Topic #4: Angiosperm Adaptations

REQUIREMENTS: Powerpoint presentations.

Objectives

1. What is a pollination vector? Give examples. Discuss the relationship of vectors to floral evolution.
2. Discuss different mechanisms of seed dispersal.
3. Discuss the abundance of atmospheric N_2 with special reference to the eukaryotes' inability to convert it to a form that they can metabolize. How is the biotic nitrogen balance maintained? Outline the nitrogen cycle.
4. Outline the steps involved in establishing the symbiosis between a legume root and a *Rhizobium* (= a type of bacterium). How does each partner benefit?
5. How does leaf shape vary from species to species, particularly with respect to water conservation?
6. Review "ordinary" photosynthetic CO_2 reduction (from BSC 2010). Review the light-harvesting reactions. Then, describe C_4 photosynthesis and explain advantages and disadvantages.
7. Discuss intraspecies variation, giving an example, and its agronomic importance.
8. Discuss various ways by which humans past and present direct evolution of agronomic species.

Lecture

Angiosperms are, of course, the most successful organisms in the current geological era. This success is due, in part, to their adaptability to specialized ecological niches. The problem is to give you an appreciation of the wealth of diversity and the extent to which some adaptations have been made without overwhelming you. I have therefore decided to present several important general areas and present only a few specific examples. (N.B.: Categories are very artificial!!!)

Ecological Adaptations

Pollination[1]

Quote from Raven, Evert, and Curtis (an earlier version of your textbook): "The evolution of the flowering plants is, to a large extent, the story of increasingly specialized relationships between flowers and their insect pollinators . . . ."

Quote from Thompson (research article): "A majority of plants would quickly become extinct without their animal pollinators."

Although some angiosperms are windpollinated, most have evolved with a vector mechanism for pollination. (Wind-pollinated plants, such as grasses, tend to grow in thick stands; pollen is shed in copious amounts and rarely travels more than 100 meters.)

In effect, these pollination vectors "help" a plant have a mobile sex life. Wide dispersal of pollen (and self-incompatibility in some cases) maximizes outbreeding and helps maintain genetic variability. Pollination vectors come in many different types:

(A) As a general rule, bees are attracted to flowers that are (1) odorous, (2) and showy at shorter wave lengths—blue and yellow (which they see; red—that is, longer wavelengths—for them is "black"), and (3) have nectar (for production of honey) and pollen (for its protein). During a "honey flow," bees are faithful to a single species[2]—therefore, pollen transfer is not random (which is why one

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[1]As indicated, this section will focus on the plant's enticement of pollinators for a visit by use of energy and protein sources (viz., nectar and pollen). Nectar is not only produced by flowers, however. Some species—maypop is a local example—have so-called extrafloral nectaries. These small organs (1–2 mm) secrete a solution of sugars and amino acids; this solution attracts ants, just as the plant "planned." For their part, the ants do not "eat and run." They hang around and protect the plant against small herbivores. Partridge pea (*Chamaecrista brachiata*) is another example of a local plant that has extrafloral nectaries. This is an important plant for beekeepers, as it provides a source of nectar when none is otherwise available.

[2]Again, this is a general statement. Sometimes bees within a single colony will visit different species and for this reason it is illegal in Florida to label a varital honey as "pure." (One may say "pure honey" and one may say "tupelo honey" and one may say "tupelo—pure honey", but he or she cannot **legally** say "pure tupelo honey.") As you know, a returning "scout" (about 7% of the field force of a colony) performs a "dance" on the "dance floor" inside the hive that directs foragers (about 93% percent of the field force) to the source of the nectar and pollen, Interestingly, her message includes two components—distance, and direction—which she expresses as an angle to the sun. Inside the hive, of course, it is dark, so she converts "sun" to "gravity." Fifty-four years after he began his studies on bee behavior, von Frisch was awarded the Nobel Prize in Medicine and Physiology, in

can buy a particular kind of honey, such as gallberry or tupelo[3]). Unlike the *general* situation for honeybees, some pollinators move from species to species when they are foraging.

POWERPOINT SLIDE: Bee on hollyhock flower (Callaway Gardens). As you see, this bumblebee was unaware of the textbook "rule" that red is not attractive to her. Note the pollen collected.

POWERPOINT SLIDE: Honeybee (*Apis mellifera*) on jujube (*Ziziphus jujuba*, north Leon County).

POWERPOINT SLIDE: Honeybee colonies (north Leon County).

