growing in the *Artemisia* genus, creosote—a shrub in the North American Desert—stands alone. Also unlike sagebrush, the whole genus that creosote belongs to only contains 4 other plants, most of which are in South America. Creosote bush (*Larrea tridentata*) gets its name from the substance creosote, which is an oil distilled from coal tar, oil tar, or wood tar. Creosote is famous for being a very old shrub, or at least a very old clone.

- ◇ The shrub of romance is the rose. Fossils of roses have been found all over the Northern Hemisphere and range from 3 to 20 million years ago, or more. All the cultivated roses around the world are descendants of naturally occurring species in the genus *Rosa*, which is divided into 4 subgenera.
- ◇ Roses are in the family Rosaceae, which includes strawberries, apples, pears, plums, apricots, and peaches. What distinguishes a rose from these other members are its prickly stems, the way the leaves grow, and the formation of the fruit of the rose, which is botanically called a hip. Although they have a reputation for being a romantic flower, and perhaps delicate because of that connotation, roses are quite hardy.



READINGS

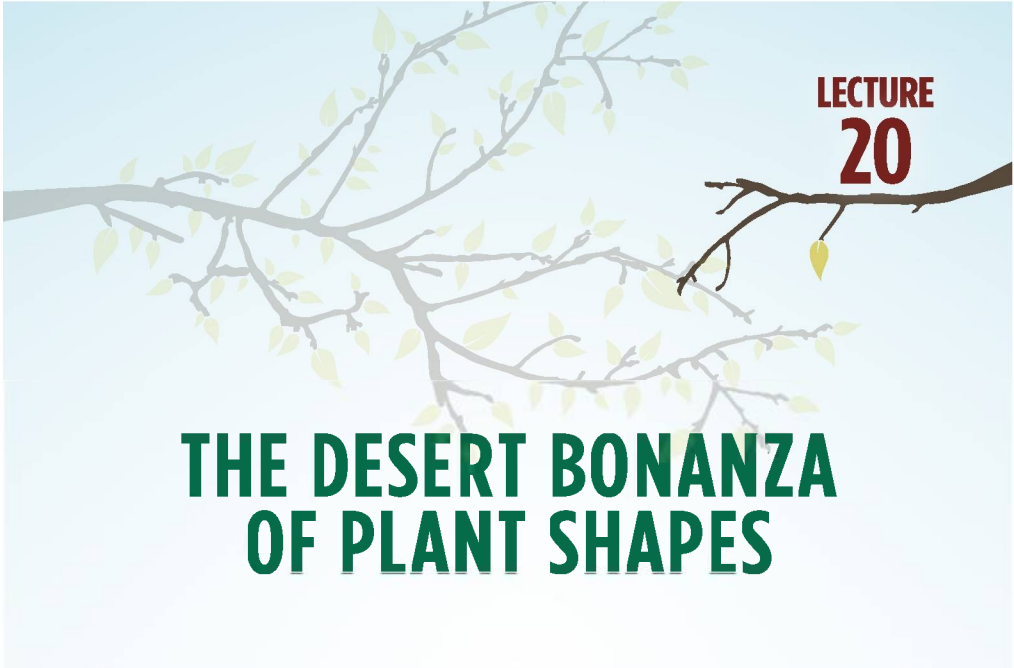
Harkness, *The Rose*.

McKell, *The Biology and Utilization of Shrubs*.

Trimble, *The Sagebrush Ocean*.

QUESTIONS

- 1 What are the advantages of the shrub growth form?
- 2 Given the advantages of the shrub form, in what kinds of habitats would you expect shrubs to dominate?



LECTURE 20

THE DESERT BONANZA OF PLANT SHAPES

Deserts are located just above tropic zones usually on the south and west of large continents. Deserts are classified by rainfall, not by temperature, so there are a number of cold deserts, such as the Great Basin Desert in the United States. Usually, deserts are areas that receive less than around 10 inches of precipitation per year. Much of the vast variety of desert plant forms are adapted to use water quickly, when it's available, and then to withstand certain periods of drought. It's this necessary adaptation that gives desert plants so many unique forms.

CRASSULACEAN ACID METABOLISM

- ◇ One of the most interesting plant adaptations to the desert is another pathway to photosynthesis. In the C₄ pathway of photosynthesis, the outside cells have a different enzyme called PEP carboxylase that only picks up carbon dioxide. Then, that carbon dioxide is moved into the regular C₃ cycle that most plants have.
- ◇ The new pathway that some desert plants have is called crassulacean acid metabolism (CAM). A common trait among CAM plants is that they have succulent leaves because their leaves are full of water.
- ◇ It seems a bit counterintuitive that a plant growing in a desert would have leaves full of water. If the plant were to have open stomata, the pores in their leaves that take in carbon dioxide, the water loss would be extreme.
- ◇ CAM plants deal with this by closing their stomata during the day and opening them at night. Although photosynthesis can't take place at night, CAM plants convert the carbon dioxide they pick up at night into malic acid and store it in the vacuole, the large liquid-filled sac that takes up most of the plant cell volume, until daylight.
- ◇ When it's sunny again, the plant goes through the light reactions just as a C₃ plant would, only the carbon comes from the malic acid, not directly from the stomata. All plants can use C₃ photosynthesis, and some are able to use all 3 types of photosynthesis—C₃, C₄, and CAM—at different times.
- ◇ The other advantage is that the main enzyme of C₃ photosynthesis, RuBisCO, cannot come into contact with oxygen. This is good because as temperatures increase, RuBisCO's affinity for oxygen will also increase. Because the plant doesn't use oxygen, this affinity for oxygen reduces the plant's efficiency.
- ◇ The malic acid that the plant is storing at night makes the leaves of a CAM plant acidic, with a lower pH, at night, which is why it's called crassulacean *acid* metabolism. As this malic acid is used during the day in the light reactions, the leaves become basic, with a higher pH.

- ◇ The CAM pathway has been detected in more than 1000 flowering plants in about 17 different families—about 0.3% of all flowering plants. Plants that are able to do CAM exist in a range of CAM activity. Plants can be obligate, meaning that they are all CAM all the time. Other plants might be facultative CAM, meaning that when conditions are good, the plant would just perform normal C3 photosynthesis, but when conditions get dry or hot, the plant can switch to CAM photosynthesis.
- ◇ Plants using CAM lose about 1/10 as much water per unit of sugars made compared to those using the standard C3 photosynthesis. But there is a trade-off: the overall rate of photosynthesis is slower, so CAM plants grow more slowly than most C3 plants.
- ◇ The CAM photosynthetic pathway is also found in members of the bromeliads (Bromeliaceae) and in some orchids (Orchidaceae). The CAM pathway evolved multiple times in the history of these families.

THE CACTUS FAMILY

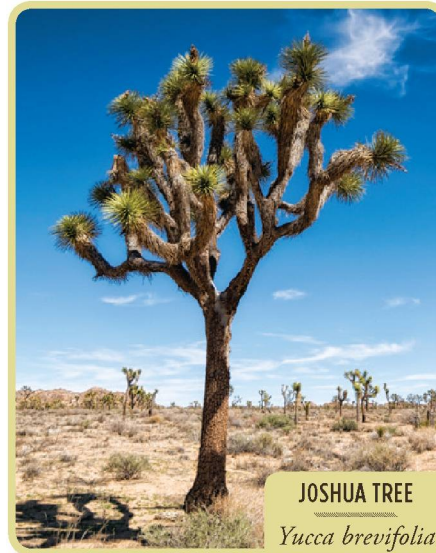
- ◇ The CAM photosynthetic pathway is also found in the cactus family, Cactaceae, which has about 1600 species, mostly distributed in the Western Hemisphere. All the cacti can perform CAM, though most seedlings use the C3 pathway.
- ◇ For the most part, the Cactaceae are unmistakable. Cacti are recognized by their green, photosynthetic stems, and what some people might think of as their needles are actually modified leaves called spines. The function of the spines is to deter animals from eating them. Many cacti are not too palatable because of the acids in their tissues, but those tissues do contain a lot of water.
- ◇ Despite the protection these plants have, they are important water sources to animals in deserts. And the fruits of many cacti are important food sources, not just for animals. In Mexico, nopalitos are a common vegetable. These are the pads of the *Opuntia*, or beavertail, cactus. Sheep, goats, and cows also eat the pads as fodder.

