Chapter 12

Biology of Non-Flowering Plants

Objectives

Overview of Non-Flowering Plants. Know the distinguishing characteristics of plants. Know the plant adaptations required for terrestrial life. Know the adaptations for terrestrial life displayed by angiosperms and how they are advantageous.

Bryophytes. Distinguish bryophytes from green algae[1] and from other plants. Understand the life cycle of *Marchantia*, a liverwort, and how it compares with the life cycle of higher plants *e.g.* gymnosperms and angiosperms. Know the structures of the bryophyte gametophyte and sporophyte and understand their function. Know the characteristics of peat moss.

Seedless Vascular Plants. Understand the advantages of a vascular system for terrestrial life. Understand the limitations associated with not having a seed. Understand how homosporous and heterosporous life cycles differ.

Gymnosperms. Know general features of gymnosperms. Understand the advantages of seeds and pollen for terrestrial life. Know the life cycle of gymnosperms. Understand how the structure of a gymnosperm leaf is adapted for terrestrial habitats.

Comparing Angiosperm and Gymnosperm Reproduction. Understand the similarities and differences in reproduction of angiosperms and gymnosperms. Understand the differences in seed formation in gymnosperms and angiosperms. Understand the advantages that each has over the other in terrestrial habitats.

Introduction to Non-flowering Plants

Several lines of evidence indicate that plants (embryophytes) evolved from green algae. Plants, unlike green algae, are, in general, terrestrial and have evolved adaptations for terrestrial life. Terrestrial plants require adaptations to avoid desiccation, provide mechanical support, transport water and nutrients, transfer "male" gametes, and protect the zygote from desiccation and harsh conditions. The three plant groups discussed in this chapter fulfill these requirements to various degrees. The basis for a comparative study of the groups of non-flowering plants is the evolution of adaptations for terrestrial life. Recall that angiosperms (flowering seed plants) are well-adapted for terrestrial life. Angiosperms have highly controlled stomata embedded in the cuticle-covered epidermis and stress-signaling hormones to avoid desiccation, complex vascular systems, efficient pollination mechanisms (characteristic flower), and seeds that are efficiently dispersed, protected, and nourished. In addition, comparing groups of plants, from bryophytes to angiosperms, notice the evolutionary advances. In addition to adaptation for terrestrial life, evolutionary advances in plants include sporophyte dominance over gametophyte dominance, the presence of seed, and oogamy over anisogamy or isogamy and non-flagellated over flagellated gametes.

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[1] p. 346

Bryophytes[2]

Bryophytes are the simplest plants, in which the gametophyte is the dominant, photosynthetic, and independent stage in the life cycle, which, recall, for all plants is alternation of generations. In bryophytes, the sporophyte is dependent, at least for a period, on the gametophyte. Bryophytes are not well adapted to terrestrial life because they have no (or rudimentary) vascular tissues, have no guard cells (although some bryophytes have rudimentary stomata), lack true roots or leaves, are seedless (recall a seed is composed of an embryo, nutritive tissue, and a seed coat), and, because they require external liquid water to complete their life cycle because they have flagellated sperm. Bryophytes are distinguishable as plants because the gametophytes of bryophytes have complex and multicellular reproductive organs, the antheridia (male) and archegonia ("female"); the archegonium protects the egg, zygote, and embryo, hence bryophytes are embryophytes[3] (distinguishing characteristic of all plants). Bryophytes are distinguishable from other plants by the sporophyte, which is unbranched (versus branched structures that are discussed with seedless vascular plants) and bears a single sporangium; thus is homosporous. Bryophytes are not considered evolutionary progenitors of other plants, but are considered an evolutionary branch. The three classes of organisms that constitute the bryophytes are the liverworts, hornworts, and mosses. The hornworts are the smallest group of bryophytes and are not discussed in this course.

Liverworts

Specimens 1 (macroscopic) and 2 and 3 (microscopic): Gametophytes of *Marchantia*, a liverwort

1. Observe the gametophyte of *Marchantia*. Like most liverworts, the gametophyte has a flat, simple structure (~10-30 cells thick) called a thallus[4] (s.; thalli, pl.).
2. Observe the underside of the thallus. Many thalli have rhizoids (but not true roots, which are defined by the presence of a vascular system) that anchor the plant to substrate. Some thalli have rudimentary stomata-like pores important for gas-exchange regulation, some have stomata similar to those found in higher plants, and some have no pores. The stomata-like pores are not regulated moment-to-moment as true stomata.
3. Observe the gemma cups. Gemma cups[5] are multicellular bodies that asexually give rise to new gametophytes.
4. Observe the reproductive structures[6] (gametangia), antheridiophores that bear "male" antheridia (flagellated sperm) and archegoniophores that bear "female" archegonia (non-flagellated and retained egg).
5. Draw the gametophyte and label the thallus, gemma cup, rhizoids, antheridiophore, and archegoniophore.
6. Next to each label, indicate the ploidy level of the structure.
7. Identify these structures in the *Marchantia* life cycle[7] sketch in your text.
8. Observe the prepared slide of the longitudinal section of the antheridiophore bearing antheridia (stained red) that contain flagellated sperm.
9. Draw and label the antheridia with sperm. Indicate ploidy level.

