Topic #2: Angiosperm Morphology and Flowering

REQUIREMENTS: Powerpoint Presentations, peanuts

Objectives

1. Give a list of characteristics of the kingdom Plantae. How can Plantae be distinguished from prokaryotes? . . . from animals?   . . . from fungi?
2. Name two major categories in the kingdom Plantae. Give common examples.
3. Name the two major categories within vascular plants. Give common examples.
4. Explain what is meant by alternation of generations. Define haploid, diploid. Define sporophyte, gametophyte. What are sporangia? What is zygotic meiosis? What is meiotic gametogenesis?
5. Distinguish between homosporous and heterosporous. Why is heterospory required for seed plants?
6. How many daughter cells result from meiosis? What happens to the ploidy level during meiosis?
7. Discuss the general trend in evolution with respect to relative dominance of the gametophyte (sporophyte) generation.
8. Name three (general) major functional components of seeds.
9. What difference in characteristics is implied by "angiosperm" and "gymnosperm"? Name other differences. What is the major nutritive tissue within gymnosperm seeds? What is the endosperm of angiosperm seeds? In general, what is the major nutritive tissue of monocot and dicot seeds? How large is the female gametophyte of angiosperms? . . . of gymnosperms?
10. Name and describe the four basic parts of a flower. List them by order of insertion on the "stem."
11. In general, how do monocot flowers differ from those of dicots?
12. List five floral characteristics that are evolutionarily advanced. Speculate on the adaptiveness of the advanced conditions.
13. Show how parietal (or marginal) placentation could give rise to more advanced types of placentation.
14. Discuss on a very elementary basis floral development. Why is *Arabidopsis* an important model plant? Discuss characteristics of model species.

15. Follow the steps of development from the megaspore mother cell to the haploid 8-nucleated female gametophyte (or embryo sac).
16. Follow the steps of development of the diploid microspore mother cell to the mature haploid male gametophyte.
17. Explain double fertilization (which gives rise to the endosperm *and* the zygote).
18. Describe some of the biochemical steps involved in seed germination. What is gibberellin? In what other plant processes (besides seed germination) is gibberellin involved?

Lecture

POWERPOINT SLIDES: Pear flower (north Leon County, Florida) + Olive flower[1] (Tuscany, Italy) + Apples[2] (north Leon County, Florida). Flowers and fruits are distinguishing characteristics of angiosperms.

---

[1]Olives were among the first trees domesticated, beginning about 4,000 B.C.E. on the east coast of the Mediterranean Sea (present day Lebanon, Israel, and Syria). (About 2,000 more years went by, however, before oil was produced from olives.) World production is now centered more westward, in Spain, Italy, and Greece although most regions bordering the Mediterranean produce some oil. As discussed further in an interesting article (*National Geographic*, September 1999), olive oil is very versatile—you can burn it, wash with it, use it as a lubricant, anoint kings with it, preserve fish, cheese, even wine, make cosmetics from it, boil it and pour it on your enemies. As a food—my favorite use—it is excellent in flavor, high in Vitamin E (an antioxidant), and devoid of cholesterol. Of course, I would not go on record, but I think that the first meal in Heaven is calamari, bread, and olive oil.

Take advantage of Florida State's subscription to the Oxford Dictionary (http://dictionary.oed.com/entrance.dtl) and you will find that the word Christ means "Lord's Anointed" or the anointed one. Powerful stuff, this plant.

[2] As a means of emphasizing the important contributions made by novice, amateur, and professional plant biologists, let's take a look at these apples. Plants must be bred and selected for growth in particular locales and times of the year. The apples pictured are Anna, named after a professor's wife in Israel. This is probably the best apple for the Deep South, like Tallahassee. Few apples will grow here because many temperate species have a very special requirement for flowering. This requirement is quantified in "chilling units (CU)" Although there is no single uniform way to express the winter requirement for breaking dormancy that many plants have, the system that seems to be the most popular is to count the number of hours in the winter when the temperature falls between 32°F and 45°F. Colder weather does not seem to be effective, and the accumulated hours must be corrected for intervening warm weather. Normally, in Tallahassee, we can expect to accumulate about 550 CU, but the winter of 1995–1996 was phenomenal (>1200 CU recorded at the agricultural station in Quincy, compared with a value of about 2200 CU in the Willamette valley). In contrast, the winter of 1996–1997 was exceptionally warm—only about 400 CU were recorded at the agricultural station in Monticello. Another apple that grows well here is Dorsett Golden, often said to be a chance seedling of Golden Delicious that was found in the Bahamas. However, chilling requirement is a multigenic trait and the chance of a low-chill cultivar "appearing" is next to nothing, so some think that a world traveler probably tossed out seeds from an apple of the Middle East and it grew to become the original Dorsett Golden.

Some plant responses overlap. Cold and drought seem to satisfy the same "need." One can therefore "fool" plants in arid environments by withholding irrigation water. Thus, peaches can be produced in some areas of South America that are warm, but dry. In southern California, where it never gets cold, some apple cultivars can be given a "winter effect" by spraying them with a chemical that causes the leaves to fall off.

Today, we will begin a series of lectures on angiosperms[3]—the most highly evolved and successful organisms on Earth today. By definition, these are the members of the kingdom Plantae that have seeds enclosed in a developed ovary (fruit). At the expense of redundancy, flowers and the fruits that develop from them are hallmarks of angiosperms.

Let us define characteristics of the kingdom Plantae:

Characteristics of Kingdom Plantae.[4]

The kingdom Plantae includes all the more specialized green organisms derived from green algae:

***** They are eukaryotic.

***** They are multicellular.

***** Their cells are vacuolate.

***** They have cellulosic cell walls. (Some green algae, and even some bacteria, also have cellulosic walls, but current thinking is that plants may have evolved the ability to make cellulose independently of green algae. Only a certain group of advanced green algae (the stone worts, e.g. *Chara*) and plants synthesize cellulose by means of the large complex rosettes that glide through the membrane extruding this polymer.)

***** Their principal mode of nutrition is photosynthesis. (They contain chlorophyll a, as do all photosynthetic eukaryotes, and they contain chlorophyll b, as do Green Algae and a few other organisms.)

***** They have a distinct evolution in relation to invasion of land.

***** They show an evolutionary trend toward organs specialized for photosynthesis (leaves), support (branches), and anchorage (roots).

Altogether, at least 1600 named and propagated apples were grown in the U.S. South prior to 1928 (C.E. Calhoun (1995) *Old Southern Apples*, McDonald and Woodward, Blacksburg, VA), of which 300 are extant. This list of 1600 does not include many new low-chill apples such as Gala and Fuji (W. Manhart (1995) *Apples for the twenty-first century*, North American Tree Co., Portland, OR), but does include such venerable cultivars as Newtown Pippin, which was a U.S. export to England in the 1770's, and Lady, a fragrant French apple of great antiquity (Appian apple of Rome?) being grown in the gardens of Louis XIII at Orleans in 1628, and which "the ladies of France carry in their pockets by reason they yield no unpleasant scent." (Thomas Burford, who conducts the annual apple tasting at Monticello, quotes a source indicating that there were 19,000 named apple cultivars (including synonyms) in 1904!) Although consumers are becoming more taste-discriminating, worldwide the greatest acreage is devoted to Red Delicious. The strains of Red Delicious that are sold today (unlike the original Red Delicious, which was first known as Hawkeye) are yucky; someone recently quipped that Red Delicious is the apple that tastes like the cardboard box that it was shipped in. But, you should try mountain-grown "old" Red Delicious from Mountain Rest, SC; these apples live up to their name.

Unfortunately, none of the PRI (for **P**urdue, **R**utgers, **I**llinois) apples, such as Enter**pri**se or **Pri**stine, appear to be adapted for the deep south. These apples have been bred to incorporate disease resistance.

[3] from Greek, "angion" means vessel and "sperma" means seed; thus, angiosperm means "seed in vessel (or carpel)."

[4] As I discuss elsewhere, the list of organisms that are included under the name "plants" is becoming larger with the development of molecular phylogenies. "Plants" in this course are restricted to organisms having the listed attributes, which may be referred to in some literature as "Land Plants."

***** They are Embryophytes[5]—fertilization occurs internally and the zygote is surrounded by protective tissues and grows within gametophytic tissue.

POWERPOINT SLIDE: Simplified key (different, but redundant with one in Topic 1). Please especially note the disclaimer on the slide that this "key" is intuitive, but has weaknesses and one is cautioned not to make the usual inferences about evolution and relatedness[6].

Major Categories of Plants.

An intuitive way to envision kingdom Plantae is to consider two major groups:

(A) the nonvascular plants or bryophyte grade[7] (a group of terrestrial green plants including the true mosses and other organisms)

(B) the vascular plants—those that contain specialized cells for conduction of water, minerals, and nutrients (these characteristics are very general and not diagnostic).