POWERPOINT SLIDE: Hive product (north Leon County). N.B. A main value of bees is in agricultural pollination, not honey, wax, or propolis.

POWERPOINT SLIDE: Butterfly collecting nectar (Calloway Gardens). For a New York minute, the proboscis extends to collect a reward for the visit.

1973. (Although I am in no position to judge the importance of them, some objections to von Frisch's theories have surfaced in the past few years. The debate is nastier than it should be. I liked the approach of one moderate who stated that, as biological organisms, bees integrate a variety of environmental cues, such as odor, along with the information conveyed by the dance. Check out http://ourworld.compuserve.com/homepages/Beekeeping/beedance.htm—you owe it to yourself. Regardless, it is quite clear now that the waggle dance does indeed convey direction and distance, as indicated by following radar-equipped bees that were removed from a hive for some distance. These bees went to the location the nectar souce "should" be had they started from the hive. For more, see *Nature* **435**, 205-207 (12 May 2005))

How bees measure distance from the hive to the nectar is an interesting question. Although it was first thought to be a measure of the energy expended to get to the floral source, data (*Nature*, May 2001) show that it is "optical flow"—essentially a measure of how many objects the bee passes. Thus, in a rich environment, the actual distance is less than the vigor of the dance might suggest.

Bee keeping is an important industry—perhaps more now for pollination than for honey, as honey from Argentina, China, Mexico, and other developing countries floods our markets. A number of good books for the lay person are available (e.g., *The Hive and the Honeybee* and *The ABC and XZY of Bee Keeping*).

Bee behavior is not some esoteric research interest; it is directly important economically. Many crops—almond is the best example—would not exist without the services of beekeepers. However, it is not just a matter of dragging the hives out. Bees have their preferences. As a local example, cucumber growers typically require bees, but if the bees are brought before the cucumber flowers are open, the bees will probably locate an alternative source of pollen and nectar. Then, as the cucumber flowers do open, the bees will fly over the fields, ignoring them, on their way to previously located sources. Bees are therefore brought in when a portion of the field is in bloom. (In other crops, however, bees are brought in before flowering begins because early pollination is necessary.)

Hodges et al. (*American Bee Journal*, May 2001) have calculated the value of beekeeping in Florida. In short, the total economic value of hive products (honey, wax, and so forth) totaled $30 million, and the total economic value of pollination, $38 million. Bear these facts in mind when you are in position to influence public policy on pesticides used in agriculture (which can devastate a beekeeping operation) or "mosquito control" programs that blanket the earth with toxic chemicals.

[3] Tupelo honey—one of about 300 kinds of honey that make up the 200-million-pound U.S. honey crop—is a prized product. It is produced in spring along the Ochlockonee, Choctahatchee, Chipola, and Apalachicola Rivers in south Georgia and northwest Florida because this is the only place that *Nyssa ogeche* (water tupelo, white tupelo, tupelo gum) grows abundantly. Because it does not granulate (high fructose content) and is mild in flavor and light in color, it is a prime dessert-quality table honey, rivaling or even exceeding that of sourwood (*Oxydendrum arboreum*). Watch the movie *Ulee's Gold* available at your local video store, which uses tupleo honey production (at the Laniers' in Wewahitchka) as the backdrop.

(B) Birds visit flowers to feed on nectar, flower parts, and insects that are attracted to the flower. (In America, the chief bird pollinator is the hummingbird.) Bird-pollinated flowers usually produce copious amounts of nectar. Birds have a keen sense of sight (in wavelengths detected, similar to humans)—"their" flowers are often colorful, especially in yellows and reds. (The "color" rule, again, is not absolute by any means, and hummingbirds sometimes visit perfectly white flowers.) Birds have a poor sense of smell—"their" flowers usually have little odor.

(C) Other examples are beetles[4] (probably the first pollinators), bats, moths, flies, etc.

POWERPOINT SLIDE: Hummingbird visiting *Macranthera flammea*[5] (courtesy of J. Alford)

POWERPOINT SLIDE: Lesser long-nosed bat pollinating a cactus (*American Scientist* 81: 460).

<u>Seed</u> <u>Dispersal</u>

(A) Many seeds are simply dispersed by wind. Wind dispersal has been a strong agent in evolution, and several specialized structures have appeared, e.g., dandelion "parachutes" and maple "helicopters."

POWERPOINT SLIDE: Maple helicopter (*Acer saccharum* subsp. *floridanum*?) (north Leon County)

POWERPOINT SLIDE: False dandelion "parachutes" (south Georgia roadside).