- ◇ It's not just the vegetative parts of cactus that are eaten. Cactus fruits are important for a variety of desert animals, and humans also eat the fruits of the *Opuntia*.
- ◇ Cacti, especially *Opuntia*, can grow very efficiently in arid lands. Within 2 years, a cultivated *Opuntia* can begin to bear fruit. But not all cacti grow so quickly. Saguaro cacti are very slow growing. In fact, they can take 75 years to produce one arm.
- ◇ Some plants in deserts are commonly called cacti but aren't. Examples of such plants include agave, aloe vera, and Joshua tree. All of these plants are monocots, so they are more closely related to lilies than they are to cacti. The Cactaceae are eudicots, and they are more closely related to carnations.



DESERT TREES

- ◇ When people think of deserts, they don't usually think of trees, but trees do live in deserts. A number of arborescent forms grow in the desert, though they are not all cacti. A desert arborescent form is the Joshua tree, or *Yucca brevifolia*, which is related to non-tree-forming yuccas. Joshua trees are in the Asparagaceae family; they are related to asparagus. The agaves are also in this family.



- ◇ Because leaves can lose so much water, many desert plants will flower during the dry season and wait for periodic rains before they produce leaves. The elephant tree of the Baja peninsula is a good example. It produces small yellow flowers during the dry season, which are an important source of nectar for pollinators.
- ◇ This delay in leaf development also enables insects to see the very small flowers without a covering of leaves. Because flowers typically don't photosynthesize, they don't transpire nearly as much, so there's little water loss for the plant to have flowers out. This tree, which is really more of a shrub, is called the elephant tree because of its thickened tree trunk, which stores water.
- ◇ A tree that has a similar kind of water-storing mechanism is the famous baobab tree of the African plains, though they also live in India, Madagascar, Australia, and the island of Socotra. All the regions where baobab trees grow are savanna, which might be desertlike half the year and grassland-like the other half of the year when the rains come. The adaptations of the baobab tree are mostly to save water.

- ◆ Like other plants in arid regions, the baobab drop their leaves during the dry season. They then put out leaves and flowers before the rains arrive again. In studies, the dominant cue seems to be photoperiod, as it is for many plants. In short, baobab trees will synchronously flower and put out leaves when the critical day length is slightly longer than 12 hours.
- ◆ Another interesting desert tree is called the boojum tree, *Fouquieria columnaris*, which is in the Fouquieriaceae, or ocotillo, family. The boojum tree is endemic to the Baja California peninsula and surrounding areas. Like the other member of this family, the ocotillo, both of these plants flush with leaves in response to rainfall. The ocotillo stems have spines, like a cactus, but the spines are made by leaves. No other plant produces spines like this.



DESERT ADAPTATIONS

- ◆ Some plants don't tolerate dryness. Perennial plants, such as the ocotillo and the baobab, time certain events, such as flowering, based on when rainfall occurs. Even most deserts have a time of year when it rains. Annual plants time their entire lives around these rainfalls.
- ◆ Every spring in the Mojave Desert, for a few weeks, the desert blooms with many desert annuals. These small wildflowers begin to germinate hours after a rainfall and then grow quickly and produce flowers, fruits, and seeds before the really hot and dry weather of the summer begins. The seeds are then dispersed into the soil by summer and wait through the winter until the next rain.

- ◇ A different way to avoid the stress of the dry season is to become dormant. A striking example of a plant like this is the resurrection plant. This plant is a lycopod, which makes it a relative of ferns. The resurrection fern is native to the Southwest United States. This plant can look dead during the dry season, and then when the rains come, it can completely revive.
- ◇ The resurrection plant prepares to have a slowdown in metabolism by storing extra sugars, such as sucrose, and amino acids, which make up proteins. Next, it starts to produce antioxidants. Lastly, it produces proteins that help the internal organelles and cell walls toughen up for the dry season.
- ◇ Another desert adaptation is to avoid leaves altogether. Some plants don't even photosynthesize. Although these plants had the ability to make chlorophyll, over time they were selected to lose this ability and instead use sugars from a host plant. These are parasitic plants, such as dodder, which is a bright orange plant that can often grow on creosote shrubs in the desert.

READINGS

Crawford, *Plants at the Margin*.

Nobel, *Environmental Biology of Agaves and Cacti*.

Tudge, *The Tree*.

QUESTIONS

- 1 Why are there so many unusual forms of plants in deserts?
- 2 How does the CAM photosynthetic pathway differ from the C₄ pathway?

LECTURE
21

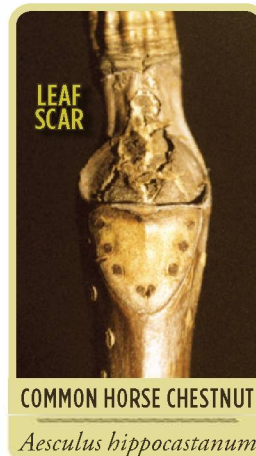
HOW TEMPERATE TREES CHANGE COLOR AND GROW

Trees are the largest, oldest, and tallest organisms on the planet. Temperate forests are dominated by trees. A tree differs from a shrub by having one main stem. Trees have wood, which distinguishes them from herbaceous plants. Unlike grasses, which grow from their base, trees grow from their tips. The total number of plant families varies with taxonomic opinion, but it's somewhere around 300 to 600 families—and many of them have trees.

HOW LEAVES CHANGE COLOR

- ◇ Deciduous means to lose the leaves, and in a temperate forest, that means to lose the leaves for the winter. Temperate trees do this because the trade-off of keeping a leaf from freezing during wintertime doesn't offset the photosynthetic gain. The sunlight is too weak, the days are too short, and the temperatures are too cold to make a living. So, the tree hibernates for winter. Before the winter comes, though, the leaves change colors.
- ◇ There are 2 main pigments that are seen when leaves change colors. Yellow and orange colors occur when the leaf has carotenoid pigments. Carotenoids have long hydrocarbon chains, which are made up of a carbon skeleton surrounded by hydrogens. Because of the hydrocarbon chains, carotenoids tend to repel water and are thus hydrophobic.
- ◇ The other major pigment class responsible for color in leaves are the anthocyanins, which are generally red and made up of carbon rings. Anthocyanins are made in the cytoplasm of the cell, where carotenes are made in plastids, usually chromoplasts, which are organelles like chloroplasts in the cell.
- ◇ These 2 pigments, carotenoids and anthocyanins, are primarily responsible for the autumn colors that light up the forest. The primary reason we see these colors is because the plant needs to break down the major green pigment, chlorophyll, which is responsible for photosynthesis. The plant needs the nitrogen that is in the chlorophyll molecule.
- ◇ Most ecosystems are nitrogen limited. If the tree can store nitrogen, it will be ready to go in the spring when it's time to put out the leaves and flower buds. So, as the plant breaks down the green chlorophyll to reabsorb the nitrogen, the other pigments, the carotenoids and anthocyanins, become visible.
- ◇ The mechanisms for their appearance, however, are quite different. Carotenoids are present in the leaf through the summer. Their purpose is to act as an antioxidant. As an accessory pigment, they can absorb extra energy if the chlorophyll molecules are at capacity. When the fall comes, these carotenoids just become more visible.

- ◇ Anthocyanins, the red pigments, are different. While present in small amounts during the summer in the leaf, they are actually synthesized in the fall as the plant begins to break down chlorophyll. Many very young leaves also have high concentrations of anthocyanins.
- ◇ This pigment helps protect a developing or dying leaf in 2 ways. First, because anthocyanins absorb the highest visible light, blue, it can protect the chloroplasts. This protection occurs because high-energy light can cause the production of free radicals, which can damage the leaf. Anthocyanins can also help neutralize chemicals in the leaf that might slow down photosynthesis.
- ◇ There are trees that just don't turn red in the fall; instead, they turn yellow. The reasons for why some trees produce anthocyanins and why others don't are not well understood. It could be that the ability to produce anthocyanins is not in the genetic history of some trees, so they don't have that ability. There could be a cost to producing anthocyanins that we're unable to detect. There could also be other environmental factors that might make anthocyanin production less efficient.
- ◇ After the leaves change color, they fall off. It's easy to understand that leaves need to go away for the winter, or for a dry spell, but leaf drop is also a good way to curb herbivore populations. If the leaves are gone, the insects and other herbivores will also go away, or at least their populations will drop, or they will switch to eating something else, which gives the tree time to recover.
- ◇ The process of leaf drop, called leaf abscission, is the same process for flowers dropping petals and ripe fruits falling off of plants. When the leaf drops, it sometimes leaves a leaf scar on the branch. By counting the leaf scars, the age of the tree can be determined. If you look closely, you can usually see the leaf scars on the twigs of most deciduous trees.