Within the category of vascular plants, one can recognize two broad categories: (1) those that produce seeds and (2) those that do not. Being the most advanced organisms, angiosperms produce seeds, but so do many plants that do not form flowers (i.e., gymnosperms; e.g. pine trees).

Without an explanation, this categorization seems unfounded, so we digress considerably for a moment to put the difference into perspective.

POWERPOINT SLIDE: Simplified plant life cycle (modified from an early edition of Raven *et al.*).

Plants (and some insects and heterotrophic protista) alternate between a gamete[8]-producing generation (in plants, called the gametophyte) and a spore-producing generation (in plants, called the sporophyte). Recall that a gamete has but one function (fusion with another gamete) and a spore has but one function (germination, perhaps after a rest period). Haploid denotes an organism or stage that has a single version of each chromosome homolog (e.g. a human sperm). Diploid denotes an organism or stage that has a double complement of DNA per cell (e.g. a human adult, in the cells of which

---

[5]It is sufficient for you to remember that plants can be distinguished from green algae because plants are embryophytes, but green algae are not. REMEMBER THIS DISTINCTION! (This situation is a bit fuzzier, however, if you are a slave to details. A few green algae form embryos, but the embryos do not advance to a large multicellular stage.)

[6]. . . a reminder to always read this text along with the Powerpoint slides. The complete presentation requires both elements.

[7]Given the introductory nature and scope of this course, we will use the term "bryophyte" more loosely than one might take the liberty of in an advanced, focused treatment. A more detailed explanation will be given later.

[8]The root "gam-" in gamete means marriage—cf. polygamy—which should help one remember the function of gametes. "Phyte," as you probably know, simply means plant.

chromosomes exist in pairs, one of which derives from the sperm and the other from the egg[9]). As noted, haploid and diploid have specific meanings, but as a matter of concept and simplicity, we will use haploid synonymously with gametophyte, and diploid, with sporophyte[10].

POWERPOINT SLIDE: Generalized overview of three kinds of sexual life cycles[11] (self-made). This chart is reproduced at the end of this topic.

Alternation of generations,[12] which all members of the kingdom Plantae exhibit, is one type of life cycle. Two other types of life cycles will be studied in this course. In some organisms (e.g. Fungi[13]), the only diploid stage is the zygote; this life cycle is referred to as zygotic meiosis. In other organisms (e.g. humans), gametes are the only haploid stage; this life cycle is referred to as meiotic gametogenesis. **It is exceedingly important that you commit these three life cycles to memory**. Regardless, it is important to remember that meiosis results in the production of four genetically dissimilar daughter cells. Over the course of the semester (and on exams), I will refer without explanation to these life cycles.

In plants, the diploid sporophyte gives rise—through meiosis—to a haploid spore. Only one type of spore is produced in *homo*sporous species, which have only one type of sporangium; in *hetero*sporous species, two types of sporangia produce two types of spores, microspores (male, regardless of size) and megaspores (female, regardless of size). The spore germinates and gives rise to the gametophyte. (In heterosporous plants (e.g. angiosperms), the microspore produces the male gametophyte, and the megaspore, the female gametophyte. In this course, we will always use the term

---

[9]Things are not all that cut and dried. Heart-muscle and liver cells range up to 16n. This phenomenon, called endopolyploidy, presumably provides for the increased transcription of various genes. (The genes that are required at high transcriptional rates in *all* cells are often redundant in the chromosome, e.g., rRNA). In an extreme example, consider *Gerris* (the water strider), which has 2n = 22. The salivary glands of this organism have as many as 2048 copies of every chromosome, or more than 40,000 chromosomes.

[10] Recall that plants are really complex and interesting. E.g., the gametophyte of wheat is triploid and the sporophyte is hexaploid in most cultivated varieties (see Introduction). Other polyploids of interest are potato (as mentioned), oats, sugar cane, cotton, alfafala, coffee, peanuts, rye, most commercial bananas (triploid), winesap apples (triploid), McIntosh apples (tetraploid), and strawberry (octoploid). Polyploids may arise in different ways, as outlined in genetic texts. As another example, often some *regions* in a plant have a doubled chromosome number, like endodermal cells (which we will study later) or those "stung" by nematodes.

In addition, some perfectly good plants are produced by the hybridization of two species (e.g., muscadines x *V. vinifiera* grapes) that have different chromosome numbers. These plants are obviously not haploid although they potentially have unpaired chromosomes.

[11]*Alternation of generations* is the same as *sporic meiosis*. *Meiotic gametogenesis* is the same as *gametic meiosis*. I strongly recommend that you commit these synonyms to memory as the alternative terms are used in different courses, exams, and literature.

[12]Hofmeister, who published his discovery in 1851 (in German) in Leipzig.

[13]This statement is made as a generality—some yeasts are diploid. We will not consider fungi that have a diploid phase of growth, but the interested student can find life cycles of these organisms in a standard advanced text, such as Lodish et al. (*Molecular Cell Biology*), which is the textbook for Molecular Biology here at Florida State

"female gametophyte," but others may use "embryo sac," which for a time, seemed to be going out of fashion.) Gametes produced mitotically by the gametophytes undergo syngamy to form the zygote, which grows into an embryo and matures into the sporophyte. At the expense of redundancy, all seed-producing plants ("higher plants") are heterosporous. More primitive plants—those that do not produce seeds—are either homosporous or heterosporous. And, finally, note that a homosporous species, with a single type of spore, produces only one kind of gametophyte, which must be bisexual (in contrast to a heterosporous species, in which the two kinds of spores give rise to two kinds of gametophytes, each of which is unisexual).[14]

In bryophytes (mosses and similar organisms), the gametophyte is the dominant form—it is nutritionally independent and is usually the larger of the two alternating generations. Among vascular plants, the sporophyte predominates, and in seed plants, the gametophyte is nutritionally dependent on the sporophyte. The trend in evolution is for a reduction of the gametophyte generation. In angiosperms, the most highly evolved organisms, the female gametophyte usually comprises but seven cells (eight nuclei) and the male gametophyte only three.[15]

The seed itself is a remarkable structure, and there are, of course, many variations. Generally, the seed contains:

PEANUTS

(A) the embryo—the new sporophyte generation—which was derived from the zygote,

(B) the outer protective seed coat, derived from the old sporophyte generation, and

(C) nutritive tissue, which may or may not be part of the embryo itself.

Thus the entire female gametophyte generation, which may or may not survive at maturity, is enclosed by the old sporophyte.

The advent of the seed was one of the most dramatic innovations in the evolution of vascular plants, appearing in the fossil record about 350 x 10^6 years ago . IT PERMITS THE YOUNG SPOROPHYTE, PROTECTED BY THE SEED COAT AND PROVIDED WITH A SUPPLY OF STORED FOOD, TO REMAIN DORMANT UNTIL CONDITIONS FAVORABLE FOR GERMINATION ARISE.

The seed plants themselves can be broken into two groups:

University. Please appreciate that the comprehensive nature of this course does not allow us to plough too deeply in the esoteric details, despite their interesting nature and importance.

[14]Later in the course, we will return to these concepts and refine them.

[15]We will teach the 8(7)/3 model described in this sentence as the gospel, as it would be treated on any standardized test. It is another example, however, of using prototypes to teach a general truth without adding in all the distracting details and exceptions. The female gametophytes of some species are larger (e.g., *Peperomia*, 64 nuclei).

(A) gymnosperms (cycads, ginkgoes, conifers, and Gnetales).

(B) angiosperms, the primary subject of this topic and evolutionary sisters of extant gymnosperms (i.e., the gymnosperms are more primitive than angiosperms, but no living gymnosperms are ancestral to angiosperms). A hallmark of angiosperms, about 250,000 extant species, is the flower. The oldest for-certain flower dates back 140 million ago.[16] Literally, "gymnosperm" means "naked seed." The seed of a gymnosperm, such as a pine, is not enclosed by a "pod"—a leaf-like structure—such as found in a typical angiosperm such as a pea.

POWERPOINT SLIDE: Pea pod with seed. Note that, botanically speaking, a fruit is a mature ovary and includes, in this case, the pea pod. This technical usage of the word "fruit" is somewhat at variance with the vernacular usage. For example, a single corn kernel is an entire fruit, not just a seed.

POWERPOINT SLIDE: Pea pod with seed (schematic) (Fig. 15.6 of Weier, Stocking, and Barbour.)

There is a more fundamental difference, however, than the name implies.

POWERPOINT SLIDE: Gymnosperm seed (schematic) (Fig. 14.4 of Foster and Gifford).

A prominent feature of the gymnosperm seed is the remains of the gametophyte, which provides nutrition to the embryo.

POWERPOINT SLIDE: Angiosperm seed (schematic) (Fig. 12-28 of Wilson, Loomis, and Steeves). (castor bean, left; corn, right).