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[4]In an interesting twist, Roger Seymour of the University of Adelaide discovered in 2001 that some flowers generate heat to attract beetles. Although this is not a widespread phenomenon, it illustrates the extent to which angiosperms and their pollinators have coevolved.

[5]This parasitic plant is a member of the Scrophulariaceae (figworts), a family that contains many parasitic species. (The figwort species that you are most likely to be familiar with is the snapdragon, *Antirrhinum majus*.) Plants that have adapted to a lifestyle of parasitism exhibit various degrees of dependence, ranging to the obligate parasitism of the mistletoe (American mistletoe, *Phoradendron flavescens*), which receives all its water and inorganic nutrients from the host plant, and to dodder (*Cuscuta* sp.), which is nonphotosynthetic. Much more subtle are the root parasites (as shown in this slide); these plants grow special processes, called haustoria (sing. haustorium), which are vascularized connections with a host plant. Because the parasitic connections are underground and because many parasites are facultative (and therefore green), this relationship escapes the attention of most passersby.

Plant parasitism has important economic consequences. A local example, mentioned before, is mistletoe, which in its most benign form is a shade in the canopy of a plant such as pecan. In its most virulent form (a leafless species), it is lethal to some gymnosperms. Dodder, also mentioned before, is a stem parasite of alfalfa (and other species). Because the seeds of dodder and of alfalfa are about the same size, they cannot be sorted mechanically; seed producers must take extreme caution to avoid distributing this parasite with commercial seeds.

Striga (witchweed) is a parasite of graminaceous species and threatens production on approximately 100 million acres in Africa, where the economic loss is estimated to be $4 billion per year and affects approximately 100 million people. It can virtually eliminate production of *Sorghum bicolor*, a staple water-efficient grain. Currently, some anxiety surrounds the veracity of claims of resistance in some newly developed lines of sorghum. (My thanks to Jill Alford, who provided assistance in the preparation of this footnote.)

(B) Plants growing around water have sometimes evolved floating fruits. E.g., because coconut fruits float, virtually all Pacific atolls are populated by this plant.

POWERPOINT SLIDE: Coconut[6] fruit (*Cocos nucifera*) (north Leon County, fruit from Homestead, Florida)

POWERPOINT SLIDE: Coco de mer[7] (*Lodoicea maldivica*) (Amanda Clark, a BOT 3015 veteran, poses with the fruit).

(C) Some plants have evolved fleshy, brightly colored, and flavorful fruits that are attractive to mammals and birds. (N.B.: Most mature fruits are colorful only at longer wavelengths, such as red; they are therefore generally not attractive to insects, which are likely to be too small to be effective in seed dispersal.) Before seed maturation, fruits are often inconspicuously colored and bitter—therefore, when the seed matures, the plant "signals" to the herbivores that it is ripe for picking!

(D) Other examples include spines (e.g., sandspur and cocklebur).

POWERPOINT SLIDE: Beggars' lice plant +beggars' lice seed on fabric (south Georgia).

POWERPOINT SLIDE: Sandspur (*Cenchrus* sp.) (south Georgia).

Physiological Adaptations

Nitrogen Fixation

Nitrogen is essential to all life. In fact, the resource excepting water that most frequently limits the growth of plants[8] (and animals) is the availability of nitrogen in a useful form (N_2—dinitrogen—

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[6] A little fun fact for you: coconut is derived from a Portuguese word that means "grinning skull."

[7] Coco de mer ("coconut of the sea") is a dioecious palm unique to the Seychelles, a group of 40 granitic islands off the east coast of Africa. Guy Lionnet tells us, "The staminate trees are however taller, by some 20 feet, than the pistillate ones, and appear thus to mount guard over their smaller, fruitful neighbors. It is perhaps this 'protective air' and the shape of the male inflorescence, which recalls a large male organ, and that of the nut, which resembles a female human pelvis, which have given birth to the curious Seychelles legend that coco-de-mer palms meet and unite by tempestuous nights, the male palms walking over to the waiting female ones, but that it is deadly to witness such an amorous encounter." Little wonder that Lionnet entitled his book, *The Romance of a Palm!* ☺

The coco-de-mer fruit is the largest; with each nut weighS up to 40 pounds and IS 18 inches long. an exceptionally large bunch, 10, can therefore weigh up to 400 pounds, and as many as two bunches may be produced a year. It is well adapted to growth on the islands. If the seed germinates and the nascent root cannot penetrate the soil, the root will grow laterally up to 12 feet to "find" a suitable site.