LEAF AND TREE GROWTH

- ◇ Broadleaf trees have many shapes. Early leaves of broadleaf trees, such as magnolias, had no teeth along the margins and no lobes. Lobing and teeth are more common in temperate trees. This is easily seen in the genus *Quercus*, the oaks. Tropical oaks have more trees with unlobed leaves, whereas lobes are the norm of the north. Lobing might be popular in the north because it expands the surface area without increasing the weight of the leaf.



NORTHERN RED OAK
Quercus rubra

- ◇ Even on the same individual tree, the size of the leaf will probably vary. Leaves that are lower in the canopy tend to be thinner and have a larger surface area to capture more light. These leaves are called shade leaves, and they are usually a darker color because chlorophyll *b* is very abundant in these leaves. The purpose of chlorophyll *b* is to improve light-capturing capability of the chloroplast.
- ◇ Leaves higher in the canopy are called sun leaves, and these leaves are thicker with multiple layers of photosynthesizing cells in the leaf because of the high light levels.

- ◇ Even the way the leaves hang on the trees will differ. Trees that are adapted to hot climates will have leaves that hang almost vertically, so as to avoid direct sunlight, which can cause too much water loss.
- ◇ Moving down from the canopy, we come to the stem, which is the trunk in trees. The wood is created by cells dividing in the vascular cambium. Whether this growth is fast or slow will generally determine the hardness of the wood. Trees that are slow growing have cells that are closer together, with less water, so the wood is harder. Fast-growing wood has cells with more water, so the wood is lighter, and usually softer.
- ◇ In addition, conifer trees lack the wood fiber cells in their wood that flowering trees have. So, the wood of conifer trees is generally referred to as softwood and that of deciduous trees is called hardwood.
- ◇ Even among the flowering trees, the hardness of the wood can vary dramatically. The weight of wood is due to cellulose and lignin in the cell walls. Cellulose is a polymer of glucose that is similar to starch. Lignin is a chemical made up of many carbon rings, called benzene rings, attached together. Lignin's ring structures give hardness and strength to the wood.
- ◇ The density of wood, and thus whether it is buoyant in water, is due to components of the cell walls. The presence of many air cavities within the cell walls of the wood make the wood become water logged. Also, the thickness of the cell walls and the amount of lignin they contain determine weight and density of the wood. Some wood is so dense that when it's dry, it sinks in water.
- ◇ Have you ever seen a tree that is leaning over, and then it straightens itself? Conifers and deciduous trees do this in 2 separate ways. As a result, there are 2 separate reactions for how trees can grow in response to a stimulus that would cause leaning. In both cases, the cells in the trunk will "react" to gravity to right the tree, so all such wood is called reaction wood. There are 2 ways to react: Conifers push themselves right, and deciduous trees pull themselves into line.



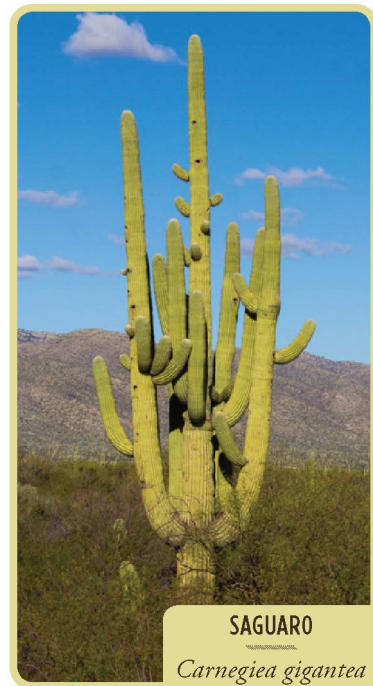
COAST LIVE OAK

Quercus agrifolia

- ◇ The pushing or pulling has to do with how the cells are growing on which side of the trunk. In conifers, the wood on the inside angle of the lean will thicken and grow with many spaces between the tracheids, which will also have a higher lignin content. This will make the wood denser and harder, but also weaker—mostly because the wood cells are not as orderly as they are in normal wood. The wood is in compression because it's pushing the rest of the tree, so it's called compression wood.
- ◇ Deciduous trees, by contrast, will pull themselves straight and produce tension wood. The cells opposite the angle of the lean will contract at the top of the stem, which will eventually pull the tree to the correct side. These cells will have gelatinous fibers but little lignin—practically the opposite of compression wood in conifers.
- ◇ The reaction wood isn't only present when trees lean; it's always in the branches so that they remain at the correct angle. This kind of wood growth can also help keep tree canopies in the light. The reaction wood growth is controlled generally by plant hormones.

TREE ROOTS

- ◇ Many trees have pretty shallow roots. Typically, most tree roots are in the top 6 to 18 inches of soil. This is usually where there will also be the greatest concentration of water, nutrients, and oxygen.
- ◇ The tree cacti, such as saguaro and Joshua trees, don't have very deep roots. There's no water table in the desert, so there's no need to have deep roots.
- ◇ Some trees have a taproot, and these are primarily found where there are water tables, such as the Midwest. Trees with a taproot include hickory, walnut, white oak, and European hornbeam.
- ◇ Regardless of how they grow, the tree root systems extend outward really far—usually about 2 to 3 times larger than the canopy area. Despite the extra area under the ground, the actual biomass distribution is different. The root-to-shoot ratio describes how much biomass the tree has put into belowground, or root, growth, versus aboveground, or shoot, growth. For most trees, the root-to-shoot ratio is around 1 to 4, so the tree aboveground is about 4 times heavier than the roots.
- ◇ Tree roots get a lot of help from mycorrhizal associations, the fungal partners that extend the surface area, and thus absorptive power, of the roots. Yet tree roots can forage through the soil. According to David Eissenstat, a professor of woody plant physiology at Penn State, thinner tree roots will send out exploratory roots or use the fungal partners to locate areas in the soil that have a high mineral content that are then exploited. Trees with thin roots that do this are oaks and maples.



- ◇ Other trees with thicker roots, such as pines and tulip poplars, don't use this strategy. These are the slow-and-steady types that produce thick roots, which will last a longer time and pay out just as many nutrients, but over a longer time frame.



READINGS

Coombes, *The Book of Leaves*.

Lee, *Nature's Palette*.

Thomas, *Trees*.

QUESTIONS

- 1 We still don't really understand how different soil types might cause different colors to appear in autumn leaves. Why do you think this is still an unknown area of botany?
- 2 How do you feel about the genetic modification of the American chestnut? Is it more acceptable to modify an organism to help it survive? Would it make a difference if that organism were on the brink of extinction?

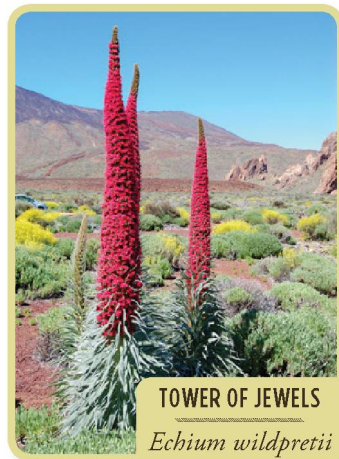
LECTURE
22

ALPINE COLD MAKES PLANTS DO FUNNY THINGS

Alpine generally means above the trees. Moving above the trees, we reach the land of alpine plants, where most plants have a short stature to deal with conditions that are too harsh for trees. When we come to mountains within the tropics—between the Tropic of Cancer and the Tropic of Capricorn—then we are arriving in what are called tropical alpine zones. Tropical alpine systems provide some of the most unique plants on the planet. But there are also alpine plants in temperate regions.