In contrast, the angiosperm seed contains an endosperm, at least during development. The endosperm ("inside seed") is formed through a process called double fertilization, which for our purposes is diagnostic for angiosperms.[17] In brief, at the time of the fertilization of the egg, other nuclei—from female and male gametophytes—unite also to form the usually triploid[18], genetically distinct endosperm. Often the female gametophyte is destroyed during seed maturation, and the

---

[16] The defining feature of an angiosperm is the presence of carpels that enclose ovules. This feature is found first in *Archaefructus*, a fossil from the Upper Jurassic of China (*Science* 282: 1692-1695, 1998). Further work (*Science* 296: 899 (2002)) suggests that this plant was aquatic.

[17] Advanced students of botany are debating (e.g., *Science* 255: 336) the significance of double fertilization events in some advanced gymnosperms, but in those organisms, the second fertilization is aborted and does not develop into an endosperm proper. Thus, as we use it, double fertilization implies the formation of an endosperm and is distinct from multiple fertilization, by which several embryos are formed within a seed. We will return to this topic when gymnosperms are discussed.

[18] For emphasis, I note again that triploid is the common genetic situation for the endosperm, but there are many exceptions, and the endosperm of some species is only diploid.

endosperm itself has been absorbed by the embryo (in which case, the embryo itself contains the stored nutrients, e.g. in the cotyledons, which will be described later).

Previously, when I introduced angiosperms, I focused on the seed, making the following points:

(A) Angiosperm seeds are contained within a protective covering or vessel (gymnosperm, you recall, means “naked seed”). In peas, for example, the vessel is the pod—a single carpel, or modified leaf[19]. Do not confuse the seed coat (on all seeds, e.g. the papery covering of Spanish-type salted peanuts) with the diagnostic modified-leaf covering that occurs only around angiosperm seeds (e.g. the hull on whole-shell peanuts).

(B) Double fertilization (with the partial minor exception noted) occurs only in angiosperms and forms the endosperm—in addition to the union of sperm and egg, (usually) three other haploid nuclei fuse to form the endosperm. The endosperm often persists in the mature seed to provide a nutritive source for the embryo, especially in monocots.[20]

We have gone forward from the seed through germination to the mature plant. Now I would like to focus on the formation of the seed, which occurs within the flower. First, let us look at the parts of a flower.

Structure of the Flower

POWERPOINT SLIDE: Flower, with parts identified. An emphasis is placed on the synonymy of microsporophyll and stamen; megasporophyll, carpel.

What we might think of as a typical, unmodified flower, such as that of a lily or flax, is made up of four sets of flower parts: (A) sepals, (B) petals, (C) stamens, and (D) pistil or pistils. The life cycle chart at the end of this topic includes a labeled drawing of a flower. The definitions, <u>taken from another source</u>, follow:

---

[19]The example of a carpel (the pea pod) is chosen because it is so easy to visualize. In the modern angiosperms, the carpels are completely sealed by the fusion of the epidermal layer. It is believed that the carpels of the first angiosperms were sealed by secretion. For a lead into that literature, see *Science* 286: 947-905 (1999)

[20]We will divide angiosperms into two groups, monocots and dicots. See the chart at the end of Topic No. 3 for a summary of the differences between these taxa. Distinguishing traits will be introduced at the relevant time. Note that our treatment is an oversimplification, as discussed in Topic 1 Progress in understanding the relationships among angiosperms has been rapid since about 1999, again thanks to molecular analyses. Three basal lineages (with a total of ca. 200 extant species) diverge near the base of the angiosperm family tree: the Amborellaceae (represented by only a single species in which the carpels are not fused!), the Nymphaeacea (water lilies), and the Illiciaceae (star anises, at least some with only a partially fused margin). These basal lineages should be considered primitive sisters of the ancestors of other modern angiosperms. The remaining angiosperms fall into three taxa: the magnoliids (perhaps 10,000 species, including magnolia, avocado, sassafras, and many others that historical treatment places at the base of dicots), the monocots (ca. 65,000 species), and the eudicots (ca. 180,000 species). As mentioned, we will simplify, as we often do, to cover the spectrum of biology that we must. See *Trends in Plant Science* 5: 330 (2000) or *National Geographic* July 2002: 103.

"Sepals. Sepals, collectively called the calyx, are the outermost parts and are commonly leaflike and green, but they may be colored like the petals and have a thinner texture, in which case they are described as being petaloid. In the unmodified flower, they are all alike in size and shape. The sepals enclose the flower in bud and or may not persist for the life of the flower. You are probably familiar with strawberry sepals, because they are conspicuous and remain attached to the fruit.

"Petals. Petals, collectively called the corolla, normally occupy a position in the flower between the sepals and the stamens. Petals are commonly delicate in texture and are often colored. They are often larger than the sepals, and they may be shed soon after the flower opens. Their color or fragrance may attract insects. The sepals and petals together make up the perianth, or floral envelope, a term that is especially useful when the distinction between sepals and petals is not obvious (e.g. in tulip flowers).

"Stamens. Stamens, collectively called the androecium, are the male reproductive parts of the flower and occupy a position inward from the perianth. They vary widely in size and number. Each stamen usually consists of two parts: (1) the anther, the sac-like part, which contains the pollen, and (2) the filament, or stalk which connects the anther to the floral axis or some other part.

"Pistils. Pistils, collectively called the gynoecium, are the female reproductive parts of the flower and occupy a central position. The gynoecium may consist of a single pistil, as in the lily, or several or many pistils, as in the buttercup. Each pistil usually consists of three parts: (1) the stigma, the pollen-receptive part at the summit, which may be single or variously lobed or branched; (2) the style, the stalklike portion below the stigma; and (3) the ovary, the enlarged portion at the base, which contains one or more ovules or immature seeds. In some pistils the style may be lacking, but the stigma and the ovary are essential to the functioning of the organ.

"The basic unit of construction of a pistil is the carpel, which is a single megasporophyll, or modified seed-bearing leaf. A pistil may consist of a single carpel, as in the sweet pea, or of two or more carpels partly or completely joined together, as in the lily (three carpels) or the mustard (two carpels). One can usually determine the number of carpels in a pistil by sectioning the ovary and counting the number of partitions or rows of ovules or seeds (placentae) or by counting the number of styles or stigmas."

If a flower contains separate carpels (pistils), it is called an apocarpous flower; if it contains a single pistil that consists of two or more united carpels, it is called a syncarpous flower.

From the model angiosperm flower, many deviations occur. A central point is that flowers are useful as taxonomic tools, a point that Linnaeus brought home to us, as discussed in the Introduction. (Wood is generally too conservative evolutionarily;[21] i.e., quite different plants have similar structures. On the other hand, vegetative characteristics are generally too plastic, being subject to variation if grown under different environmental conditions. Floral morphology and anatomy are "just right.")

---

[21] Obviously, I am painting with a very broad brush and soiling the truth. As an example of the taxonomic value of wood anatomy in the distinction of closely related plants, consider the two major genera in the walnut family. *Juglans* (walnuts) has partitions in the pith of branchlets, whereas the other genus, *Carya* (hickory, pecan) lacks these partitions. As an example of the taxonomic value of vegetative characteristics in the distinction of closely related plants, consider *Vitis rotundifolia* (the muscadine), which has unbranched tendrils. In contrast, Euvitis grapes (i.e., the source of most wines, grape juice, raisins, dessert grapes) have forked tendrils. These and all the

Actually, flowers are prime taxonomic tools, so let us briefly review some of the characteristics that give an indication of how “advanced” a flower is. (In biology, “advanced” has a specific meaning, which is “appearing late in the fossil record.” It does **not** mean “improved,” “more elaborate,” “complicated,” or “efficient.”)

Trends in Floral Evolution

(A) Reduction in the number of parts. *Magnolia*, one of the oldest angiosperms, has many petals.

POWERPOINT SLIDE: *Magnolia* (near Strozier Library, FSU)

The most advanced flowers have few parts. Sometimes by looking at the arrangement of parts in advanced flowers, it is possible to infer where, e.g., a ring of stamens “should” have been. If a flower is hermaphroditic, i.e., it has both “male” and “female” parts, it is called a perfect flower (e.g. the flower shown). Imperfect flowers lack either pistils or stamens. In some cases, both types of imperfect flowers are borne on the same individual plant. Such a plant, e.g. all squash (and many other members of the Cucurbitaceae (gourd family)), is monoecious (“one house”).

POWERPOINT SLIDE: Monoecious vs. dioecious (self-made)

POWERPOINT SLIDE: Cucumber flowers, cv Orient Express (north Leon County, Florida)—an example of a monoecious[22] plant.

In a few species, e.g. marijuana, some of the plants will bear “male” flowers, and others, “female” flowers; such a species is called dioecious (“two houses”).

---

other exceptions that one might imagine—not to mention the auxiliary use of these characteristics in descriptions—do not invalidate the general truth as stated in the text of these notes.