[8] A central thread in this course is that our Use of plants for the production of food, fiber, shelter and so forth has economic impacts (U.S. ag exports in 1995: $55 billion, *Florida Market Bulletin*, August 15, 1996) and environmental impacts. In the latter context, I will briefly discuss nitrogen fertilization. Provision of optimum

makes up 80% of the earth's atmosphere, but it cannot be used by eukaryotic organisms). Nitrogen is continuously recycled.

POWERPOINT SLIDE: Haber,[9] developer of commercial process for producing ammonium from N_2 gas (energetically expensive).

POWERPOINT SLIDE: Nitrogen cycle (self made).

Although the bulk of nitrogen is recycled (through ammonification and nitrification), some is lost ($NO_3^- \rightarrow N_2$). The amount of nitrogen in the cycle is replenished by some atmospheric actions (volcanoes, lightning—10^7 tons annually) and by nitrogen fixation 2 x 10^8 tons annually) ($N_2 \rightarrow NH_4^+$), which is catalyzed only by prokaryotic organisms[10]. Many of these are "free-living,"

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nitrogen to plants takes several forms, one of which is the energy-intensive production of NH_4 as described in the main lecture portion on this page.

An insidious cost of nitrate fertilization is the leaching of fertilizer from the soil into surface and groundwater. As an example, NO_3^- is often given to plants as the sodium or ammonium salt. In our neighboring state Georgia, 3.8% of the tested shallow wells exceeded EPA's 10 ppm standard for drinking water (*Georgia Farmers and Consumers Market Bulletin*, August 7, 1996). (Sources of this contaminant, in addition to leaching of fertilizer, include animal waste at feedlots, breakdown of residual nitrogen in soils and crop residues, nitrate-bearing minerals, septic tanks, and municipal wastes.)

From an article on the Second International Nitrogen Conference, 2001: "To get a handle on one of the world's biggest environmental headaches, think about dinner. Say that tonight you eat 100-gram helpings of both rice and chicken. Producing those foods in rice paddies and chicken farms required 40 grams of nitrogen in fertilizer, 90% of which was wasted, leaking into the soil, water, an air. Add the 4 grams of nitrogen from the meal that you'll leave in the toilet, and that's part of your daily contribution to nitrogen related problems such as as algal blooms and smog, ..."

[9]It is almost impossible to exaggerate the importance of this person's work. To get quickly to the point, use of recycling and green manures as nitrogen sources for fertilization would limit the carry capacity of the Earth to about 2 billion fewer people than presently live. Indeed, the sudden increase in Earth population, beginning about 1950, is mirrored by the increase in the consumption of nitrogen fertilizer to its present level of 85 megatons (*Trends in Plant Sciences* 3: 389, 1998) to 110 megatons (*Science* 294: 1268, 2001) of nitrogen per year. One can say, then, that about 1/3 of Earth's population **can** exist because of Haber! (Of course, agriculture does not reach its potential in terms of nitrogen fixation, and some nitrogen fertilization is in the form of nitrates, so roughly 2/3 of fixed nitrogen applied to agricultural systems arises from synthetic fixation and 1/3 from biological fixation.)

Unfortunately, though, Haber lived a tragic life. His chemistry, coupled with Bosch's innovation to prevent the reaction chamber from deterioration at the extreme temperatures and pressures, led to the first commercial ammonium factory in Germany in 1913. He was awarded a Nobel Prize for the work in 1919. By 1919, however, Haber had been labeled a war criminal because, as Director of the Kaiser Wilhelm Institute for Physical Chemistry during World War I, he developed the use of chlorine gas for the German army. He thought that this gruesome weapon would bring a swift victory to Germany and, overall, limit the suffering in the war. Before its first use against Allied troops, his wife—tormented by her husband's work—committed suicide. A Jew, he fled Germany and died in 1934 at the age of 66 in Switzerland. For more details of this interesting story, see the July 1997 issue of *Scientific American*.

[10] . . . and, as mentioned previously, about 100 megatons from synthetic fertilizers. As a means of comparison, although about 200 megatons of nitrogen enters the nitrogen cycle from nitrogen fixation, only about 50 megatons of this 200 megatons is agricultural.

but some form mutualistic and highly specific associations with plants[11], e.g., the *Rhizobium*-legume symbiosis.[12, 13, 14]

POWERPOINT SLIDE: Nodules on *Vicia faba* roots (FSU lab).

