CHAPTER 30

PLANT DIVERSITY II: THE EVOLUTION OF SEED PLANTS

OUTLINE

I. Overview of Reproductive Adaptations of Seed Plants
   - A. The gametophytes of seed plants became even more reduced than the gametophytes of seedless vascular plants
   - B. In seed plants, the seed replaced the spore as the main means of dispersing offspring
   - C. Pollen became the vehicles for sperm cells in seed plants

II. Gymnosperms
   - A. The Mesozoic era was the age of gymnosperms
   - B. The four divisions of extant gymnosperms are the cycads, the ginkgo, the gnetophytes, and the conifers
   - C. The life cycle of a pine demonstrates the key reproductive adaptations of seed plants

III. Angiosperms (Flowering Plants)
   - A. Terrestrial adaptation continued with the refinement of vascular tissue in angiosperms
   - B. The flower is the defining reproductive adaptation of angiosperms
   - C. Fruits help disperse the seeds of angiosperms
   - D. The life cycle of an angiosperm is a highly refined version of the alternation of generations common to all plants
   - E. The radiation of angiosperms marks the transition from the Mesozoic to the Cenozoic era
   - F. Angiosperms and animals have shaped one another's evolution
   - G. Agriculture is based almost entirely on angiosperms

IV. The Global Impact of Plants
   - A. Plants transformed the atmosphere and climate
   - B. Plant diversity is a nonrenewable resource

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. Describe the adaptations of seed plants that have contributed to their success on land.
2. List the four divisions of gymnosperms.
3. Describe the structures of ovulate and pollen cones of a pine and distinguish between the two.

4. Describe the life history of a pine and indicate which structures are part of the gametophyte generation and which are part of the sporophyte generation.
5. Point out the major life cycle differences in ferns and pines.
6. Distinguish between pollination and fertilization.
7. Describe a pine seed and indicate which structures are old sporophyte, gametophyte, and new sporophyte.
8. Describe how the needle-shaped leaves of pines and firs are adapted to dry conditions.
9. List and give examples of the two classes of Anthophyta.
10. Compare the life cycles of mosses, ferns, conifers, and flowering plants in terms of:
    a. Dominant life cycle stage (gametophyte/sporophyte)
    b. Whether they are homosporous or heterosporous
    c. Mechanism of gamete transfer
11. Describe some refinements in vascular tissue that occurred during angiosperm evolution.
12. Explain how evolution of the flower enhanced the reproductive efficiency of angiosperms.
13. Identify the following floral structures and describe a function for each:
    a. Sepals
    b. Petals
    c. Stamens
    d. Carpels
    e. Filament
    f. Anther
    g. Stigma
    h. Style
    i. Ovary
14. Describe four commonly recognized evolutionary trends in floral structure found in various angiosperm lineages.
15. Define fruit and explain how fruits are modified in ways that help disperse seeds.
16. Diagram the generalized life cycle of an angiosperm, identify which structures are haploid, and explain how it differs from the life cycle of a pine.
17. Explain the process of double fertilization and describe the fate of the polyploid nucleus.
18. Explain how an angiosperm seed differs from that of a pine.
19. Explain why paleobotanists have difficulty piecing together the origin of angiosperms and describe some current theories on how flowering plants may have evolved.
20. Explain how animals may have influenced the evolution of terrestrial plants, and vice versa.

KEY TERMS

nucellus	fiber	anther	cross-pollination
integuments	flower	stigma	double fertilization
ovule	sepal	style	cotyledons
seed	petal	ovary	endosperm
conifer	stamen	fruit	coevolution
tracheids	carpel	pollen grains	
vessel elements	filament	embryo sac	

LECTURE NOTES

The emergence of seed plants further transformed the Earth. Seeds and other adaptations of gymnosperms and angiosperms heightened the ability of plants to survive and reproduce in diverse terrestrial environments; these plants became the principal producers in the food webs of most ecosystems on land.