[22] The definition of *monoecious* given in your text is “having the anthers and carpels produced in separate flowers on the same individual.” The definition of *dioecious* given in your text is “unisexual; having the male and female (or staminate and ovulate) elements on different individuals of the same species.” I define these two words in the same way (as does Campbell (whose book is used for the 2000-level courses here at FSU))—i.e., these words apply to the sporophytes of *flowering* plants. However, you should be aware that this most restrictive definition is not used by everyone. For example, Berg, in his nonmajors botany book, applies these words to all seed plants. Ditto, for Scagel et al. in their advanced plant morphology book. Even further afield, one dictionary lists monoecious as a zoological term synonymous with hermophroditic.

As far as I am aware, no one has ever applied these two words to the gametophytic generation of plants. Almost identical terms are used, however, by some to describe the analogous condition with gametophytes. (For example, Scagel et al. define *dioicous* as “condition of bryophyte gametophyte in which the gametophore bears only one kind of sex organ; unisexual.)

POWERPOINT SLIDE: *Cannabis sativa* ("male," left) and *Cannabis sativa* ("female," right) (Linnaeus' specimen, courtesy of L. Anderson).

The typical situation, however, is for a flower to be "complete," that is, to have the four types of flower parts. Sex may not always be fixed, however. Interestingly, in the case of kaki persimmons.[23] at least in some of the cultivars (abbreviation for '*culti*vated *var*iety') investigated early in the 20th century, some plantings would sometimes become fruitless because the flowers were producing only "male" parts.

POWERPOINT SLIDE: Kaki persimmon, cv Fuyugaki (Havinam Orchards, east Leon County, Florida).

POWERPOINT SLIDE: Native persimmons (North Leon County, Florida).

Interestingly, in the case of *Musa* (banana[24]), completeness of the flower changes over the developmental course of the inflorescence.

POWERPOINT SLIDE: Banana inflorescence showing fruit at top and scars from flower abortions at bottom. (north Leon County, Florida).

---

[23] *Diospyros kaki* (the oriental or kaki persimmon, shown) and *D. virginiana* (the persimmon native to Tallahassee) are fascinating plants. Literally, "diospyros" means "fruit of the gods." I could go on for days, and sometime I might, but for the moment, let me simply note that many have been captivated by this plant. On November 4, 1862, George H. Ewing (Company K, 20th Michigan Volunteers (Infantry)) discusses stealing foods from Southern folks ("best pork we could eat," "we take every thing that we can get hol of," "get a goose," "lots of honey," "I dont see what thay are a going to live on for the nex coming year it loock hard you can bet to see the girls and wimons and Childen cry when we com") but he had time to worry about the future ("I will put in some persimons seeds you must put them in the ground this winter and let them freeze.") (Note that George understood that persimmon seeds have a chilling requirement in order to germinate. More will be said on this topic later.) By January, his original unit of 96 men could only muster 35. George himself had a bout with dysentery in October and stepped on a nail in January. George never saw those persimmons grow (from his friend Smith J. Williams, to his sister Susan, January, 1864, ". . . you wished me to write whether george realized his situation. I dont think he did he was struck by a shell and killed instantly he never moved or groaned after he was hit. we were in the rifel pits at the time.") Quotes from J. T. Greene (ed.) (1994) *The Ewing family civil war letters*. Michigan State University Press, East Lansing, MI.

My daughter, who is degreed in anthropology, points out that persimmons were important long before they were "discovered" by whites. Perhaps you would be interested in reading John Swanton's collection of Native American myths, which include something akin to a persimmon diety. Or, perhaps, the book by John White, who lived early at Roanoke—persimmon fruits were eaten fresh, or dried into a kind of fruit leather, or made into a sweet bread by mixing the pulp with maize by many Indians in the U.S. Southeast. John Casada (*South Carolina Wildlife* 5, 1994), like Bill Outlaw, likes to eat these fruits also ("succulent fruits . . . to please the most finicky gourmet" or "stuff from which gustatory dreams are made."). He goes on to point out that persimmon wood is so strong that it has been used for a variety of tasks, such as in the crafting of agricultural implements (e.g., moldboards—the part of the plow that "turns" the soil), croquet mallets and balls, and even golf club heads. (Most of these uses have been lost with the development of composites and metals.)

[24] According to some counts, banana (including plantain) annual production is 95 million tons and provides the main food source for one-half billion people. This count would place banana as the fourth-largest staple food crop. (See *Trends in Plant Science* 6: 454 (2001)).

Why would there be an evolutionary trend toward reduction in number of flower parts? I put this question to FSU's Dr. Alice A. Winn and several FSU graduate students, who provided an explanation that I condense here: (a) Evolution of more efficient pollination systems permits less resource investment in pollen, so anther size or number could be reduced (similar arguments could be given for other parts). (b) Complete loss of functional parts (i.e., imperfect flowers) would promote outcrossing.[25]

(B) Cyclic arrangement of parts, each kind at a separate level. Arrangement in whorls is more advanced than a spiral arrangement (spiral arrangement is seen, for example, in buttercup, which is reminiscent of a pinecone). The lily flower that we saw had parts in whorls.

POWERPOINT SLIDE: Spiral insertion of floral organs vs. organs arranged in whorls. (graphics courtesy of K.Womble.)

(C) Fusion of organs. We have already noted the fusion of the corolla in flowers, which is more advanced than having separate petals. On the other hand, the carpels can be fused even if the corolla is not. Sometimes, the fusion of parts may give rise to a different interpretation.

Dr. Winn and her colleagues suggest that fusion of parts confers specificity to pollen vectors and hence "refuses the reward" to those other visitors that do not have the "right" feeding apparatus.

---

[25]Even plants that have perfect flowers or monoecious species may have evolved means to promote outcrossing. As an example, pecan (from the Illinois *pakani*, meaning stone; *Carya illinoinensis*) produces flowers of both sexes, but the pollen is released either too early or too late, generally, for self-pollination. For this reason, it is recommended that cultivars for cross-pollination be selected carefully for timing of pollen release and pistil receptivity.

Historically, pecans have been an important dooryard plant in north Florida, and there is limited commercial production. Indeed, the name of Talpeco Road (perpendicular to Monroe, about a mile north of I-10) is not at all some Indian-derived word but instead is a contraction of *Tal*lahassee *Pe*can *Co*mpany. In our neighboring state Georgia, pecans are more important, and the production there is about 100 million pounds per year. A tiny part of this production comes from a few trees set out by my great-grandfather, J. S. "Buck" Sutton, after he bought his place from Old Man Steve Lewis in 1878. (As an aside, Old Man Lewis sold an adjoining farm to another one of my great-grandfathers, Sam Watson, but Old Man Lewis kept most of his property. Interestingly Old man Lewis did not leave much to his son, Lonnie, who himself acquired a fortune. It is a twisted story: Old Man Lewis' daughter Delia married L. G. Outlaw, my grandfather and the son of W. H. Outlaw. Delia heard the rooster crow for her one evening and, by the power of this omen, expired in the hours following; she had issued progeny. L.G. then married Della, one of Buck's daughters. Buck himself was prosperous, but he was positioned between two tragic generations—his father died of dysentery at Staunton (no battle honors, no tales of bravery, just graves containing multiple sons, fathers, and husbands) and his daughter Della, my grandmother, was murdered when she was a young woman. But I digress . . . .) Pecan culture has moved westward, to drier climates where scab is not such a problem. Actually, the pecan is the state tree of Texas and was so loved by Gov. Hogg that he requested that one be planted at his grave. (Gov. Hogg is often remembered because he named his daughter Ima (a shortening of Imogene); contrary to popular belief, he did not have another daughter named Ura.)

POWERPOINT SLIDE: Example of fused corolla (*Datura inoxia*, undisclosed location, latitude, ~ 30° 23’ N).

POWERPOINT SLIDE: Example of fused filaments (okra, north Leon County, Florida).

POWERPOINT SLIDE: Inferior and superior ovaries &c. (modified from Fig. 12-9 of Wilson, Loomis, and Steeves).

The left panel of this slide shows a flower with a superior ovary. All the flower parts—including the pistil—are attached to a common base, the receptacle. The center panel also shows a superior ovary, but the flower parts have fused, forming a floral tube. This is an intermediate evolutionary position. Finally, on the right, the floral tube is fused with itself, the sepals, petals and stamen appear to grow from the top of the ovary. Thus, the ovary appears to be below the rest of the flower and is called inferior, the advanced condition.

(D) Away from parietal placentation.[26]

POWERPOINT SLIDE: Marginal placentation (pea, with a single carpel, Fig. 53 b of Porter) + free-central placentation (chickweed, cross section) (Fig. 57 of Porter) + basal placentation (e.g. grasses and roses) and free-central placentation (e.g. *Primula*, primrose) (Fig. 58 or Porter).

The carpel is a single modified leaf (recall the pea pod). If this carpel were unfolded, the point of seed attachment would obviously be along the leaf margin, which is parietal placentation (the primitive condition). In fact, the placentation in pea is marginal, and—because of the way that the carpel margin is fused—the placentation is also parietal.

Observe that several carpels can fuse (to form a “compound” ovary, an advanced characteristic) and that further changes can result in the more advanced placentation types.