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[2] Chapter 16, p. 345
[3] pp. 350-351
[4] Fig. 16-5
[5] Fig. 16-14
[6] Fig. 16-12 (macroscopic) and 16-7 (microscopic)
[7] Fig. 16-15 (Life cycle of a liverwort)

10. Observe the prepared slide of the longitudinal section of the archegoniophore bearing archegonia containing a single egg.
11. Draw and label an archegonium with egg. Indicate ploidy level.

Specimen 4: Sporophyte of *Marchantia*, a liverwort

The sporophyte of *Marchantia* is formed after fertilization of the egg, within the archegonium, by the sperm. Following fertilization, the diploid zygote divides mitotically to form a diploid embryo[8], which grows further to form an adult sporophyte[9]. In *Marchantia*, the sporophyte is simple, microscopic, and dependent on the gametophyte for nutrition. The function of the sporophyte is to produce spores through meiosis.

1. Observe the prepared slide of the sporophyte, which is within the archegonia (of the "female" gametophyte).
2. Identify the sporophyte in the life cycle sketch of *Marchantia* in your text.
3. Observe the oval-shaped chamber, the "capsule," which contains the haploid spores (red), and is attached to the gametophyte by a stalk and a foot (at interphase of sporophyte and gametophyte). Sporophytes produce a single type of sporangium and, thus, release mature spores that are morphologically similar (making liverworts homosporous) that germinate to form a new gametophyte.
4. Draw and label the *Marchantia* sporophyte, capsule, spores, foot, and stalk. Also, indicate the ploidy level of the structures and the position of the gametophyte relative to the sporophyte.

Mosses. The mosses are the most complex group of bryophytes. They have a "leafy," erect gametophyte[10], which is more complex than that of liverworts. They do not have complex vascular systems, but have a rudimentary conducting system[11] with complex, multicellular rhizoids (root-like structures). In addition, many mosses have stomata[12] present on the sporophyte.

The antheridia and archegonia of liverworts are formed at the tips of the "male" and "female" gametophytes respectively[13]. Fertilization occurs within the archegonia and the zygote develops into the sporophyte by mitosis. The sporophyte is attached to and dependent on the gametophyte, even at maturity. The sporophyte of mosses is more conspicuous than that of liverworts. The sporophyte produces spores by meiosis and releases them by a dehiscence mechanism[14]. Mosses, like liverworts, are homosporous.

Peat Moss (*Sphagnum*) is common in wet places, predominantly in temperate and arctic regions. Its peculiar leaf-like structure[15], large, barrel-shaped, dead, colorless cells and a network of thick, living, photosynthetic cells between them, serves as a highly efficient water storage system.

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[8] Fig. 16-8
[9] Fig. 16-9
[10] Fig. 16-21
[11] Fig. 16-24
[12] Fig. 16-28
[13] Fig. 16-25 (Life cycle of a moss)
[14] Fig. 16-20
[15] Fig. 16-20b

Peat moss often forms extensive sphagnum bogs that can reach an age of 10,000 years or more. Because of the chemical activity of peat moss, the water stored in the bog is acidic, an environment that does not favor the activity of decomposing bacteria and fungi. Dead *Sphagnum* and other plants, including wind-carried pollen grains from other plants, accumulate in the deeper layers of bogs. The examination of cores from peat bogs can yield important information. For example, pollen-grain analysis in peat bogs reveals the composition and history of the surrounding vegetation because plants can be identified by their pollen grains, thus revealing the history of changes in climate (paleoclimatology).

Many remarkable archaeological finds have also been recovered from peat bogs. In 1986, human remains from thousands of years ago were discovered in a peat bog in central Florida. The remains were well-enough preserved to permit analysis of DNA recovered from the body tissues.

Seedless Vascular Plants[16]

A vascular system[17] and support mechanisms allow plants to attain size and complexity in terrestrial habitats. In addition, most seedless vascular plants have a cuticle covering the epidermis that prevents desiccation and stomata that regulate gas exchange. These structures evolved in the diploid sporophyte. In vascular plants, the sporophyte is the dominant, photosynthetic, macroscopic generation that is only dependent on the gametophyte only for initial development. However, free-living (exposed to the environment) gametophytes and flagellated sperm, which need external liquid water to move to the egg, are hindrances to terrestrial life for these plants.