I. Overview of Reproductive Adaptations of Seed Plants

Three life cycle modifications contributed to terrestrial seed plant success:

1. Reduction of the gametophyte. They were retained in the moist reproductive tissue of the sporophyte generation (not independent).
2. Origin of the seed
   - Zygotes developed into embryos packaged with a food supply within a protective seed coat.
   - Seeds replaced spores as main means of dispersal.
3. Evolution of pollen. Plants were no longer tied to water for fertilization.

A. The gametophytes of seed plants became even more reduced than the gametophytes of seedless vascular plants

While the gametophytes of seedless vascular plants develop in the soil as an independent generation, those of seed plants are reduced in size and retained within the moist reproductive tissue of the sporophyte generation.

- This evolutionary trend reverses the gametophyte-sporophyte relationship observed in bryophytes (see Campbell, Figure 30.1).
- Dominance of the diploid generation may afford protection from solar radiation-induced mutations of the genome (damaging radiation is more extensive on land than in aquatic habitats).

B. In seed plants, the seed replaced the spore as the main means of dispersing offspring

The relatively harsh terrestrial environment led to the development of resistant structures for the dispersal of offspring.

- Bryophytes and seedless vascular plants produce and release hardy single-celled spores.
- Seeds are more hardy because of their multicellular nature.

A seed consists of a sporophyte embryo together with a food supply surrounded by a protective coat.

- The sporophytes do not release their spores, but retain them in their sporangia, as a result, the sporophyte also contains a gametophyte.

All seed plants are heterosporous in that they possess two different kinds of sporangia, each producing a different type of spore.

- Megasporangia produce megaspores that give rise to female egg-containing gametophytes.
- Microsporangia produce microspores that give rise to male sperm-containing gametophytes.

The development of the seed is associated with the megasporangia.

- The megasporangium of seed plants is not a chamber, but a fleshy structure called a *nucellus*.
- Additional tissues called *integuments* surround the megasporangium (contribute to the protective coat).

- The resulting structure—megaspore, megasporangium, and integuments—is called an *ovule* (see Campbell, Figure 30.2a).
- The female gametophyte develops within the wall of the megaspore and is nourished by the nucellus.
- If the egg cell of a female gametophyte is fertilized by a sperm cell (see Campbell, Figure 30.2b), the zygote develops into a sporophyte embryo.
- The resulting sporophyte-containing ovule develops into a seed (see Campbell, Figure 30.2c).

C. Pollen became the vehicles for sperm cells in seed plants

The microspores develop into pollen grains, which in turn, mature to form the male gametophores of seed plants.

- Pollen grains are coated with a resilient polymer, sporopollenin (see Chapter 29).
- Pollen grains can be carried away by wind or animals (e.g., bees) following release from microsporangia.

A pollen grain near an ovule will extend a tube through sperm cells into the female gametophyte within the ovule.

- In some gymnosperms, the sperm cells are flagellated (ancestral condition).
- Other gymnosperms (including conifers) and angiosperms do not have flagellated sperm cells.

II. Gymnosperms

A. The Mesozoic era was the age of gymnosperms

Gymnosperms appear in the fossil record much earlier than flowering plants. Gymnosperms most likely descended from Devonian progymnosperm and were seedless.

- Seeds evolved by the end of the Devonian.
- Adaptive radiation during the Carboniferous and Permian periods led to today's divisions.
- During the Permian, Earth became warmer and drier; therefore, lycopods, horsetails, and ferns (previously dominant) were largely replaced by conifers and their relatives, the cycads (two divisions of gymnosperms).
- This large change marks the end of the Paleozoic era and the beginning of the Mesozoic era.

Gymnosperms lack enclosed chambers (ovaries) in which seeds develop.

B. The four divisions of extant gymnosperms are the cycads, the ginkgo, the gnetophytes, and the conifers

Campbell, Figure 30.3, shows the four divisions of living gymnosperms.

The *conifers* are the largest division of gymnosperms.

- Most are evergreens: pines, firs, spruces, larches, yews, junipers, cedars, cypresses, and redwoods all belong to this division.
- Includes some of the tallest (redwoods and some eucalyptus); largest (giant sequoias); and oldest (bristle cone pine) living organisms.
- Most lumber and paper pulp is from conifer wood.