ALPINE PLANTS

- ◇ Alpine plants face a number of problems. They typically have a short growing season. In temperate regions, it can be as short as 6 weeks. If they're growing on rocky soil, it can be very dry. It's usually very windy above the tree line, and it can freeze pretty much any night of the year. In addition, light levels can be extraordinarily high on cloudless days. To meet these challenges, many temperate alpine plants are small and low to the ground.
- ◇ There are a number of different adaptations that alpine plants have to cope with these stresses. One adaptation is their small stature. Being small is good for a number of reasons. First, plants can overwinter under the snow, so as not to freeze. Although they are dormant, their tissues still need protection from the extreme cold that can occur in the alpine. Being under the snow for the winter provides a blanket of temperatures that won't go much below freezing, unlike the air temperatures above the snow.
- ◇ Small stature is also great because the ground absorbs solar radiation. Alpine soil surface temperatures above 100° Fahrenheit have been measured in Rocky Mountain National Park. At night, the soil will reradiate the heat to the air above it. This reradiation can help keep plants from freezing.
- ◇ The plant morphologies of alpine plants are also related to helping keep warm. There are 2 unique growth forms among alpine plants. One is the rosette, which is classically defined as having a set of leaves that radiates out from a single location on a stem, with very small distances between where these leaves insert on the stem. Rosettes typically have a circular outline or shape. Some rosettes hug the ground while others tower on a long stalk or even a trunk. The leaves in a rosette are arranged so



that there is very little overlap, and this is an efficient way for the leaves to gather sunlight.

- ◆ Unlike the tree rosettes of the tropical alpine, the temperate alpine rosettes grow almost flush with the ground. In addition to absorbing heat from the ground, this growth form also prevents the leaves from losing too much moisture.
- ◆ Because the leaves are against the ground, there is little wind blowing over the stomata, which are pores for the exchange of carbon dioxide and oxygen. When these stomata are open, as they must be for photosynthesis to occur, evaporation of water from the leaves will occur, and minimizing this loss is paramount for the plant.
- ◆ A rosette also has a sort of parabolic shape in the leaves that can concentrate heat to the center of the plant, which is often where the meristem, or growing part of the plant, is located.
- ◆ The other unique growth form is that of the cushion plant. These unique plants are called cushions because they have a mounded, hemispherical appearance, like that of a pincushion.
- ◆ The cushion growth form solves several alpine growing problems. First, the form creates a boundary layer within its small canopy. Just like the rosette leaves growing against the ground, cushion plant leaves lose less water because there is not much wind movement through the cushion.
- ◆ Cushion plants can also store a fair amount of heat in their canopies. Just as the soil will warm up during the day, so will a cushion.



- ◇ Cushions also collect dead material at the base of their canopies, which basically makes a compost heap at the base of the cushion. As more debris collects, the cushion grows over it as it gets larger, creating a bigger and more mound-shaped plant. And all of this decomposing debris also creates some heat and provides more nutrients to the plant.

AVOIDING FREEZING

- ◇ Alpine plants have interesting physiological traits to avoid freezing. The problem for alpine plants is not so much the cold temperatures in winter. By the time winter hits, plants are already dormant for the year. They look dead above ground, but their roots are still living, and they are hardened for the winter.
- ◇ The major stress for alpine plants involves a late freeze—that is, a freeze that would happen in the very late spring after plants have already started their comeback from winter, or after they’ve started to flush, which is when they start to produce their summer leaves and flowers. Early fall freezes can also damage a plant if it hasn’t already become frost hardened for the winter.
- ◇ Plants have essentially 2 ways to avoid freezing: supercooling and supersaturation. In supercooling, water can go down to temperatures below freezing, but plants avoid the formation of ice crystals in their cells. When an ice crystals form, it’s called nucleation, and when that happens, ice will begin to form rapidly. But if there isn’t anything for the water to form a nucleation event around, then water won’t freeze—even below the normal freezing point.
- ◇ That’s what the plant is doing when it uses supercooling. The water is below 0° Celsius, but the water has been moved into vacuoles and into cell walls. For an herbaceous plant, this mechanism is only good for a few hours and can usually only avoid damage at temperatures down to -10° Celsius.

- ◇ For woody tissues, dense, thick walls can prevent water from nucleating, so these tissues can survive freezing in temperatures down to -50° Celsius, which is the freezing point for supercooled water. But even the most winter-hardy plants cannot survive formation of ice crystals in the cytoplasm, which is not within the contents of the cell.
- ◇ When plants use supersaturation to avoid freezing, they are basically using the same principle behind antifreeze and road salts. By adding solutes to the water in their cells, plants can reduce the freezing point, but usually only by up to -5° Celsius.
- ◇ Aside from growth form and leaf physiology, many plants avoid freezing by insulating their leaves with hairs, also called trichomes. Many alpine plants look white because the leaves are covered in a very dense, thick mat of woolly-like hairs, and these are for insulation. These hairs can also prevent the leaf from getting too wet, and they can shield the leaf from fungal spores. These hairs also act as sunscreen.



- ◇ The alpine sun can be very strong because there is less filtering by the atmosphere at high elevations. Just as alpine plants can avoid freezing by being close to the ground, they can also risk heat damage on warm days.
- ◇ In a paper from 1984, a botanist measured the surface temperature of a cushion plant at 45° Celsius, or 113° Fahrenheit. He then reported that this same part of the plant had brown leaves the next day. One way to avoid this overheating is by keeping the leaves shaded with many hairs. Interestingly, ultraviolet radiation doesn't seem to have that great of an effect on plant growth, not even at alpine elevations.

- ◇ It's not just heat damage that plants at high elevations have to worry about. The strong sunlight can also cause photo-oxidation, in which too much light overexcites the electron transport chain in the light reactions, and electrons can run amok.
- ◇ When this happens, a plant can undergo photorespiration as a way to deal with the excess energy. This process, photorespiration, is photosynthesis happening in the presence of light. Although this process protects the plants from damage, it costs the plant in terms of lost carbon fixed into sugars. The plant can avoid this with some hairs on its leaf.

ALPINE FLOWERS

- ◇ For an alpine plant, there are 3 ways to flower: early, midseason, and late. Early-flowering plants flower as the snow is melting. An example is the glacier lily. Midseason plants flower at the peak of the growing season. Many cushion plants fall into this category. The last category is late flowering, which flower after the main part of the growing season is over. The genus *Sedum*, also called the stonecrops, tend to flower a bit later.



- ◇ All the early-flowering and many midseason-flowering alpine plants preform their flowers during the end of the previous growing season, which ensures that they are ready to go when the temperatures get warm enough. Preformed flower buds are more common in alpine areas than in other habitats.
- ◇ Some plants that flower won't reproduce sexually. This can happen through apomixis, which is seed development without pollination. Although seeds are produced, they are clones of the parent plant. But even clones can benefit from the advantages of seed dispersal; that is, even though that seed may be a clone, it can still travel farther than vegetative reproduction through a runner or a rhizome.
- ◇ Alpine plants with a wide distribution are able to do this facultatively. When conditions are very harsh and the elevation is very high, these species will tend to produce more clonal seeds. As the elevation decreases and growing conditions become more favorable, plants will produce more seeds through sexual reproduction. Apomixis can also be a successful strategy because of the volume of seeds produced. Dandelions are a great example of this strategy.
- ◇ Alpine areas, at least those in North America, are known for their variations in color. Alpine plants come in a wide variety of pinks, reds, whites, yellows, and purples, including some blue flowers. This is not the case with all alpine flowers.
- ◇ A curious thing about the alpine flora of New Zealand is that it is mostly white. According to Sir Alan Mark, the premiere alpine botanist in New Zealand, the lack of color is due to a lack of pollinators that prefer such flowers. Colorful flowers tend to be visited by insects that can see color and are attracted to color. In other alpine regions, this would include long-tongued bees, which are absent in the alpine of New Zealand, and butterflies, which are scarce.

- ◇ Another curious, but very effective, attribute of virtually all alpine flowers is heliotropism, or sun tracking, in which the flower tracks the Sun as it moves across the sky. The alpine snow buttercup is a tiny yellow flower that does this. The prevailing thought is that flowers track the Sun to keep the center of the flower warm, which would be attractive to pollinators in the cool alpine air.

READINGS

Körner, *Alpine Plant Life*.

Rundel, Smith, and Meinzer, *Tropical Alpine Environments*.

Zwinger and Willard, *Land above the Trees*.

QUESTIONS

- 1 Why do you think giant rosettes flourish in tropical alpine regions but fail to grow in temperate alpine regions?
- 2 What advantages does the cushion plant growth form offer to another developing plant?