POWERPOINT SLIDE: Placentation types, evolutionary series (Fig. 6 of Lawrence).

It is important to note that some, but not all, botanists accept the interpretation given. In a general course like this one, our time constraints do not permit more than an overview.

---

[26] In this course, we will not distinguish between marginal and parietal placentation, and, *for our purposes*, you may consider any simple, longitudinal ovary (composed of a single carpel) to exhibit parietal placentation.

Dr. Winn and her colleagues suggest that seeds may be better protected from seed predators if placentation is not marginal.

(E) Away from regularity.

The flowers that we have examined so far have displayed radial symmetry. That is, if you were to look at these flowers from the top, it would be possible to "slice the pie" in a number of ways and get equal halves.

POWERPOINT SLIDE: Garden pea flower (schematic) (Fig. 12-11 of Wilson, Loomis, and Steeves).

POWERPOINT SLIDE: *Salvia*—irregular flower (north Leon County, Florida).

POWERPOINT SLIDES: Floral development—custom, but using a diagram from *Scientific American*, Nov, 1994), emphasizing floral organ identity.

What stimulates flowering? Why does a normal vegetative meristem turn into a floral meristem? In brief, we know a great deal about the environmental factors that result in flowering, but how these factors play out is species specific. Plants must be of a certain physiological age before any influence will cause them to flower. Said another way, a plant has a period of juvenility in its development. Some plants are exquisitely sensitive to photoperiod—some require short days, and some require long days. Often, a period of cold weather is necessary, but a period of water stress can sometimes substitute. Even physically damaging a plant might cause it to flower. In contrast to the effect of environmental factors, we know less about the signal propagation.

POWERPOINT SLIDE: One pear has reached its chilling required, the other not. (North Leon County, FL)

We know from grafting experiments that a signal can be sent from a leaf to the meristem, where it is effective. We know that the signal moves in the phloem. But—despite decades of work—we do not know the chemical identity of **the** signal ("florigen"), but in some species, it seems to be simply one of the gibberellic acids. In other cases, maybe the signal is not one simple chemical but is encoded in the ratios of many known chemicals.

POWERPOINT SLIDES (CONTINUED): Floral development—custom, but using a diagram from *Scientific American*, Nov, 1994), emphasizing floral organ identity.

Floral morphology is studied actively by plant developmental biologists, and now we turn to a few comments concerning their findings. In brief, a floral meristem proceeds in three steps. **First**, there are genes, whose expressions determine the kind of meristem (floral or vegetative). **Second** in this cascade is the expression of genes that position the appendage. **Third**, and our focus here, are three major classes of genes set the pathway for development of the floral appendages. For example, if certain classes of gene A are expressed alone, the appendage will take the characteristics of sepals, typically the first whorl. If classes A and B are expressed, the gene products "turn on" genes involved in petal development and turn others off; B[27] and C, stamens; C alone, carpels. In addition to the genes that determine the types of floral whorls, many many genes act as promoters or repressors of flowering. Overall, an implication of developmental pathways or cascades is that a trait selected independently (e.g. petal fusion to eliminate foraging on nectar or pollen by an inefficient vector) *might* be carried over to fusion of other floral parts, if no deleterious effects result. Thus, it is not necessarily valid to "demand" in isolation that a particular trait be more "fit."

The preceding information on flowering has been discovered, in large measure, through research on a small member of the mustard family, *Arabidopsis thaliana*. *Arabidopsis* is a model system for many kinds of studies in plant biology (analogous to the fruit fry, the mouse); it was the first plant to have a sequenced genome.[28] *Arabidopsis* was selected as a model organism because it is small and does not demand stringent conditions for successful culture (i.e., it is inexpensive and easy to grow), it has a rapid growth cycle (6–8 weeks from seed to seed), and it has a small genome size (smaller gene families or less redundancy implies a greater likelihood of observing a phenotype).

As organ development can be changed by a single ("controller") gene mutation, we can explain the development of some horticultural plants (as I mentioned earlier, horticultural varieties often do not provide "typical" examples of plants). Let us take the case of roses, which are dicots. As you would expect from our discussions, roses should have 4 or 5 petals, or integral multiples thereof. This apple blossom is an example of a member of the rose family:

POWERPOINT SLIDE: Apple blossom (north Leon County, Florida).

---

[27] As noted, B is involved in petal and stamen specification. Interestingly, this class of homeotic genes is found in gymnosperms, where it has a role in the microsporophyll development. Thus, this class of genes has an origin in the common ancestor of gymnosperms and angiosperms (it is absent in other plants). For more, see Crit Rev Plant Sci 23: 129 (2004).

[28] In 2002, the draft sequences of *O. japonica* and *O. indica* rice were published in *Science* magazine. This was an important accomplishment for many reasons. First, rice is an important food crop. Second, the rice genome is relatively small (430 Mb, only 3–4x the size of that of *Arabidopsis*), and it also serves as a model for the larger genomes of other important cereals (e.g. wheat has 16,000 Mb).

The Cherokee rose is the state flower of Georgia. As it is very ornamental, it is a good example with which to compare cultivated roses (and its use permits the introduction of another important concept (invasive species[29]) in an oblique fashion).

POWERPOINT SLIDE: Cherokee rose, overview and close-up (north Leon County, Florida).

What could be more "American" than the Cherokee rose? Much . . . .

POWERPOINT SLIDE: Trail of Tears, probably southern Missouri, I forget exactly.

POWERPOINT SLIDE: Some latter-day stragglers (taken in Missouri of specimens originating in Georgia).

The genocide of the Cherokees[30] is, as you well know, memorialized. These Amerinds are synonymous with "native." The contribution of their name to this rose would imply by association that it is native also, but it is not. It is a native of China, an introduced invasive species. In fact, 37% of the vascular plant species in Florida are *not* native. My friend Kathy Burks estimates at about one in five the chance that any particular roadside plant in Leon County is not native. These exotic species displace native plants and change the plant-community structure. As you infer, this problem is not simply limited to the plants that have "bad-guy" reputations (e.g. *Kudzu*, a legume; chinaberry, *Melia*,

---

[29] For more information, read *Strangers in Paradise: impact and Management of Nonindigenous Species in Florida*. Island Press, Washington, D.C. (1997).

[30] Georgia volunteer Z. A. Zele (later a Confederate colonel), reflecting on the 1838 removal, "I fought through the Civil War and have seen men shot to pieces and slaughtered by the thousands, but the Cherokee removal was the cruelest work I ever saw." J. G. Burnett, a former army private, tells his eightieth birthday story on December 11, 1890, "Being acquainted with many of the Indians and able to fluently speak their language, I was sent as interpreter into the Smokey Mountains country in May 1838, and witnessed the execution of the most brutal order in the history of American warfare. I saw the helpless Cherokees arrested and dragged from their homes, and driven at the bayonet point into the stockades. And in the chill of a drizzling rain on an October morning I saw them loaded like cattle or sheep into . . . wagons and start toward the west. One can never forget the sadness and solemnity that morning. Chief John Ross led in prayer and when the bugle sounded and the wagons started rolling many of the children rose to their feet and waved their little hands good-bye to their mountain homes, knowing they were leaving them forever. . . . murder is murder whether committed by the villain in the dark or by uniformed men stepping to the strains of martial music. Murder is murder and somebody must answer, somebody must explain the streams of blood that flowed in the Indian country in the summer of 1838. Somebody must explain the four thousand silent graves that mark the trail of the Cherokees to their exile. I wish I could forget it all, but the picture of . . . wagons lumbering over the frozen ground with their cargo of suffering humanity still lingers in my memory." (Quotes from Mankiller, W., and M. Wallis (1993), *Mankiller: a Chief and her People,* St. Martin's Press, New York.) Now, as one botanist to another, explain to me why "Some 2,200 Cherokees fought on the Union side during the Civil War. A total of 3,530 men from the Indian nations served in the Union army, and 1,018 of that number died during their enlistment. Thus 28.8 percent or more than one-fourth of all Indians in the Union army died of disease, were killed in battle, or died of wounds. No state had a higher percentage of losses than the Indian nations." (W. G. Gaines (1989), *The Confederate Cherokees. John Drew's Regiment of Mounted Rifles*. Louisiana State University Press, Baton Rouge).

in the Mahogany family; or mimosa, an erroneous name for the "silk tree," also a legume). Perhaps one of the most serious exotic pests in Florida is Brazilian pepper, which takes over pine rock barrens in the Everglades—so much so that it is better to continue to farm the land on the edge of the Everglades than to let it become overrun with Brazilian pepper and be a seed source for the adjacent areas.

POWERPOINT SLIDE: Brazilian pepper, inset and whole plant (left, *Schinus terebinthefolius*) and the silk reed (right, *Negraudia regnaudiana*) (Edge of the Everglades).