Specimen 5: *Psilotum* (whisk fern), homosporous seedless vascular plant

1. Observe the sporophyte of *Psilotum*[18], which has a green, dichotomously (equally) branched stem that is photosynthetic and has vascular tissue. (Unequal branching leads to more complex structures, thus dichotomous branching is a simple trait.)
2. Observe, on the stem, the presence of small leaf-like structures call enations. Enations do not have vascular tissue within them.
3. Observe the sporangia near the tips of the branches. Sporangia make spores and release them when they are mature. Released spores germinate to form a free-living gametophyte, which makes antheridia and archegonia. *Psilotum* is homosporous; thus, each spore forms a bisexual gametophyte.
4. Draw the stem, showing dichotomous branching. Label the stem, enations, and sporangia. Indicate the ploidy level of each structure.

Specimen 6: *Selaginella*, heterosporous seedless vascular plant

Selaginella[19] is sometimes called a "resurrection plant," because, after severe desiccation, it is one of the few plants that can be restored. *Selaginella* has a bushy appearance with true leaves borne on a true stem and true roots. The tip of the sporophyte bears strobili (pl.; strobilus, s.). Strobili are cone-like structures that bear the spore-producing parts of the plant.

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[16] Chapter 17 p. 368
[17] Fig. 17-3
[18] Fig. 17-34 (Life cycle of *Psilotum*)
[19] Fig. 17-17

1. Observe the prepared slide of the whole-mount of the strobilus of *Selaginella*. The leaves on the strobilus are called sporophylls.
2. At the base of each sporophyll is a sporangium, which bears spores. There are two types of sporangia, the megasporangium bears megaspores (large spores) and the microsporangium bears microspores (small spores). Megaspores and microspores are released and germinate to form the "female" and "male" gametophytes respectively. The flagellated sperm produced in the antheridia of the "male" gametophyte fertilize the eggs produced in the archegonia of the "female" gametophytes, thus returning to the diploid generation.
3. Draw and label the micro- and megasporophylls, micro- and megasporangia, and micro- and megaspores. Indicate the ploidy level of each labeled structure.

Although most seedless vascular plants are homosporous, *Selaginella* is hetersporous. Heterospory is an evolutionary advancement in vascular plants and is the precursor to the production of seeds, which form the basis for the success of higher plants.

Specimen 7: Fern sori

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1. Observe the underside of the leaf-like sporophyll of a true fern[20]. The brown structures are sori[21] (pl.; sorus, s.), which are specialized structures bearing clusters of sporangia.
2. Draw the underside of a fern sporophyll with sori.
3. Scrape a small amount of the brown "powder" onto a slide (not a wet mount). Observe and note the sporangia (elliptical sacs with thick-walled cells) that contain haploid spores.
4. Heat the slide gently. Observe the sporangia again under the microscope and notice that the spores have been released. The heating causes the thick-walled cells that line the wall of the sporangium to lose water, shrink, and cause the sporangia to release the spores. Ferns are homosporous; thus, each spore forms a bisexual gametophyte that is free-living and photosynthetic. Fertilization occurs within the archegonia, where the new sporophyte begins development.
5. Draw and label sporangia, spores, and the thick-walled cells lining the sporangia. Indicate the ploidy level of each labeled structure.

Gymnosperms

The four groups of living gymnosperms are cycads, ginkgos, gnetophytes, and conifers. As in ferns, the sporophyte dominates the gymnosperm life cycle; however, all gymnosperms are obligatorily heterosporous because they produce seeds. Gymnosperms have two structures that make them better adapted to a terrestrial environment than the seedless plants, seeds and pollen. In addition, gymnosperms have well-developed vasculature, including a vascular cambium that produces secondary growth.

The mature sporophyte (the familiar tree) of gymnosperms[22] produces microspores and megaspores that are born in sporangia of separate, morphologically distinct cones. Each scale of a "male" cone bears two microsporangia, which contain numerous microspore mother cells that, through meiosis, give rise to haploid microspores that each develop into a four-celled pollen grain. Each scale of a "female" cone bears two ovules, each containing a megasporangium that is surrounded by an integument. Each ovule contains a single megaspore mother cell that undergoes meiosis. Three of the four megaspores produced from meiosis of the megaspore

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[20] Fig. 17-30
[21] Fig. 17-27; 17-28
[22] Fig. 18-17

mother cell disintegrate and the remaining megaspore forms into the female gametophyte, which is never shed by the sporophyte (another important attribute required for seed production). During pollination, two sperm nuclei enter the egg cell, but one disintegrates and the other unites with the egg-cell nucleus to form the zygote. The ovule develops into a seed, which is covered by a seed coat. The seed provides protection from unfavorable environments for the embryo and provides nutrients for early development of the new sporophyte. The development of seeds and pollen freed plants from the requirement of liquid water for reproduction.