LECTURE
23

BAD PLANTS AREN'T SO BAD

Poisonous plants, invasive plants, and carnivorous plants are not similar in terms of their habitats, chemistry, ancestry, or even the way they make a living. It's interesting that not all plants are poisonous, given the wide variety of those that are, and even a plant that is harmful at one level might be beneficial in a different dose or context. Invasive species can be feared, but some research says that they increase diversity, and, at least for some invasive plants, animals in their new habitats sometimes learn to eat them, and other plants will eventually compete with them. Carnivorous plants are revered by humans because they go against the norm of what we expect plants to do.

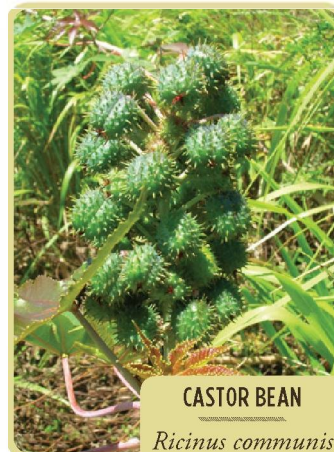
POISONOUS PLANTS

- ◇ There are many poisonous plants, such as poison ivy and poison oak. The poison in poison oak and poison ivy is urushiol, which causes a red, itchy rash and maybe a puss-filled blister.
- ◇ If you rub against the ortiga plant, expect a rash and even hives. This plant is a type of stinging nettle, called nettle tree. Both of these plants come from the Urticaceae family, which is basically a whole family of stinging plants. Many of these plants have very hairy leaves that are arranged opposite of each other on the stem.
- ◇ Botanically, the stinging hair is just a trichome, which is what all plant hairs are called. In the case of the nettle, the trichome is made of brittle silica, the primary component of glass, and it's equipped with a small spherical bulb on the tip. When the trichome is disturbed—for example, by your hand accidentally brushing up against it—the trichome will break and stick into your skin, and the toxin from the bulbous tip will move into your skin.



ORTIGA BRAVA
Urera baccifera

- ◇ The nettle toxin is composed of several chemical compounds. It contains histamine, which triggers an inflammatory response, and this is why you take an antihistamine to treat the symptoms of nettle. The toxin also contains the neurotransmitters acetylcholine and serotonin, which is supposed to be a happy neurotransmitter, but in this case, it causes pain. It also has a few acids, including formic acid, the stinging component of ant venom. There is some evidence that stinging nettle has antimicrobial properties and could be useful for ulcers.
- ◇ There are many other poisonous plants, such as oleander, castor bean, deadly nightshade, and poison hemlock. The cecropia tree is a fast-growing pioneer tree in Central America. A pioneer is a species that grows best in a disturbed area, such as a landslide or an area that has a gap in the forest canopy, perhaps from a tree falling down. Most pioneers are relatively fast growing.
- ◇ Although the cecropia contain latex, this doesn't fend off all of the herbivores that would feast on them. Their ultimate protection comes from their symbiosis with ants. A whole genus of ants, *Azteca*, is found with different species of cecropia. The tree provides a home and snacks for the ants in exchange for protection. The ants will attack any animal that tries to eat the cecropia, and they will nibble off any plants that try to grow on it.



INVASIVE PLANTS

- ◇ Another type of plant that is to be feared is an invasive plant, which is a plant that is not only a nonnative plant in that it has been introduced from elsewhere, but also that it's invaded into natural ecosystems and is taking over the habitat.
- ◇ One reason why invasive plants are able to take over so well is that, typically, none of their enemies or competitors get introduced too, so there are no other organisms to keep it in check, so it grows out of control.
- ◇ Cheatgrass is a good example. Cheatgrass came to the United States in grain feed accidentally and was well distributed across the West by 1930. Cheatgrass gets its name from the way it would cheat ranchers out of good forage for their livestock. Because cheatgrass flourishes in disturbed habitats, it's difficult to eradicate.
- ◇ Another invader found in the West is the diffuse knapweed, *Centaurea diffusa*. A knapweed is a shrub in the sunflower family, and it's sort of a cross between a thistle and a tumbleweed. Not good as forage and an excluder of native plants, diffuse knapweed is a pretty unwelcome visitor from the Mediterranean region.
- ◇ Unlike some plants that are successful in new habitats because their competitors and herbivores didn't come with them, knapweed outcompetes native North American grasses more so than grass species from its old neighborhood.



- ◇ Knapweed's offense is a cocktail of exudates from its roots that prevent the growth of grasses from North America. Apparently, grasses from the Mediterranean are immune to these exudates, or at least not as repelled by them. This type of chemical defense against competitors is called allelopathy, and native shrubs, such as creosote, do it as well.
- ◇ A more famous invasive plant, at least in the Southern United States, is the infamous kudzu vine, which was brought to the United States from Japan to control soil erosion around the time of the Great Dust Bowl in the 1930s. It's rumored that this plant covers more than 7 million acres and that it will take over the South, but a 2015 issue of *Smithsonian* reports that the U.S. Forest Service assessed that the actual area consumed by kudzu was only about 227,000 acres of forestland.



- ◇ Not just small herbaceous plants are invasive. In the Eastern United States, the Norway maple can displace the sugar maple. They are pretty similar, but their leaves are different: The sugar maples lobes are deeper to the midrib, or the hinge between the 2 parts of the leaves, and the serrations, or teeth, on the margins are different.



- ◆ As if it weren't bad enough to be deadly or invasive, some plants are both. The *Abrus precatorius*, or jequirity, is both terribly invasive and extremely toxic. A native of India, it is a member of the pea family, Fabaceae. This plant has become naturalized throughout the tropics and subtropics, including Florida. The entire plant contains the toxin abrin, which is similar in chemical makeup to the toxin ricin, which is the poison found in castor bean. If the plant's seeds are chewed, the toxin can cause death.

CARNIVOROUS PLANTS

- ◆ There are about 600 species of carnivorous plants, and they can live in a variety of habitats. The most well-known carnivorous plant, the Venus flytrap, is native to North and South Carolina, where it lives in bogs and swamps. However, carnivorous plants can also live in sandy or rocky areas, in forests, and even in bodies of water.



- ◇ Carnivorous plants still photosynthesize, but one thing that unites most of the habitats where they live is the paucity of minerals in the soil. These plants are often located in environments that are low in nitrogen. A soil that is low in nitrogen would likely be a wet soil that has leached much of its nitrogen away. As rain constantly bathes the soil in water, the minerals, including nitrogen, dissolve into the water and are carried off by gravity and erosion. This process is called leaching.
- ◇ At the other extremes, desert soils and soils that are very sandy or rocky also lack nitrogen because there is little decayed organic material in them.
- ◇ Because carnivorous plants live in regions without a lot of nitrogen, they have found a way to augment their diet with insects. Generally, plants will secrete an enzyme that will speed up the decomposition of the insect, and then the plant will absorb the minerals that were in the insect's body.

- ◇ Carnivory probably evolved several times among the flowering plants. There are 2 main ways to be a carnivorous plant, both of which involve liquids: A plant can trap insects in water, such as the carnivorous tank plants, or a plant can trap insects on sticky leaves. The wide variety of ways leaves have evolved to do this trapping shows the flexibility of leaf development.
- ◇ Water traps are found in plants like pitcher plants. Even though the most famous carnivorous plant, the Venus flytrap, is in one of these families, the Droseraceae family, it doesn't have a water trap or a sticky leaf. Other members of the Droseraceae family are the sundews, which are so called because they look like they are glistening with dew in the sun.
- ◇ These plants have flattened leaves that are covered with trichomes, or leaf hairs, and these hairs have glands at that base that produce digestive enzymes that decompose the trapped prey. These digestive enzymes increase in production once a prey has been captured, peaking about 4 days after an insect has been captured.



- ◇ The Venus flytrap is only one species in one genus, *Dionaea*. There are trichomes that line the inside of 2 modified leaves that form the trap. Two trichomes have to be triggered within a short time for the physical stimulus on the leaves to turn into an electrical stimulus inside the leaves. The electrical stimulus goes to the midrib, or the hinge between the 2 parts of the leaves.
- ◇ What happens next is basically an educated guess because there isn't strong evidence to support the exact mechanism. In the big picture, changes will happen in the cells of the midrib that will cause a snap-buckle response. In their open state, the flytrap's leaves are spring loaded. Then, when an insect lands on a flytrap's leaf, the midrib cells swell with water, snapping the leaves closed to a position that has no stored energy. Apparently, it's fairly difficult to reset the trap. A Venus flytrap can only reset about 7 times before it dies.