POWERPOINT SLIDE: Establishing *Rhizobium* symbiosis (modified from Fig. 19.10 of Kirk).

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[11]Put this into the WOW category: Termites, which are major decomposers of Earth's biomass (lignocellulosic plant-wall residue), consume a diet low in nitrogen. Spirochetes (a kind of bacterium) in the termite gut contain the nitrogenase gene and fix nitrogen. For more, see *Science* 292: 2495 (2001).

[12]Rhizobium means root-living. In addition to the genus *Rhizobium*, other bacterial taxa (*Sinorhizobium*, *Bradyrhizobium*, also associate with legumes. As an interesting aside, the generality is that bacteria have a single chromosome, and plasmids may also be present. In the case of *Sinorhizobiium* the single chromosome is 3.65 mb, but the two megaplasmids (1.68 and 1.35 mb) contain almost as much DNA.

[13] The word symbiosis means different things to different people; you will need to be alert to this fact as you read. To give you a feel for the range of definitions that are currently in use, please read the following, which were taken from various textbooks.

Textbook 1: The living together in close association of two or more dissimilar organisms; includes parasitism (in which the association is harmful to one of the organisms) and mutualism (in which the association is advantageous to both).

Textbook 2: Two different kinds of organisms living together.

Textbook 3: Intimate association between members of different species.

Textbook 4: The close association of organisms of different species within an environment. Commensalism, mutualism, and parasitism are symbiotic relationships.

Textbook 5: An intimate and protracted association between two or more organisms of different species. Includes mutualism, in which the association is beneficial to both; commensalism, in which one benefits and the other is neither harmed nor benefited; and parasitism, in which one benefits and the other is harmed.

Textbook 6: [The living together of] . . . two or more dissimilar organisms . . . in close association with each other. The association may be beneficial to both organisms (mutualism) or harmful to one organism (parasitism).

Textbook 7: The living together of two organisms in an intimate relationship.

Textbook 8: An ecological relationship between organisms of two different species that live together in direct contact.

[14]The problem for agriculture is, of course, that the symbiosis between the legume and the bacterium is specific—particular legumes even require particular strains of the bacterium. In general, most plants (and most crop plants) do not form associations with N_2-fixing bacteria. Indeed, none of the top five crops (wheat, rice, maize, potato, barley) associates with nitrogen-fixing bacteria although current research on maize suggests some possibilities. One long-term goal of plant researchers is to "create" organisms that would enter into this symbiosis. For example, if maize were a nitrogen-fixer, our dependence on fossil fuels to feed this nitrogen-hungry plant would be diminished. (I briefly note that reduction of N_2 to NH_4^+ is an expensive 6-electron reduction; the sunlight harvested and used for this process would not be available to reduce C.) As a perspective on this problem, I quote from Bergman et al. (*Trends in Plant Sciences* 6: 196): "The development of artificial, nitrogen-fixing symbioses in economically and agriculturally relevant host plants is a highly desirable alternative to the use of chemical fertilizers. Nitrogen-fixing symbioses only need light-generated energy to convert atmospheric nitrogen into a bio-available form—ammonia—while the synthesis of chemical nitrogen fertilizer depends on diminishing fossil fuels, and may cause eutrophication (excessive nutrient enrichment in the environment, leading to oxygen depletion). Although the development of artificial symbioses is seen as a long-term research effort, hope of success has been provided by recent progress in the development of molecular techniques, in combination with an expanding knowledge of signalling events between symbionts. Cyanobacteria are excellent candidates for artificial symbioses, with their unparalleled symbiotic competence and wide host and organ range. Moreover, there is no requirement for cyanobacteria to invade the host cells, and they are equipped with their own nitrogenase protection devices, the heterocysts."

The legume releases a chemical that attracts bacteria. Usually, this chemical is a flavinoid. This chemical is "recognized" by soil bacteria that are appropriate for nodulation of this plant species. In response, the bacteria release chemicals (nodulation factors) that cause deformation of root hairs, formation of an infection tread, and proliferation or root cortex cells to form a nodule. These signals or nodulation factors are complex, containing a backbone of 4-5 sugars that is attached to a fatty acid such as a C_{18}. Even in plants that do not form the symbiosis (e.g., tobacco), these compounds are biologically active, suggesting that the bacterium has commandeered a "normal" developmental pathway that is usually controlled by endogenous plant growth regulator. Next, bacteria are encapsulated in membranous vesicle and they proliferate.