Needle-shaped conifer leaves are adapted to dry conditions.

- Thick cuticle covers the leaf
- Stomata are in pits, reducing water loss
- Despite the shape, needles are megaphylls, as are leaves of all seed plants.

C. The life cycle of a pine demonstrates the key reproductive adaptations of seed plants

The life cycle of pine, a representative conifer, is characterized by the following:

- The multicellular sporophyte is the most conspicuous stage; the pine tree is a sporophyte, with its sporangia located on cones.
- The multicellular gametophyte generation is reduced and develops from haploid spores that are retained within sporangia.
  - ⇒ The male gametophyte is the pollen grain; there is no antheridium.
  - ⇒ The female gametophyte consists of multicellular nutritive tissue and an archegonium that develops within an ovule.

Conifer life cycles are heterosporous; male and female gametophytes develop from different types of spores produced by separate cones.

- Trees of most pine species bear both pollen cones and ovulate cones, which develop on different branches.
- Pollen cones have microsporangia; cells in these sporangia undergo meiosis producing haploid microspores, small spores that develop into pollen grains—the male gametophytes.
- Ovulate cones have megasporangia; cells in these sporangia undergo meiosis producing large megaspores that develop into the female gametophyte (see Campbell, Figure 30.4). Each ovule initially includes a megasporangium (nucellus) enclosed in protective integuments with a single opening, the micropyle.

It takes nearly three years to complete the pine life cycle, which progresses through a complicated series of events to produce mature seeds.

- Windblown pollen falls onto the ovulate cone and is drawn into the ovule through the micropyle.
- The pollen grain germinates in the ovule, forming a pollen tube that begins to digest its way through the nucellus.
- A megaspore mother cell in the nucellus undergoes meiosis producing four haploid megaspores, one of which will survive; it grows and divides repeatedly by mitosis producing the immature female gametophyte.
- Two or three archegonia, each with an egg, then develop within the multicellular gametophyte.
- More than a year after pollination, the eggs are ready to be fertilized; two sperm cells have developed and the pollen tube has grown through the nucellus to the female gametophyte.
- Fertilization occurs when one of the sperm nuclei unites with the egg nucleus. All eggs in an ovule may be fertilized, but usually only one zygote develops into an embryo.
- The pine embryo, or new sporophyte, has a rudimentary root and several embryonic leaves. It is embedded in the female gametophyte, which nourishes the embryo until it is capable of photosynthesis. The ovule has developed into a pine seed, which consists of an embryo (2n), its food source (n), and a surrounding seed coat (2n) derived from the integuments of the parent tree.
- Scales of the ovulate cone separate, and the winged seeds are carried by the wind to new locations. Note, that with the seed plants, the seed has replaced the spore as the mode of dispersal.
- A seed that lands in a habitable place germinates, its embryo emerging as a pine seedling.

III. Angiosperms (Flowering Plants)

Flowering plants are the most widespread and diverse; 250,000 species are now known.

- There is only one division, Anthophyta, with two classes, Monocotyledones (monocots) and Dicotyledones (dicots).
- Most use insects and animals for transferring pollen, and therefore, are less dependent on wind and have less random pollination.

A. Terrestrial adaptation continued with refinement of vascular tissue in angiosperms

Vascular tissue became more refined during angiosperm evolution.

- Conifers have *tracheids* (see Campbell, Figure 30.5), water-conducting cells that are:
  - ⇒ An early type of xylem cell
  - ⇒ Elongated, tapered cells that function both in mechanical support and water movement up the plant
- Most angiosperms also have *vessel elements* that are:
  - ⇒ Shorter, wider cells than the more primitive tracheids
  - ⇒ Arranged end to end forming continuous tubes
  - ⇒ Compared to tracheids, vessel elements are more specialized for conducting water, but less specialized for support
- Angiosperm xylem is reinforced by other cell types called *fibers*, which are:
  - ⇒ Specialized for support with a thick lignified wall
  - ⇒ Evolved in conifers. (Conifer xylem contains both fibers and tracheids, but not vessel elements.)