To return to flower structure—the point is that an unselected rose has five petals (or it is 5-merous). Because the "master" genes, as discussed, control floral development, a single mutation can result in large morphological changes[31] (analogously to the homeotic genes that direct *Drosophila* development, which you have studied in BSC 2012). In this way, petal proliferation results in the cultivated roses and in the camellias (tea family).

POWERPOINT SLIDE: Cultivated roses (from the governor's garden, Tallahassee).

POWERPOINT SLIDE: *Camellias* (from a show at Tallahassee Mall).

Examples of Advanced Families

(A) Orchids[32] are the second-largest family of flowering plants and exhibit many advanced characteristics. They have three fused carpels, an inferior ovary, usually one (sometimes two) stamen, and irregular flowers. The stamen, style, and stigma are fused into a single unit.

POWERPOINT SLIDES: 4 orchids
a-c. from the greenhouse of my father's sister, the late Lena Belle Outlaw
d. from the Missouri Botanical Garden.

---

[31] The situation in which a single gene alters many characteristics is called pleiotropy. In your consideration of "why a certain trait is favored," bear in mind that you have probably considered the sporophyte only. (Some genes are expressed only in the gametophyte, some only in the sporophyte, and some in both.) In the case of the fern *Athyrium distentifolium*, a single locus controls a large number of morphological traits. It turns out that one allele (A^F) is favored in the gametophytic generation and the other allele (A^D) is favored in the sporophytic generation. This is, therefore, a case of antagonistic pleiotropy, and simple analysis of the sporophytic generation would never answer your question.

[32] from Latin *orchis*, from Greek *orkhis* for testicle.

At one time or another, we have touched on several important monocots (e.g. wheat, maize), so, as a matter of interest, I will show examples of another exceedingly important moncot, rice, and of sugar cane, a very important monocot, especially to Florida.

POWERPOINT SLIDE: Harvesting rice in Sierra Leone.

POWERPOINT SLIDE: Rice field (near Crowley, LA)

POWERPOINT SLIDE: Konrico Rice Mill—the oldest rice mill in continuous operation in the U.S. (Crowley, LA)

POWERPOINT SLIDE: Sugar cane field (near Abbeyville, LA)[33]

(B) Asters (composites) are the largest family of flowering plants and the most advanced dicot family. Ray flowers (looking superficially like petals) are sometimes sterile or lack stamens; in other flowers, the stamens are fused to each other and to the corolla; sepals are absent or reduced. The ovary is inferior.

POWERPOINT SLIDE: Composites (flower schematic showing composite nature of inflorescence) (Fig. 19-11a of Raven, Evert, and Curtis).

POWERPOINT SLIDES: 6x composites

a. *Gazania*, from Tübingen University Botanical Garden,
b. golden aster (*Heterotheca*)
c. *Gerbera* (daisy) + dissected *Gerbera* + ray flower of *Gerbera* from collection of my mother, the late Christine Outlaw
d. goldenrod (*Solidago*) (north Leon County, Florida)
e. cv Mammoth sunflowers with subadult human female for scale—note at the lower left that the female is standing near the top of a ladder (north Leon County, Florida).

A dicot of extreme importance to Florida deserves at least one slide! . . . hence, this photograph of a bearing citrus plant.

POWERPOINT SLIDE: Ponkan mandarin (from the Citrus Germplasm Repository, Leesburg, FL)

[33] I have a special interest in sugar cane. Please visit http://www.southernmatters.com. Learn how plant biology, traditional food production, and food technology blend.

Confusion in the Interpretation of Floral Parts

A warning: interpretation of flowers and flower parts is not always as simple as it has been described here.

POWERPOINT SLIDE: Dogwood[34] flower (north Leon County, Florida). White petal-like structures are bracts, not petals.

POWERPOINT SLIDE: Tulip field (near Lisse, the Netherlands). Petals and sepals are identical and colored.

POWERPOINT SLIDE: Rape seed field (Thüringer Wald, Germany)

POWERPOINT SLIDE: *Fuchsia* "Dark Eyes" (Callaway Gardens, Georgia).

POWERPOINT SLIDE: *Amorphophallus titanum*, with Hugo de Vries[35] for scale (inflorescence—several flowers) (Fig. 9-15 Raven, Evert, and Eichhorn).

The size of flowers ranges from very small to larger than a human being.

POWERPOINT SLIDE: The syconium of a common edible fig (*Ficus carica*, north Leon County, Florida). The pistillate flowers point inward from the walls of the syconium, which comprises a fused shoot system.

Angiosperm Life History[36,37]

---

[34]This footnote was copied directly from http://www.bright.net/~dogwood: "The word 'dogwood' comes from a custom in England to wash dogs with a concoction made from dogwood bark to cure mange.
"There is a legend, that at the time of the Crucifixion the dogwood had been the size of the oak and other forest trees. So firm and strong was the tree that it was chosen as the timber for the cross. To be used thus for such a cruel purpose greatly distressed the tree, and Jesus, nailed upon it, sensed this, and in his suffering said to it: Because of your regret and pity for My suffering, never again shall the dogwood tree grow large enough to be used as a cross. Henceforth it shall be slender and bent and twisted and its blossoms shall be in the form of a cross . . . two long and two short petals. And in the center of the outer edge of each petal there will be nail prints, brown with rust and stained with red, and in the center of the flower will be a crown of thorns, and all who see it will remember."

[35]In 1890, this botanist, de Vries, confirmed the botanist Mendel's theories on numerical ratios and plant hybridization. Again, my grand explanation of everything is to count, count, count (all the while tempering that obsession with the realization that all things that need counting cannot be counted, and that some things that can be counted easily don't need to be counted—thanks, e, for allowing that bit of plagiarism). To zoom forward by a century, I quote FSU professor Susan Blessing (2005): "But if you can't do math or math is scary, science is not for you."

[36]The "textbook" definition of alternation of generations, as it applies to plants, is copied from *New Phytologist* 152: 365 (2001) to provide you with an alternative explanation: "**Diploid sporophytes and haploid gametophytes.** Alternation between diploid sporophytes and haploid gametophytes is universal among plants (although the relative structural complexity of the two generations varies from group to group, and . . .). In mosses . . ., the haploid gametophyte stage is free-living and perennial whereas the sporophyte is relatively ephemeral and completes its entire development attached to the maternal gametophyte. In ferns, both generations

The remainder of our time on this section will be devoted to filling in the gaps represented by this slide—going from ovule to seed (b $\rightarrow$ a). Please note that angiosperm life history is covered well in any introductory text. In addition, there is a summary drawing in these notes.

The Male Gametophyte

POWERPOINT SLIDE: Maize anther (from the *Plant Cell*).

POWERPOINT SLIDE: Microsporogenesis and microgametogenesis.

Microsporogenesis (literally, origin of small spores) is the formation of microspores within the sporangia, or pollen sacs, of the anther (a–c in the following sequences).

Microgametogenesis (literally, origin of small gametes) is the development of microspores into the microgametophyte (= pollen grain) (c–h in this sequence). (The microgametophyte contains the gametes.)

As seen in the previous slide, within the anther, four groups of fertile (= sporogenous) diploid cells differentiate. The outer cells are sterile and serve as a nutritive source.

(c) The sporogenous cells differentiate into microspore mother cells (= microsporocytes); each spore mother cell divides meiotically to give rise to a tetrad of . . .

(d) single-celled haploid microspores. (Note that between tetrad formation and pollen-grain formation, the exact sequence of events—e.g. separation of the individual microspores from each other—may vary.)

The microspore enlarges and has a complex cell wall (which often is sufficient to identify the plant).

(e) Microgametogenesis begins by division of the microspore into two cells—one is the vegetative (or tube) cell; the other is the generative cell. In most species (but not maize), the gametophyte is in this two-celled stage when it is released from the anther.

(f) After resting on the stigma of the pistil, the generative nucleus divides to give rise to two male gametes (= sperm), and the pollen tube grows as will be discussed later.

---

are free-living, although it is the sporophyte that is perennial and large whereas the gametophytes are smaller and relatively ephemeral. As is well known, the gametophyte stage of seed plants is even smaller and, indeed, the entire female or megagametophyte develops endosporically, and the male or microgametophyte completes most of its development within the confines of the microspore wall."

[37] The sequence of events is typical of about 70% of angiosperms. Most of the differences are "trivial," but a few angiosperms (the Podostemaceae and some primitive groups) do not undergo double fertilization at all (V. Raghavan (2003) *New Phytologist* 159:565-583).

The Female Gametophyte[38]

Early in development, a single megasporocyte (= megaspore mother cell) arises in the nucellus.

POWERPOINT SLIDE: Ovule/megaspore mother cell (Fig. 15.24 of Raven and Curtis).

Megasporogenesis is the process of megaspore formation within the nucellus (= megasporangium).

Megagametogenesis is the development of the megaspore into the megagametophyte. (The megagametophyte contains the gametes.)

Early in development, a single megasporocyte (= megaspore mother cell) arises in the nucellus. The nucellus develops one or two covering layers, the integuments. Note the opening called the micropyle.