The plant provides energy (generally carbohydrate) and a favorable environment (a very special one: low $[O_2]$ by leghemoglobin, which is similar to hemoglobin in blood and which gives nodules a pink color), and the bacteria supply the nitrogen-fixation machinery (an enzyme, nitrogenase that converts N_2 to NH_4^+ and that is denatured by O_2).

POWERPOINT SLIDE: Bluebonnet, example of a nitrogen-fixing plant (Austin, Texas).

POWERPOINT SLIDE: Red clover, example of a nitrogen-fixing plant (north Leon County, Florida).

Other examples of organism-to-organism interactions include (A) fungal association with roots, as discussed earlier[15] and (B) production of chemicals that prevent growth of other plants nearby (e.g., walnut, creosote bush).

Biochemical Adaptations

$\underline{C_4}$ Photosynthesis

POWERPOINT SLIDE: Crabgrass-invaded disturbed sunny habitat (north Leon County, Florida).

POWERPOINT SLIDE: Grass leaves (Fig. 19.10 of Esau). Observe the so-called "kranz" anatomy in the leaf cross-section at left, and compare this abundance of plastids in the bundle-sheath cells to the leaf cross-section at right (from a C_3) species.

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[15]Interestingly, formation of a nodule and of a mycorrhizal association have many features in common. E.g., a pea mutant defective in its ability to form nodules is also defective in its ability to form mycorrhizal associations. Similarly, novel genes turned on during nodulation are also turned on during formation of the mycorrhizal association. Fungal-plant associations are very old (~400 million years) and indeed these represent early fungal fossils. Symbioses with bacteria came much later (~ 70 million years ago) and it is therefore thought that bacteria commandeered existing mechanisms. For a brief general overview, see *Science* 304: 234-237 (2004).

POWERPOINT SLIDE: *Cynodon dactylon* (Bermuda grass) (Fig. 19.11 of Esau). Note the dimorphic chloroplasts.

POWERPOINT SLIDE: Clanton Black (Satilla River, Georgia)

POWERPOINT SLIDES: C_4 photosynthesis (self made)—series of slides that outline the pathway and describe the costs and benefits.

C_4 photosynthesis, in its simplest terms, follows: Two kinds of photosynthetic cells "cooperate" to fix and reduce CO_2 photosynthetically. The mesophyll cells have a special very active and efficient enzyme, PEPC, that removes CO_2 from the intercellular leaf spaces and incorporates it into organic form. (3-C precursor + $CO_2 \rightarrow$ 4-C product). PEPC can utilize CO_2 even when $[CO_2]$ is very low; for reasons we cannot explore now, the Calvin-cycle enzyme, rubisco, that incorporates CO_2 into that cycle is not efficient and cannot lower the $[CO_2]$ in the leaf to the levels that PEPC does. The 4-C product of the PEPC reaction is transported to the other photosynthetic cell type, the bundle-sheath cells, where the original carbon of CO_2 is released as CO_2. This CO_2 is fixed by the Calvin cycle, which is present in the bundle sheath cells. (The Calvin cycle is not present in the mesophyll cells.) Overall, therefore, the initial fixation of CO_2 by PEPC and transport of this C to the bundle-sheath cells constitute a CO_2-concentrating mechanism. The concentrating mechanism "overcomes" rubisco's inability to extract CO_2 from air, which contains only a small amount of this gas. Obviously, the auxiliary mechanism evolved at a cost. What advantages does the plant gain? Primarily two: (1) C_4 plants typically require less water. Their stomata need not be so widely open to admit CO_2 because the driving force is higher. (The driving force is proportional to the $[CO_2]_o$ - $[CO_2]_i$, and C_4 plants have a low $[CO_2]_i$.) (2) C_4 plants are typically more nitrogen-use efficient. Rubisco is a huge sluggish enzyme, so much so that a normal leaf is >25% of this one protein. Because C_4 plants have the above-mentioned CO_2-concentrating mechanism, much less rubisco is required, so less N is "tied up" in the protein. (Disclaimer: This paragraph should not be used as reference because my simplification left out chemical intermediates and alternative pathways. From a conceptual viewpoint, the essence has been conserved.)

Morphological Adaptations

<u>Leaf</u> <u>Response</u> <u>to</u> <u>Dryness</u>

(A) Reduction in air spaces.