READINGS

Largo, *The Big, Bad Book of Botany*.

Laws, *Fifty Plants That Changed the Course of History*.

Stewart, *Wicked Plants*.

Wilhelm, Porembski, Seine, and Theisen, *The Curious World of Carnivorous Plants*.

QUESTIONS

- 1 Would you plant a nonnative plant in your garden? Why or why not?
- 2 Why do you think people are so fascinated by carnivorous plants?

LECTURE
24

MODIFYING THE GENES OF PLANTS

Genetically modified organisms (GMOs) are typically created by transferring a piece of DNA from one organism into another organism. The genome of an organism is the combination of all the DNA. If you add a snippet of DNA from some other organism and insert it into the original organism, you have modified it. Humans can manipulate genes within an organism to provide all kinds of benefits, both economic and ecologic.

GENETICALLY MODIFIED ORGANISMS

- ◇ People are skeptical that we understand all the repercussions of genetically modifying organisms—particularly those that we eat. But there are compelling reasons to want to genetically modify an organism.
- ◇ One of the most popular GMOs that virtually everyone in the United States has eaten is Bt corn. The “Bt” stands for *Bacillus thuringiensis*, which is a type of bacteria that lives naturally in the soil. Organic farmers have known since the 1960s that it produces a protein that can ward off a major corn pest, the European corn borer. A borer is a type of moth that has a larval stage that eats the leaves and stems of the corn.
- ◇ If this type of bacteria was harmful to the European corn borer, what was it specifically that harmed the moth? Because most bacteria cause harm by creating proteins called endotoxins, the Bt endotoxin was the likely candidate, and Bt was already sprayed on plants to kill pests.
- ◇ To genetically modify the corn, there needs to be a piece of DNA from another organism, and the donor organism in this case is *Bacillus thuringiensis*. This bacterium has a gene that produces the protein that is the Bt endotoxin.
- ◇ So, if you can get this one gene from the *Bacillus thuringiensis* into the corn, then the corn plant can make its own pesticide against the European corn borer. If the corn plant has the gene from the *Bacillus thuringiensis*, then it can create Bt endotoxin and destroy its own pests, with no help from pesticides needed.
- ◇ In this way, one might think that everyone would love GMOs, as they could bring about the end to the use of pesticides. Since the invention of Bt corn, there is now Bt cotton, Bt potatoes, Bt eggplant, and Bt soybeans. The idea is that if the plants are making their own defense, then we are not using pesticides on them, and workers who would normally have to treat these plants are also not being exposed.

- ◇ Although there is speculation about many different negative consequences of Bt crops, the strongest and most potentially damning evidence thus far comes from natural selection.
- ◇ These corn borers and other lepidopterans, such as butterflies and moths, are just trying to make a living. If any of them just happen to have a bit of resistance to this Bt toxin, they are going to do well, while all of their friends die off. The ones that have resistance find mates that also have resistance, because they're the only ones left, and they mate.
- ◇ Chances are that many of their offspring will also have resistance to the Bt endotoxin, and suddenly Bt corn doesn't work as well. There is evidence of instances where this has happened. Just because the toxin is produced by the plant doesn't mean that insects won't evolve to resist the toxin. Pesticide resistance develops no matter where the pesticide comes from.



INSERTING GENES

- ◇ Interestingly, you insert a gene from a bacterium into the genome of a corn plant by using another bacterium. Bacteria are so useful in this process because they contain something that most eukaryotic cells, such as our cells, don't have. They have plasmids, which are small circular pieces of DNA that are separate from the regular chromosomes of the bacteria. These plasmids are one of the reasons that bacteria can develop antibacterial drug resistance so quickly—because these plasmids can be shared between bacteria.
- ◇ The DNA within the plasmid can be sliced up using restriction enzymes. An enzyme is just a protein that speeds up a reaction. A restriction enzyme will search for particular sequences of DNA and cut the DNA in the same location. When this cut occurs, the ends of the DNA are now sticky, which means that they will glom onto another piece of DNA, if they happen to meet up with one. The DNA they're going to meet up with is the donor gene from the bacteria.
- ◇ Now there are gene guns, which use nanometer-sized gold or tungsten bullets that are coated with the DNA of interest to insert into the plant's DNA. Gene gun technology was invented in the mid-1980s.

THE POTENTIAL HARM OF GMOS

- ◇ There are several concerns about the potential harm of GMOs, but most of these concerns don't have strong evidence—yet.
- ◇ One concern about GMOs is that you're putting in a different gene, which will make a new protein, that wasn't found in the original organism. For example, if you put a gene to make a bacterial protein into a soybean, people who have never been allergic to soybeans might now be allergic to a GMO soybean because it has a new protein from the bacteria. The concern seems to be one of knowledge to the consumer and potential for allergies.

- ◇ Another concern with GMOs is that the gene that is put in the crop will find its way into other plants, causing them to be resistant to herbicides or be able to make their own pesticides. The concern is that the gene of interest—for example, the Bt gene that was bred into corn—would find its way into a relative of corn.
- ◇ Corn is a grass, and there are many grasses that are considered weeds, and many plants cross-pollinate to form new varieties. Because plants hybridize, the concern is that the pollen from Bt corn may fertilize a non-corn grass and give it the Bt gene, which would prevent it from being harmed by the corn borer.
- ◇ So far, there's not strong evidence of superweeds, but there has been a problem with pollen contamination. Corn pollen is very light and can easily travel miles away and pollinate other cornfields. Pollen from Bt corn has made its way onto fields that are not Bt corn, thus conferring the Bt gene to that corn, even though the farmer hasn't paid for it and may not want it. Because corn is wind pollinated, it would be very difficult to keep Bt pollen off a nearby cornfield if you were trying to maintain a non-GMO crop.
- ◇ The concern is protecting farmers who don't want their crops cross-pollinated with GMOs, as well as consumer confidence that a small grower who claims that his or her corn is non-GMO should actually be able to protect that crop from GMO pollen.
- ◇ Another concern with GMOs is that friendly insects, or at least insects that aren't pests, will eat the plant that makes pesticide and get killed, or pollen from a plant that has been genetically modified to make its own pesticide will get eaten by a friendly insect, which will die.
- ◇ Other arguments against GMOs pertain to sustainable agriculture and profit for smaller farmers versus larger corporations. Depending on the type of GMO used, the seed might have to be purchased every year. If left to their own reproductive strategy, genetically modified genes may or may not be passed onto offspring. To ensure that every plant has the gene, a farmer must buy all new seeds. If farmers have to buy these seeds every year, then they are making less money.

- ◇ The contrary argument is that companies that did the research to develop the seed deserve the money to pay for that research and development and that the farmers are saving money by buying fewer pesticides. But pests such as the corn borer will continue to develop a resistance to the Bt toxin, even if the corn produces it in its own Bt toxins. The problem of resistance still remains.
- ◇ Another concern about GMOs is that biotechnology will not solve world hunger problems. In most parts of the world, hunger is an economic or political problem, or a problem of distribution—not one of production. When countries have a drought or a severe food shortage, the main issues become distribution of donated food.
- ◇ But GMOs can provide new varieties of crops that would be more drought tolerant or that would produce more nutritious foods. Scientists in Egypt have developed a drought-resistant form of wheat by inserting a gene from barley. Experiments indicated that the new wheat strain outperformed the non-GMO variety under normal rainfall conditions. Currently, Egypt has to import wheat because it can't meet its need, but if the wheat range could expand, then perhaps Egypt could meet its demand.
- ◇ Because many of the objections to GMOs can, in principle, be met through further research into GMOs, the eventual promise of GMOs can seem limitless. For example, plants can be genetically engineered to make vaccines.
- ◇ Because of the contention with GMOs, some botanists wondered if there was an alternative pathway to changing aspects of plants without changing their genes. In a 2016 report, scientists in Germany showed that just spraying RNA on leaves of barley reduced the amount of fungal infection of the sprayed leaves. Apparently, the RNA they sprayed on the barley leaves was able to silence, or turn off, some major genes in the fungal pathogen. Techniques like this demonstrate that there are different ways to give plants resistance to disease without modifying their genes.