Cycads[23]**.** Many cycads grow to heights of small trees and are frequently mistaken for palms because their unbranched stems are topped with a crown of palm-like leaves. *Cycas* is the most primitive living cycad. The pollen grains, which contain the sperm, are deposited on the ovule. Upon reaching the fluid-filled chamber above the female gametophyte, their pollen tubes burst and release flagellated sperm, which swim the rest of the way to the egg.

Specimen 8: *Cycas* megasporophyll

1. Observe the megasporophyll of *Cycas*, noting the position of the ovule.
2. Observe a preserved seed and note the presence of the female gametophyte at the center.
3. Outside the gametophyte is a distincy layer called the nucellus (remains of the megasporangium).
4. Outside the nucellus is the integument that will form the seed coat.
5. Draw and label the megasporophyll and ovule. Draw a section of the ovule and label megasporangia and female gametophyte. Indicate the ploidy level of each labeled structure.

Ginkos[24]**.** Like the cycads, the ginkgos were once distributed worldwide and formed extensive forests. Now, they are represented by a single species, *Ginkgo biloba*, which is native only to southeastern China. *G. biloba* is a highly branched tree with fan-shaped leaves, which are deciduous (shed each fall), but attractive ornamental plants in the United States.

Conifers. The dominant and most conspicuous gymnosperms are the conifers, which include the pines, spruces, firs, cedars, yews, junipers, and redwoods. Conifers are woody, perennial plants, either trees or shrubs. Most conifers are bisexual, meaning each individual produces both male and female cones. The leaves of conifers are either scale-like or needle-like in shape. Most conifers are also evergreen (retain each leaf for several years).

Specimen 9: Cross-section through a pine needle

Conifers tend to be drought-tolerant plants. The small leaves of conifers have a thick epidermis and cuticle and relatively few stomata. The stomata of pine needles are sunken in the epidermis, thus decreasing the driving force for water loss.

1. Observe the cross-section of a pine needle[25] and notice the thickness of the cuticle.
2. Look for sunken stomata.
3. At the center of the needle is a patch of vascular tissue (with tracheids and sieve cells), which is surrounded by photosynthetic cells.

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[23] Fig. 18-33
[24] Fig. 18-35
[25] Fig. 18-12

4. The two large holes in the photosynthetic part of the leaf are resin ducts. Resin ducts are also found in the stems and roots of many conifers. The cells surrounding these ducts produce terpenes and resinous compounds that protect the plant against insect and fungal attacks.
5. Draw and label the epidermis, stomata, resin ducts, tracheids, and photosynthetic cells of the pine needle.

Specimen 10: Longitudinal section of the "male" cone (microsporangium) of pine[26]

1. Note the microsporophylls, scales, which bear the microsporangia[27].
2. Observe, within the microsporangia, the presence of several winged pollen grains[28]. Each mature pollen grain is a haploid male gametophyte.
3. Draw and label microsporophylls, microsporangia, and pollen grains.

Comparison of Angiosperm and Gymnosperm Reproduction

The angiosperms, or flowering plants, are the most advanced, diverse, and numerous group of plants. Several major changes in reproduction occurred as the angiosperms evolved, making them more successful on land than other groups of plants. As in all vascular plants, the diploid sporophyte of angiosperms and gymnosperms is dominant in the life cycle of flowering plants. Reproduction by the sporophyte involves the production of microspores and megaspores by meiosis.

In angiosperms the microspores are produced in the anther (collection of microsporangia), which, in turn, is part of the stamen, which may be thought of as the fusion product of microsporophylls. The microspores develop into male gametophytes, or pollen grains. The angiosperm pollen grain is similar to that of the gymnosperms; however, pollination in most angiosperms is aided by animals rather than by wind. This proved to be an extremely important adaptive advance.

The female reproductive structures of both angiosperms and gymnosperms are enclosed in a structure called the ovule. In gymnosperms, the ovule is borne on the megasporophyll. In angiosperms, the ovule is borne on the carpel (megasporophyll) and the carpel(s) form an ovary in which the ovule(s) are enclosed. In the ovule, a single haploid megaspore is formed by meiosis. The angiosperm megaspore develops into a haploid female gametophyte, which consists of only 7 cells (containing a total of 8 nuclei).

After fertilization in gymnosperms the nutritive cell layer in the seed is the remnant of the female gametophyte. In angiosperms, the seed produces a triploid nutritive tissue (the endosperm) and the ovary wall develops into the flesh of the fruit.

Review Questions

1. Compare and contrast the alternation of generations that occurs in bryophytes and in gymnosperms. Give at least two similarities and two differences.

2. Contrast the fate of the spores in *Selaginella* with the fate of the spores in angiosperms.

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[26] Fig. 18-15
[27] Fig. 18-17
[28] Fig. 18-16

3. Describe the evolutionary and adaptive advances displayed by each of the following groups of plants: ferns, gymnosperms, and angiosperms.