POWERPOINT SLIDE: Cross-section of *Sphaeralcea* leaf (Fig. 19.1a of Esau). The mesophyll in this plant is differentiated into only palisade parenchyma.

In contrast:

POWERPOINT SLIDE: Cross-section of *Nymphaea* leaf (Fig 19.6 of Esau).

This dicot water plant contains large air spaces. (Note, also, as an aside, that this plant—a water lily—also has another unusual adaptation. After flowering, the stem "corkscrews," so that the fruit (a tomato-like berry) is developed at the lake bottom.)

(B) Reduction of surface-to-volume ratio.

POWERPOINT SLIDE: Cross-section of *Greggia* (Fig. 19.1d and e of Esau).

This plant has a high volume-to-surface area ratio.

(C) Development of water-storage tissues.

POWERPOINT SLIDE: Cross-section of *Salsola* (Fig. 19.1b and c of Esau).

Salsola has specialized water-storing cells.

(D) Development of trichomes (hairs, etc.) on leaf surface.

POWERPOINT SLIDE: Cross-section of *Atriplex* (Fig. 10.1f and g of Esau). Hairs that increase boundary layer.

(E) Sunken stomata.

POWERPOINT SLIDE: Cross-section of *Banksia* (Fig. 180a Eames and MacDaniels).

(F) Thick cuticle.

POWERPOINT SLIDE: Contrasting cuticle thickness (Fig. 33 of Eames and MacDaniels).

(G) Leaf rolling.

POWERPOINT SLIDE: Grass leaves (Fig. 19.8 of Esau). Note the bulliform cells, which can cause "twisting" as shown on the inset at left.. [Keep this image of modern maize in your mind, to compare with corn grown by southeastern U.S. Indians later in the topic.]

A discussion of plant adaptations would not be complete without at least a mention of the various and sundry ways that we have selected plants for particular modifications to suit our agricultural purposes. In the following series of slides, we will acknowledge some of these modifications.

Genetic Variation of Plants

As mentioned quite early in this course, man has taken advantage of the genetic variation of plants and directed their evolution, a process called domestication. This process is far from finished, and work needs to be done on several fronts. Many scientists feel that we rely on a too narrow base of species of plants—the big five (wheat, rice, maize, potato, barley) account for the bulk of calories consumed by humans throughout the world. These scientists fear that a disease could strike and abolish food supplies, and clearly they can find precedents of such catastrophic events (e.g., the potato famine). Therefore, few scientists and some lay people are exploring the domestication of new species[16] to broaden the genetic base of our civilization or to produce products on marginal land or by use of salt-water irrigation or for the production of new products, such as superior oils for lubrication or fibers for industry. Other scientists focus not so much on new species as on the genetic diversity of plants that we now use. They are also able to point to near disasters that happened because the crop plant used was so uniform in genetic composition (e.g., so-called Texas cytoplasm, which makes the plants male-sterile, was used in the production of hybrid corn to save detassling labor, but this genetic trait also caused the corn to be susceptible a mutant form of a fungus). These concerned people maintain federally funded germplasm repositories (such as the Citrus Repository near Leesburg, Florida, and the other one near Riverside, California) or private repositories such as Seed Savers Exchange, Decorah, Iowa. So far, this discussion has had two main foci: the vulnerability we accept when we rely on too few species, and the importance of having "genetic warehouses" for use by plant breeders to transfer desired traits from one strain to another ("Extinction is forever."). Now, however, plant biologists are not limited in their efforts of combining or transferring traits by sexual crosses or even asexual ones (such as polyethylene-glycol induced cell fusion). Many, many transgenic plants—i.e., plants that have a foreign gene incorporated into them—are either available or on the way. Prime

[16] An example is buffalo gourd, a member of the squash family. The vines of this plant are digestible and have a high protein content and, thus, could serve as a source of forage. The roots, which can weigh up to 40 kg after three or four years, have a high starch content and could be a source of calories and sweeteners. The seeds are rich in oil, and after expression of the oil, the meal is a livestock foodstuff . . . .