POWERPOINT SLIDES: Megasporogenesis/fertilization (modified from Fig. 15.23c–j of Raven and Curtis).

(c–d, keyed to slide) The diploid megaspore mother cell divides meiotically to form four haploid megaspores, which are arranged in a linear tetrad.

(e) Three nuclei disintegrate; the one distal to the micropyle survives.

(f–g) Megagametophyte. The megaspore enlarges at the expense of the nucellus and undergoes three mitotic divisions to form two groups of four nuclei each.

(h) One nucleus from each pole moves to the center. These two nuclei are the polar, or fusion, nuclei.

The three nuclei at the micropylar end become the egg apparatus, which consists of an <u>egg cell</u> and the remaining two nuclei (called synergids). The three nuclei at the other end are the so-called antipodals. Cell-wall formation occurs around each of these nuclei, leaving a central binucleate cell (i.e., a 7-cell structure (with 8 nuclei) = mature female gametophyte = embryo sac). (Compare your notes with the microgametophyte.)

<u>Fertilization</u>

---

[38] The angiosperm female gametophyte often goes by the name of “embryo sac.” I use “gametophyte” to keep the terminology parallel with lower plants. Embryo sac is not such a bad name, however, because the female gametophyte in angiosperms is so small and does not even contain remnants of an archegonium. Gametophyte does not fit in those cases in which asexual reproduction occurs through failed meiosis of the megaspore mother cell, which gives rise to the embryo sac, which—through mitosis—gives rise to the embryo.

The pollen grain can be transferred to the style by a variety of vectors, including wind (the primitive condition). The pollen grain germinates, as you recall, and forms a tube. (If the generative nucleus has not yet divided, it does so now to form two sperm cells.)

The pollen tube grows[39] down through the style of the pistil (either through a channel between cells or in the thick cell walls). We believe that synergids release a chemical and the pollen tubes grow in response to the concentration gradient of this chemical. Commonly, the pollen tube enters the ovule through the micropyle and penetrates and kills one of the synergids. A hole develops near the end of the pollen tube. Two sperm[40] and the tube nucleus are released.

Ultimately, one of the sperm nuclei unites with the two polar nuclei and one unites with the egg nucleus. The latter is true fertilization (= syngamy). The triploid nucleus (= 2 polar + 1 sperm, all haploid) gives rise to endosperm.

the zygote → the embryo[41]

the triploid nucleus → endosperm

the integuments → the seed coat

the ovary wall (and other) → the fleshy part of the fruit

POWERPOINT SLIDE: Angiosperm life cycle for recapitulation (custom-made)

Angiosperm Development.

---

[39] Pollen-tube growth is impressive. Consider maize: The pollen grain lands on the silk tip, it germinates and the tube grows at 1 cm·hr^{-1} through the silk to the nascent kernel.

[40] These are indeed cells with a membrane, as first shown by my major professor, D.B. Fisher, who was then a post-doctoral student with William Jensen at UC Berkeley. The sperm cells are inside the larger vegetative cell.

[41] The lecture text discusses the normal case, i.e., a seed has one embryo, and that embryo is formed from a zygote. A zygote, recall, is the product of syngamy; in other words, in a somewhat roundabout way, the new plant that grows from a seed is a more-or-less equal product of the sporophyte "parents." But plants are interesting. In some plants, the embryos arise from the nucellus (which is strictly maternal sporophyte tissue). That means that the embryo is exactly like the seed-bearing sporophyte. Thus, plants grown from such seeds are genetic copies of the mother plant, just as if the daughter plants had been propagated vegetatively. Plants that develop nucellar embryos often develop more than one ("polyembryony"), and sometimes the zygote-derived embryo will also survive. Thus, when the dwarfing, cold-hardy, *Phytophthera*-resistant citrus rootstock *Poncirus trifoliata* cv. Flying Dragon is propagated from seeds, "off-types" (i.e., those from sexual embryos) must be rogued. Fortunately, in this case, it is easy to identify the off-types, which have straight thorns. For more information on the formation of asexual embryos, including by means not discussed in this footnote, read the review by A. M. Koltunow (1993), Apomixis: embryo sacs and embryos formed without meiosis or fertilization in ovules. *Plant Cell* 5: 1425.

An example of a plant that you can grow "true" from seeds is Orlando tangelo, which you can buy in the markets in Florida in mid-winter. This is a genetically complex plant. Tang-elo is a combination of Tangerine (a name given to reddish mandarins, the name derives from Tangiers) + pumelo (for our purposes, essentially a grapefruit). I might talk later about growing citrus from seeds (as opposed to graftage), which has some advantages, but is usually discouraged.

Now, let us turn to the development of a plant from a seed. The embryo in the seed consists of

(A) a stemlike axis that bears

(B) one (for *mono*cot) or two (for *di*cots) cotyledons, which are the seed leaves. In most dicots, the food reserve is stored in the cotyledons at seed maturity, whereas in monocots, the reserve is still in the endosperm and the cotyledon serves to absorb this reserve for the seedling during growth.

Point B was discussed earlier and is emphasized in the following micrographs.

POWERPOINT SLIDE: Immature *Capsella* seed + mature *Capsella* seed (Fig. 20-5F of Raven, Evert, and Curtis).

Capsella is a dicot, and the immature seed has a great deal of endosperm, which is absorbed by the embryo during seed maturation.

POWERPOINT SLIDE: Longitudinal section of seed of wheat[42] (a monocot) (Fig. 20-4a of Raven, Evert, and Curtis). Be sure to follow the germination on this PPT!

Seed germination is, of course, important to the survival of the plant, not to mention the farmer and brewmaster. Timing of germination is all important. Wild plants often sense environmental cues. Seeds of temperate plants often require a period of cold, e.g. 1000 hours near 40°F, before they will germinate. This trait has an obvious adaptive significance—the seed "should" germinate in spring. Some seeds will germinate only after given a light treatment; again, the adaptiveness of this trait is obvious—should a small seed germinate too deeply in the soil, it could not emerge before the nutritional supplies were exhausted. Some seeds have a more special requirement (e.g. some must be acid treated, as they are when they pass through the digestive tract of a bird). A plant growth regulator, gibberellin[43], is a key player in seed germination of many, if not all, dicots and monocots. The embryo makes it when the seed is given water. Our knowledge is most complete in this regard for grass seeds, such as barley. In these plants, the GA diffuses to the cell layer just inside the seed coat (the aleurone layer) and stimulates this layer to make and secrete hydrolytic enzymes that break up the polymers in the endosperm. These hydrolytic products, sugars and amino acids, provide the "food" for growth. Gibberellin application to seeds overcomes the requirement for cold or light, indicating that this substance in an intermediate in the signal-transduction cascade that senses these environmental cues.

---

[42]White flour comes from the endosperm; wheat germ comes from the embryo; bran comes from the hard tissue (the pericarp) that surrounds the grain. (The wheat "seed" is actually an entire fruit, so the outer covering is not the seed coat, as it would be easy to think.)

[43]Gibberellin is a general name that refers to a class of naturally occurring heterocyclic compounds, which to date number 126 (see *Journal of Plant Growth Regulation* vol 20, 2001). (Some of this number may not act directly but must be converted to an active form first). The most famous of these is GA_3, which is often called gibberellic

Although it is somewhat peripheral to the question of seed germination, it is useful to note other functions that gibberellin has in plant metabolism. In a word, gibberellin causes cell elongation. Thus, it is involved in many aspects of normal development, such as typical shoot elongation. Plants that have an impaired ability to make or use gibberellin remain short (i.e., as rosettes[44]).

(C) apical meristem of the root and shoot on the axis below and above cotyledon(s) (meristematic cells are physiologically young and capable of repeated divisions).

(D) epicotyl ("epi-" means "above"), the axis above the cotyledon(s) (the epicotyl together with the young leaves is called the plumule).

(E) hypocotyl ("hypo-" means "below"), the axis below the cotyledon, which becomes the radicle or embryonic root at tip.

Now I would like to show some morphological aspects of emergence.

POWERPOINT SLIDES: Germination (epigeous, castor bean, Fig. 20-2b of Raven, Evert, and Curtis and soybean, FSU lab + hypogeous, pea, Fig. 20-2 of Raven, Evert, and Curtis and *Vicia faba*, FSU lab).

In summary, you do not need to know the names of any of the representative plants, but you do need to know the generalities.

Dicots typically use the cotyledons themselves (part of the embryo) as a food reserve for germination and growth. Most often, in dicots, the endosperm does not persist to seed maturity.

In many plants, the cotyledons emerge from the soil, expand manyfold, and become photosynthetic (i.e., form the "seed leaves").