- ◇ There is an even newer and greater technique on the plant biotechnology horizon. Scientists have observed certain patterns in the genomes of some bacteria. The pattern is that some base pairs, which make up the DNA, would be repeated over and over again. In between these repeated segments would be normal areas of DNA. These patterns are called clustered regularly interspaced short palindromic repeats (CRISPR).
- ◇ Why the bacteria had these repeats was a mystery until scientists figured out that these repeats matched the DNA of viruses that prey on bacteria. CRISPR holds onto pieces of viral DNA so that the bacteria will recognize future attacks from viruses, much like our own immune system. The bacteria with CRISPR also have a group of enzymes called CRISPR-associated proteins that will cut DNA in precise locations. Using these 2 tools, scientists can add and delete genes from genomes with unprecedented accuracy and speed.

READINGS

Endersby, *A Guinea Pig's History of Biology*.

Slater, Scott, and Fowler, *Plant Biotechnology*.

Wood and Habgood, *Why People Need Plants*.

QUESTIONS

- 1 How do you feel about genetically modified organisms? Does it make any difference if the modified piece of DNA is from another organism or if the primary modified organism is created in the lab using CRISPR technology?
- 2 How has this course changed the way you think about botany?

BIBLIOGRAPHY

Attenborough, D., and N. Graham. *The Private Life of Plants: A Natural History of Plant Behaviour*. Princeton University Press, 1995.

Bernhardt, P. *Wily Violets and Underground Orchids: Revelations of a Botanist*. University of Chicago Press, 2003.

Blackburne-Maze, P. *Fruit: An Illustrated History*. Firefly Books, 2003.

Bock, Jane, et al. *Identifying Plant Food Cells in Gastric Contents for Use in Forensic Investigations: A Laboratory Manual*. U.S. Department of Justice, National Institute of Justice Research Report, January 1988.

<https://www.ncjrs.gov/pdffiles1/Digitization/110008NCJRS.pdf>.

Bone, M. *Steppes: The Plants and Ecology of the World's Semi-Arid Regions*. Timber Press, 2015.

Buchmann, S. *The Reason for Flowers: Their History, Culture, Biology, and How They Change Our Lives*. Scribner, 2016.

Capon, B. *Botany for Gardeners: An Introduction and Guide*. Timber Press, 1990.

Chamovitz, D. *What a Plant Knows*. Scientific American/Farrar, Straus and Giroux, 2013.

Chase, T. D., and R. Llewellyn. *Seeing Seeds: A Journey into the World of Seedheads, Pods, and Fruit*. Timber Press, 2015.

Cooke, I. *Grasses and Bamboos: A Practical Guide*. Ball Publishing, 2006.

Coombes, A. J. *The Book of Leaves: A Leaf-by-Leaf Guide to Six Hundred of the World's Great Trees*. Edited by Zsolt Debreczy. University of Chicago Press, 2010.

- Crane, P., and P. von Knorring. *Ginkgo: The Tree That Time Forgot*. Yale University Press, 2015.
- Crawford, R. M. *Plants at the Margin: Ecological Limits and Climate Change*. Cambridge University Press, 2008.
- Darke, R. *The Encyclopedia of Grasses for Livable Landscapes*. Timber Press, 2007.
- Endersby, J. *A Guinea Pig's History of Biology*. Harvard University Press, 2008.
- Essig, F. B. *Plant Life: A Brief History*. Oxford University Press, 2015.
- Farjon, A. *A Natural History of Conifers*. Timber Press, 2008.
- Farmer, E. E. *Leaf Defence*. Oxford University Press, 2014.
- Fenner, M. *Seeds: The Ecology and Regeneration in Plant Communities*. CABI Publishing, 2000.
- Fenner, M., and K. Thompson. *The Ecology of Seeds*. Cambridge University Press, 2005.
- Gibson, D. J. *Grasses and Grassland Ecology*. Oxford University Press, 2009.
- Gilbert, E. *The Signature of All Things: A Novel*. Penguin, 2013.
- Glover, B. *Understanding Flowers and Flowering: An Integrated Approach*. Oxford University Press, 2007.
- Halle, F. *In Praise of Plants*. Timber Press, 2002.
- Hanson, T. *The Triumph of Seeds: How Grains, Nuts, Kernels, Pulses, and Pips Conquered the Plant Kingdom and Shaped Human History*. Basic Books, 2016.
- Harder, L. D., and S. C. Barrett. *Ecology and Evolution of Flowers*. Oxford University Press, 2006.

- Harkness, P. *The Rose: An Illustrated History*. Firefly Books, 2003.
- Hodge, G. *Practical Botany for Gardeners*. University of Chicago Press, 2013.
- Hogarth, P. J. *The Biology of Mangroves and Seagrasses*. Oxford University Press, 2007.
- Howell, C. E. *Flora Mirabilis: How Plants Have Shaped World Knowledge, Health, Wealth, and Beauty*. National Geographic, 2009.
- Karban, R. *Plant Sensing and Communication*. University of Chicago Press, 2015.
- Kessler, R., and W. Stuppy. *Seeds: Time Capsules of Life*. Firefly Books, 2006.
- Kimmerer, R. W. *Gathering Moss*. Oregon State University Press, 2003.
- King, J. *Reaching for the Sun: How Plants Work*. Cambridge University Press, 2011.
- Körner, C. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer Press, 2003.
- Kourik, R. *Understanding Roots: Discover How to Make Your Garden Flourish*. Metamorphic Press, 2015.
- Large, M. F., and J. E. Braggins. *Tree Ferns*. Timber Press, 2004.
- Largo, M. *The Big, Bad Book of Botany: The World's Most Fascinating Flora*. William Morrow Paperbacks, 2014.
- Laws, B. *Fifty Plants That Changed the Course of History*. Firefly Books, 2011.
- Lee, D. *Nature's Palette: The Science of Plant Color*. University of Chicago Press, 2007.
- Mabey, R. *Cabaret of Plants*. W. W. Norton Press, 2015.

- MacAdam, J. W. *Structure and Function of Plants*. Wiley-Blackwell, 2009.
- McKell, C. M. *The Biology and Utilization of Shrubs*. Academic Press, 1988.
- Mehlreter, K., L. R. Walker, and J. M. Sharpe, eds. *Fern Ecology*. Cambridge University Press, 2010.
- Moore, M. *Medicinal Plants of the Mountain West*. Museum of New Mexico Press, 1979.
- Moran, R. C. *A Natural History of Ferns*. Timber Press, 2004.
- Nobel, P. S. *Environmental Biology of Agaves and Cacti*. Cambridge University Press, 2003.
- Richardson, D. M. *Ecology and Biogeography of Pinus*. Cambridge University Press, 1998.
- Royte, E. *The Tapir's Morning Bath*. Houghton Mifflin Company, 2001.
- Rundel, P. W., A. P. Smith, and F. C. Meinzer. *Tropical Alpine Environments: Plant Form and Function*. Cambridge University Press, 1994.
- Slater, A., N. W. Scott, and M. R. Fowler. *Plant Biotechnology*. Oxford University Press, 2003.
- Speer, J. H. *Fundamentals of Tree-Ring Research*. University of Arizona Press, 2010.
- Stewart, A. *Wicked Plants: The Weed That Killed Lincoln's Mother and Other Botanical Atrocities*. Algonquin Books, 2009.
- Stuppy, W. *Fruit: Edible, Inedible, Incredible*. Earth Aware Editions, 2013.
- Thomas, P. A. *Trees: Their Natural History*. Cambridge University Press, 2014.
- Trewavas, A. *Plant Behaviour and Intelligence*. Oxford University Press, 2014.

Trimble, S. *The Sagebrush Ocean: A Natural History of the Great Basin*. University of Nevada Press, 1999.

Tudge, C. *The Tree: A Natural History of What Trees Are, How They Live, and Why They Matter*. Crown Publishers, 2007.

Vogel, S. *The Life of a Leaf*. University of Chicago Press, 2012.

Whitelock, L. M. *The Cycads*. Timber Press, 2002.

Wilhelm, B., S. Porembski, R. Seine, and I. Theisen. *The Curious World of Carnivorous Plants: A Comprehensive Guide to Their Biology and Cultivation*. Timber Press, 2007.

Wood, C., and N. Habgood. *Why People Need Plants*. Kew Publishing; Open University, 2010.