examples include several so-called delayed-ripening tomatoes,[17] one of the first of which was Flavr Savr (under the McGregor label, but not sold now), a product of research at Calgene, which was subsequently bought out. All these delayed-ripening tomatoes have some kind of genetic mechanism that slows ripening, e.g., antisense mRNA to the gene that makes a normal tomato-fruit cell-wall degrading enzyme. In another product-oriented case, an enzyme that makes a unique oil has been transferred into rapeseed. Perhaps the greatest benefit, however, will come not from plant products, but from plant protection. We spend a great deal of time and money in, and accept rather severe environmental penalties for, protecting plants. As an example, cotton is a "dirty" crop and relies on nominally 10 pesticide applications, depending on disease and insect pressure. BolGard cotton, a product of Monsanto Company, is so called because the bolls are "guarded" against the bollworm, and to some extent, the boll weevil. This cotton was produced by incorporation of a bacterial gene that codes for a protein that is toxic to certain kinds of insects but is otherwise harmless. Use of this cotton eliminates about 3–5 of the required insecticide sprays each year. A variant of this gene has been incorporated into corn, as protection against the corn borer. Finally, as an example of a strategy for protection against fungal pathogens, I note that transgenic grapes that have a fungal-cell-wall-degrading enzyme transferred to them are under study. In summary, then, the genetic resources for development of plants with new characteristics may be found within the species, or may be found in a species even a kingdom away! (Extinction is *really* forever.)

Everyone is aware of the growth habit of maize, and it therefore can serve as a good example of the variation of an important crop plant. (This single-species variation is intended to complement the discussion of adaptations earlier that emphasized how one species may evolutionarily adapt to a particular environment and another species to different one.) One of the harshest environments for plant culture is the North American Southwest, and indeed, generally, water is the most limiting resource for a terrestrial plant. As the following two slides show, however, the pre-Colombian Hopi, the Zuni, and the Navajo selected maize that produced fair crops even under these conditions.

POWERPOINT SLIDE: A field of Zuni maize, ca. 1910 (Zuni, New Mexico; *Journal of Agricultural Research* 1: 293).

POWERPOINT SLIDE: The basal portion of a Navajo maize plant from which the leaves and husks have been removed. The ears from this plant weighed nearly 1 kg. (source as above).

In order to achieve growth and production, the Amerinds exploited two major adaptations, as shown below:

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[17]Typically, commercial tomatoes are picked when they are green. Then, they are stored in their green state. When the market is right, they are "gassed," i.e., given a treatment with ethylene, a plant hormone that speeds senescence. After this treatment, they are shipped to grocers and ripen on the way. Once the ripening process kicks in however, they have a short shelf life.

POWERPOINT SLIDE: A seedling of Hopi maize (source as above).

The left plate shows that this plant has the ability to grow even if the seed is planted 45 cm below the surface of the soil. If planted that deeply, regular unselected maize would never push leaves to the soil surface,[18] and a typical commercial planting depth today is about 3–5 cm. The second special feature of this corn is the development and persistence of a primary root, and, at an early stage, the relatively feeble adventitious root system. This primary root allows the plant access to moisture far below the surface of the soil.

I will finish this topic by reviewing some common plants that have been selected for their edible parts.

POWERPOINT SLIDE: Teosinte, the wild plant from which maize is probably derived (Duke University Gardens) + kernels of maize (Missouri).

POWERPOINT SLIDE: Market potatoes (swollen underground stem) and market onions (leaves) (New Dehli).

POWERPOINT SLIDE: Onions (terminal parts of leaf are dried, whereas bulb remains succulent) (Missouri).

POWERPOINT SLIDE: Leeks (elongate leaf blades bleached by covering with soil) (Beijing).

POWERPOINT SLIDE: Cauliflower (modified inflorescence) (Helsinki) Cauliflower, cabbage, rape, collards, broccoli, Brussels sprouts are all different modifications of the same species (*Brassica oleracea*).

POWERPOINT SLIDE: Chinese cabbage (enlarged midrib) (north Leon County, Florida).

POWERPOINT SLIDE: Stacks of Chinese cabbage outside a dorm food-service facility (Beijing).

POWERPOINT SLIDE: Sugar beet field (for roots) (California).

POWERPOINT SLIDE: Carrot (for roots) (Beijing).

POWERPOINT SLIDE: Ginger (for root) (Beijing).

POWERPOINT SLIDE: Turnip (for root) (Yangling).

POWERPOINT SLIDE: Taro (for root) (Beijing).

POWERPOINT SLIDE: Water chestnut (for stem) (Beijing).

POWERPOINT SLIDE: Edible-stem lettuce (Beijing).

POWERPOINT SLIDE: Bananas (Jefferson County, Florida). Banana is an infertile hybrid (2N, 3N, 4N) of two wild species.

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[18] As a general horticultural rule, a seed is placed about 1.5–2.0 seed diameters below the soil surface.