---

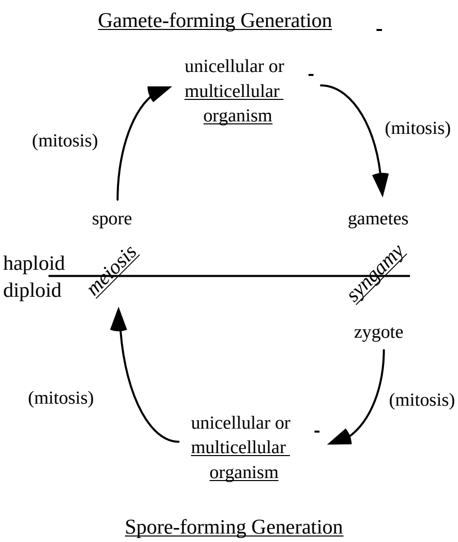
acid. Gibberellins have many physiological effects, and some of the particular gibberellins are more effective than others in eliciting certain responses, indicating a differentiation of function.

[44]Some agricultural plants are rosettes, and they are "released" from this growth form by a cold treatment (i.e., winter) or by a light treatment. As an example, cabbages are actually biennials. They evolved to produce a mature plant full of stored energy during the first year and, during the second year, to bolt and flower. Just as gibberellins overcome the cold or light requirement of seeds, gibberellins can be used to overcome the cold or light treatment for development of sexually mature plants.

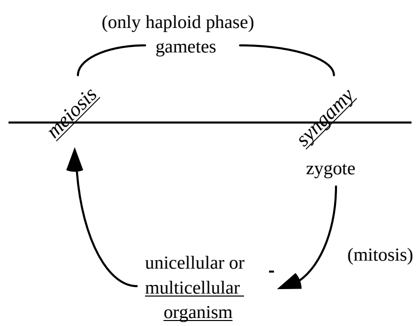
Such a powerful substance has not, of course, been overlooked by agriculturists. Judicious (that's a key word) application of gibberellin enhances blueberry production. It also causes larger fruit when applied to manmade seedless fruits, such as some varieties of euvitis grapes. (Don't we all look forward to the development of a truly seedless muscadine!!)

Generalized Overview of Three Sexual Life Cycles

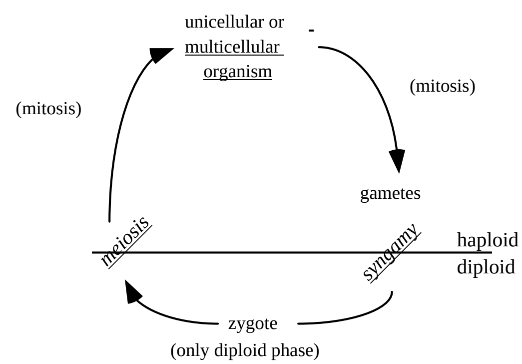
Alternation of Generations



Meiotic Gametogenesis



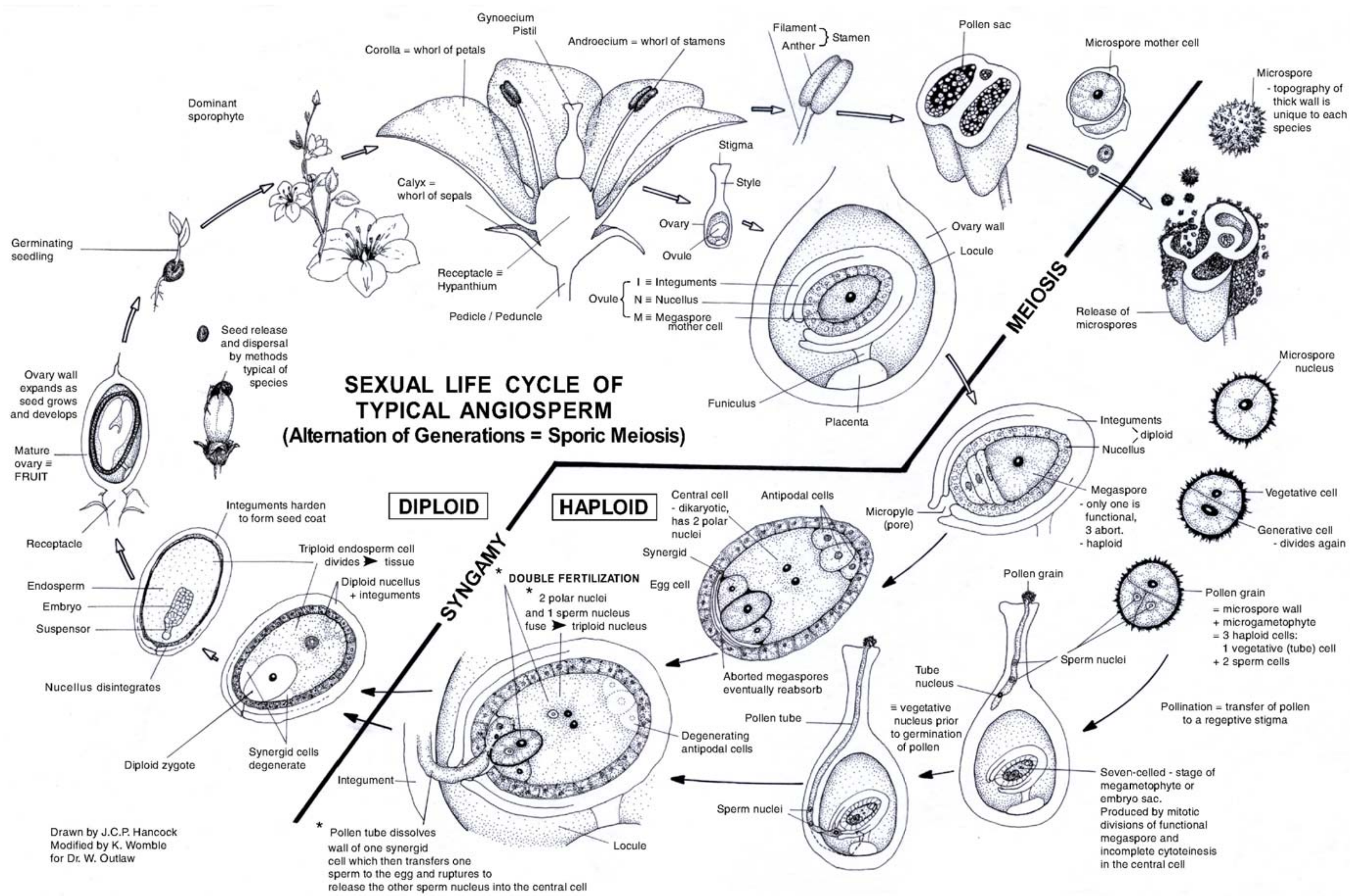
Zygotic Meiosis



Example: All plants

Example: Mammals

Example: *Chlamydomonas*


SEXUAL LIFE CYCLE OF
TYPICAL ANGIOSPERM
(Alternation of Generations = Sporic Meiosis)
DIPLOID
HAPLOID
MEIOSIS
SYNGAMY
Dominant sporophyte
Gynoecium
Pistil
Corolla = whorl of petals
Androecium = whorl of stamens
Calyx = whorl of sepals
Receptacle ≡ Hypanthium
Pedicle / Peduncle
Filament
Anther
Stamen
Stigma
Style
Ovary
Ovule
Ovule
I ≡ Integuments
N ≡ Nucellus
M ≡ Megaspore mother cell
Ovary wall
Locule
Funiculus
Placenta
Pollen sac
Microspore mother cell
Microspore
- topography of thick wall is unique to each species
Release of microspores
Microspore nucleus
Vegetative cell
Generative cell
- divides again
Integuments
Nucellus
diploid
Megaspore
- only one is functional, 3 abort.
- haploid
Micropyle (pore)
Pollen grain
= microspore wall
+ microgametophyte
= 3 haploid cells:
1 vegetative (tube) cell
+ 2 sperm cells
Pollen grain
Sperm nuclei
Tube nucleus
≡ vegetative nucleus prior to germination of pollen
Pollination = transfer of pollen to a regeptive stigma
Seven-celled - stage of megametophyte or embryo sac.
Produced by mitotic divisions of functional megaspore and incomplete cytoteinesis in the central cell
Pollen tube
Sperm nuclei
Central cell
- dikaryotic, has 2 polar nuclei
Antipodal cells
Synergid
Egg cell
Aborted megaspores eventually reabsorb
Degenerating antipodal cells
* DOUBLE FERTILIZATION
* 2 polar nuclei and 1 sperm nucleus fuse ➤ triploid nucleus
Integument
Locule
* Pollen tube dissolves wall of one synergid cell which then transfers one sperm to the egg and ruptures to release the other sperm nucleus into the central cell
Integuments harden to form seed coat
Triploid endosperm cell divides ➤ tissue
Diploid nucellus + integuments
Synergid cells degenerate
Diploid zygote
Endosperm
Embryo
Suspensor
Nucellus disintegrates
Receptacle
Mature ovary ≡ FRUIT
Ovary wall expands as seed grows and develops
Seed release and dispersal by methods typical of species
Germinating seedling
Drawn by J.C.P. Hancock
Modified by K. Womble
for Dr. W. Outlaw