B. The flower is the defining reproductive adaptation of angiosperms

Flower = The reproductive structure of an angiosperm which is a compressed shoot with four whorls of modified leaves (see also Campbell, Figure 30.6)

Parts of the flower:

Sepals - Sterile, enclose the bud

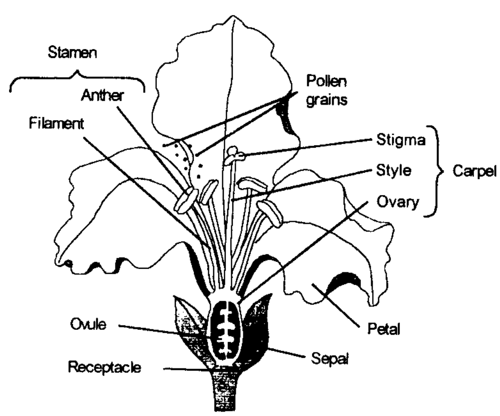
Petals – Sterile, aid in attracting pollinators

Stamen – Produces the pollen

Carpel – Evolved from a seed-bearing leaf that became rolled into a tube

Stigma – Part of the carpel that is a sticky structure that receives the pollen

Ovary – Part of the carpel that protects the ovules, which develop into seeds after fertilization



There are four evolutionary trends in various angiosperm lineages:

1. The number of floral parts have become reduced.
2. Floral parts have become fused.
3. Symmetry has changed from radial to bilateral.
4. The ovary has dropped below the petals and sepals, where the ovules are better protected.

C. Fruits help disperse the seeds of angiosperms

Fruit = A ripened ovary that protects dormant seeds and aids in their dispersal; some fruits (like apples) incorporate other floral parts along with the ovary (see Campbell, Figure 30.7)

Aggregate fruits = Several ovaries that are part of the same flower (e.g., raspberry)

Multiple fruit = One that develops from several separate flowers (e.g., pineapple)

Modifications of fruits that help disperse seeds include:

- Seeds within fruits that are shaped like kites or propellers to aid in wind dispersal
- Burr-like fruit that cling to animal fur
- Edible fruit with tough seeds which pass through the digestive tract of herbivores unharmed, dispersing seeds miles away

D. The life cycle of an angiosperm is a highly refined version of the alternation of generations common to all plants

Life cycles of angiosperms are heterosporous (in common with all seed plants) and the two types of sporangia are found in the flower (see Campbell, Figure 30.8):

- Microsporangia in anthers produce microspores that form male gametophytes.
- Megasporangia in ovules produce megaspores that develop into female gametophytes.

Immature male gametophytes:

- Are *pollen grains*, which develop within the anthers of stamens
- Each pollen grain has two haploid nuclei that will participate in *double fertilization* characteristic of angiosperms.

Female gametophytes:

- Do *not* produce an archegonium
- Are located within an ovule
- Consist of only a few cells: an *embryo sac* with eight haploid nuclei in seven cells (a large central cell has two haploid nuclei)
- One of the cells is the egg

An outline of the angiosperm life cycle follows:

- Pollen from the anther lands on the sticky stigma at the carpel's tip; most flowers do not self-pollinate, but have mechanisms to ensure *cross-pollination.*
- The pollen grain germinates on the stigma by growing a pollen tube down the style of the carpel.
- When it reaches the ovary, the pollen tube grows through its micropyle and discharges two sperm cells into the embryo sac.
- Double fertilization occurs as one sperm nucleus unites with the egg to form a diploid zygote; the other sperm nucleus fuses with two nuclei in the embryo sac's central cell to form triploid ($3n$) endosperm.
- After double fertilization, the ovule matures into a seed.

The seed is a mature ovule, consisting of:

1. Embryo. The zygote develops into an embryo with a rudimentary root and one (in monocots) or two (in dicots) *cotyledons* or seed leaves.
2. Endosperm. The triploid nucleus in the embryo sac divides repeatedly forming triploid endosperm, rich in starch and other food reserves.
3. Seed coat. This is derived from the integuments (outer layers of the ovules).