Zwinger, A. H. and B. E. Willard. *Land above the Trees: A Guide to American Alpine Tundra*. Johnson Books, 1996.

IMAGE CREDITS

title page	© Ohmega1982/iStock/Thinkstock.
lecture titles	© andrekaulitzki/iStock/Thinkstock.
5	© dhobern/flickr/CC BY 2.0.
7	© Jannoon028/iStock/Thinkstock.
8	© USDA.
14	© Jirawat Jerdjamrat/iStock/Thinkstock.
15	The Teaching Company Collection.
17	The Teaching Company Collection.
21	© PFMphotostock/iStock/Thinkstock; © pellaee/flickr/CC BY 2.0.
22	© treegrow/flickr/CC BY 2.0.
23	© jacilluch/flickr/CC BY-SA 2.0.
24	© Martin Cooper/flickr/CC BY 2.0.
26	© jph9362/iStock/Thinkstock.
32	© pichaitun/iStock/Thinkstock.
33	© Holcy/iStock/Thinkstock.
34	© Ian_Redding/iStock/Thinkstock.
38	© GaryKavanagh/iStock/Thinkstock.
40	© Dorling Kindersley/Thinkstock.
41	The Teaching Company Collection.
42	© Gerald Holmes, California Polytechnic State University at San Luis Obispo, Bugwood.org/CC BY-NC 3.0.
44	© tonrulkens/flickr/CC BY-SA 2.0.
47	The Teaching Company Collection.
48	© Starr Environmental/flickr/CC BY 2.0.
50	The Teaching Company Collection.
51	© pawpaw67/flickr/CC BY-SA 2.0.
52	© jhfearless/flickr/CC BY 2.0; The Teaching Company Collection.
56	© Starr Environmental/flickr/CC BY 2.0.

- 57 © Alexander Rozhenyuk/Hemera/Thinkstock;
..... © Elena Elisseeva/Hemera/Thinkstock;
..... © Gratsyanna/iStock/Thinkstock.
- 58 © BSANI/iStock/Thinkstock;
..... © Rob Routledge, Sault College, Bugwood.org/CC BY 3.0;
..... © born1945/flickr/CC BY 2.0.
- 59 © Bruce Ackley, The Ohio State University,
..... Bugwood.org/CC BY 3.0.
- 63 The Teaching Company Collection.
- 64 The Teaching Company Collection.
- 67 © Designua/Shutterstock.
- 72 The Teaching Company Collection;
..... © Nadezhda_Nesterova/iStock/Thinkstock.
- 74 © inra.dist/flickr/CC BY 2.0.
- 79 © MWCPPhoto/iStock/Thinkstock.
- 81 © v_apl/iStock/Thinkstock.
- 83 © t_y_l/flickr/CC BY-SA 2.0;
..... © Psumuseum/Wikimedia Commons/CC BY-SA 3.0;
..... © alexlomas/flickr/CC BY 2.0.
- 87 © Dave Powell, USDA Forest Service (retired),
..... Bugwood.org/CC BY 3.0.
- 89 © Arturo Reina Sánchez/Wikimedia Commons/CC BY-SA 3.0.
- 90 © Paul Wray, Iowa State University,
..... Bugwood.org/CC BY 3.0;
..... © Mark-Poley/iStock/Thinkstock;
..... © Sten Porse//CC BY-SA 3.0.
- 91 © Bill Cook, Michigan State University,
..... Bugwood.org/CC BY 3.0.
- 92 © tamara_kulikova/iStock/Thinkstock;
..... © picture_istock/iStock/Thinkstock.
- 97 © Scott Zona/Wikimedia Commons/CC BY 2.0.
- 98 The Teaching Company Collection.
- 102 © AlessandroZocc/iStock/Thinkstock;
..... © John Tann/flickr/CC BY-SA 2.0;
..... © Björn S.../flickr/CC BY-SA 2.0;
..... © John D. Byrd, Mississippi State University,
..... Bugwood.org/CC BY 3.0;
..... © Jan Samanek, Phytosanitary Administration,
..... Bugwood.org/CC BY 3.0.

- 103 © Dave Powell, USDA Forest Service (retired),
Bugwood.org/CC BY 3.0;
© emmor/iStock/Thinkstock;
© jacilluch/flickr/CC BY-SA 2.0;
© Daniel J. Layton/Wikimedia Commons/CC BY-SA 4.0;
© ArturoYee/flickr/CC BY-SA 2.0.
- 104 © John D. Byrd, Mississippi State University,
Bugwood.org/CC BY 3.0;
© Deanster1983 who's mostly off for a while/flickr/CC BY-SA 2.0;
© Aries Tottle/flickr/CC BY-SA 2.0;
© Muffet/flickr/CC BY 2.0;
© Aries Tottle/flickr/CC BY-SA 2.0;
© RPFerreira/iStock/Thinkstock.
- 105 © asavliuk/iStock/Thinkstock;
© wplynn/flickr/CC BY-ND 2.0;
© siur/iStock/Thinkstock;
© DeaPeaJay/flickr/CC BY-SA 2.0;
© Michael Wunderli/flickr/CC BY-SA 2.0.
- 110 © AJC1/flickr/CC BY-SA 2.0.
- 111 © mb-fotos/iStock/Thinkstock.
- 112 © DanielaC173/flickr/CC BY-SA 2.0.
- 116 © johan63/iStock/Thinkstock.
- 117 The Teaching Company Collection.
- 118 © Jonas Janner Hamann, Universidade Federal de Santa Maria
(UFSM), Bugwood.org/CC BY 3.0.
- 119 © Starr Environmental/flickr/CC BY 2.0.
- 120 © Amawasri/iStock/Thinkstock.
- 124 © TANAKA Juuyoh (田中十洋)/flickr/CC BY 2.0.
- 125 © HildaWeges/iStock/Thinkstock.
- 126 © standret/iStock/Thinkstock.
- 127 © Purestock/Thinkstock.
- 131 © richcarey/iStock/Thinkstock.
- 135 © hakoar/iStock/Thinkstock.
- 139 © odmeyer/iStock/Thinkstock.
- 142 © cassinga/iStock/Thinkstock.
- 143 © Starr Environmental/flickr/CC BY 2.0.
- 146 © Starr Environmental/flickr/CC BY 2.0.
- 147 © pjimalsbury/iStock/Thinkstock.

148 The Teaching Company Collection.

149 © Lomvi2/Wikimedia Commons/CC BY-SA 3.0.

152 © Forest and Kim Starr, Starr Environmental,
Bugwood.org/CC BY 3.0;
© Dun.can/flickr/CC BY 2.0.

155 © Roblre/iStock/Thinkstock.

157 © Joanna Wnuk/Hemera/Thinkstock.

159 © andrey_zharkikh/flickr/CC BY 2.0.

160 © Morn the Gorn/Wikimedia Commons/CC BY-SA 3.0.

164 © joedecruyenaere/flickr/CC BY-SA 2.0.

165 © Patrick_Lienin/iStock/Thinkstock.

166 © Tomas Castelazo/Wikimedia Commons/CC BY 3.0.

170 © Bill Cook, Michigan State University, Bugwood.org/CC BY 3.0.

171 © Maria_Ermolova/iStock/Thinkstock.

173 © Franco Folini/flickr/CC BY-SA 2.0.

174 © Lacy Mayberry/iStock/Thinkstock.

175 © magicflute002/iStock/Thinkstock.

177 © slava296/iStock/Thinkstock.

178 © AlexTerrill/iStock/Thinkstock.

180 © adrianciurea69/iStock/Thinkstock.

181 © billmiky/flickr/CC BY-ND 2.0;
© randihausken/flickr/CC BY-SA 2.0.

185 © Dick Culbert/flickr/CC BY 2.0.

186 © Forest and Kim Starr, Starr Environmental,
Bugwood.org/CC BY 3.0;
© Eurico Zimbres/Wikimedia Commons/Public Domain.

187 © Matt Lavin/flickr/CC BY-SA 2.0.

188 © Kerry Britton, USDA Forest Service, Bugwood.org/CC BY 3.0.

189 © Pthiti/iStock/Thinkstock.

190 © monica-photo/iStock/Thinkstock.

191 © Koldunov/iStock/Thinkstock.

195 © jcarillet/iStock/Thinkstock.