Monocots and dicots use endosperm differently.

- Monocot seeds store most food in the endosperm.
- Dicots generally restock most of the nutrients in the developing cotyledons.

In a suitable environment the seed coat ruptures and the embryo emerges as a seedling, using the food stored in the endosperm and cotyledons.

E. The radiation of angiosperms marks the transition from the Mesozoic to the Cenozoic era

Angiosperms showed a relatively sudden appearance in the fossil record with no clear transitional links to ancestors.

- Earliest fossils are early Cretaceous (approximately 130 million years ago)
- dominant, as they are today.

There are two theories about their sudden appearance:

1. Angiosperms originated where fossilization was unlikely (they are an artifact of an imperfect fossil record).
2. Angiosperms evolved and radiated relatively abruptly *(punctuated equilibrium)*.

Perhaps angiosperms evolved from seed ferns, an extinct group of unspecialized gymnosperms.

F. Angiosperms and animals shaped one another's evolution

Terrestrial plants and animals have coevolved, a consequence of their interdependence.

Coevolution = Reciprocal evolutionary responses among two or more interacting species; adaptive change in one species is in response to evolutionary change in the other species.

Coevolution between angiosperms and their pollinators led to diversity of flowers.

- Some pollinators are specific for a particular flower. The pollinator has a monopoly on a food source and guarantees the flower's pollen will pollinate a flower of the same species (see Campbell, Figure 30.9).
- Often, the relationship between angiosperms and their pollinators is not species specific; a pollinator may not depend exclusively on one flower species, or a flower species may not depend exclusively on one species of pollinator. However, flower color, fragrance, and structure are usually adaptations for *types* of pollinators, such as various species of bees or hummingbirds.

Edible fruits of angiosperms have coevolved with animals that can disperse seeds. Animals become attracted to ripening fruits as they:

- Become softer, more fragrant, and higher in sugar
- Change to a color that attracts birds and mammals, animals which are large enough to disperse the seeds

G. Agriculture is based almost entirely on angiosperms

Angiosperms provide nearly all our food: fruit, vegetable crops, and grains, such as corn, rice, wheat.

Flowering plants are also used for other purposes, such as:

- Fiber
- Medication
- Perfume
- Decoration

Through agriculture, humans have influenced plant evolution by artificially selecting for plants that improved the quantity and quality of foods and other crops.

- Many of our agricultural plants are so genetically removed from their origins that they probably could not survive in the wild.

- As a consequence, cultivated crops that require human intervention to water, fertilize, provide protection from insects and disease, and even to plant their seeds, are vulnerable to natural and human-caused disasters.

V. The Global Impact of Plants

A. Plants transformed the atmosphere and the climate

In addition to being the primary producers of the terrestrial environment, plants also changed the physical environment of Earth.

- They decreased atmospheric carbon dioxide, resulting in global cooling.
- The cooler environment may have made terrestrial life more habitable for other organisms.

B. Plant diversity is a nonrenewable resource

Plant diversity is a nonrenewable resource, and the irrevocable extinction of plant species is occurring at an unprecedented rate.

- The exploding human population demands space and natural resources.
- The toll of habitat destruction is greatest in the tropics because this is where:
  - ⇒ Most species live
  - ⇒ More than half the human population lives and human population growth is fastest
  - ⇒ Most deforestation is caused by slash-and-burn clearing for agriculture

As the forest disappears, so do thousands of plant and animal species.

- Habitat destruction also endangers animal species that depend on plants in the tropical rainforest.
- Habitat destruction by humans has not been limited to the tropics. Europeans eliminated most of their forests centuries ago, and in North America, destruction of habitat is endangering many species.

There are many reasons to value plant diversity and to find ways to protect it.

- Ecosystems are living treasures that can regenerate only slowly.
- Humans depend on plants for products such as medicines, food and building materials.
- We still know so little of the 250,000 known plant species. (Food agriculture is based on only about two dozen species.)

REFERENCES

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