

Chapter 30 - Plant Diversity II: The Evolution of Seed Plants

Overview: Transforming the World

- The seed arose about 360 million years ago.
 - A seed consists of an embryo and its food supply, surrounded by a protective coat.
 - When mature, seeds are dispersed from their parent.
 - Because it nourishes and protects the embryo yet can separate from the mother plant, a seed is analogous to a detachable, mobile womb.
- Seeds are the key adaptation that enabled seed plants to be the dominant producers on land, making up the great majority of plant biodiversity.
- Agriculture, the cultivation and harvest of plants (especially angiosperms), began 13,000 years ago.
 - Humans began to cultivate plants independently in various regions, including the Near East, East Asia, Africa, and the Americas.
- The cultivation of plants was the single most important cultural change in the history of humanity; it made possible the transition from hunter-gatherer societies to permanent settlements.

Concept 30.1 Seeds and pollen grains are key adaptations for life on land.

- A number of terrestrial adaptations contributed to the success of seed plants.
- These adaptations, including the seed, the reduction of the gametophyte generation, heterospory, ovules, and pollen, provided new ways for seed plants to cope with terrestrial conditions such as drought and exposure to ultraviolet radiation.
- Novel adaptations enabled seed plants to reproduce under a broader range of conditions.

Seed plants have reduced gametophytes.

- Bryophyte life cycles are dominated by the gametophyte generation, whereas seedless vascular plants have sporophyte-dominated life cycles.
- The trend to gametophyte reduction continued in the lineage of vascular plants that led to seed plants.
 - Seedless vascular plants have tiny gametophytes that are visible to the naked eye.
 - The gametophytes of seed plants are microscopically small and develop from spores retained within the moist sporangia of the parental sporophyte.
- In seed plants, the delicate female gametophyte and the young sporophyte embryo are protected from environmental stresses, including drought and ultraviolet radiation.
- The gametophytes of seed plants obtain nutrients from their parents, whereas the free-living gametophytes of seedless vascular plants must fend for themselves.

Heterospory is the rule among seed plants.

- Nearly all seedless plants are homosporous, producing a single kind of spore that develops as a

- bisexual gametophyte.
- Seed plants likely had homosporous ancestors.
- All seed plants are heterosporous, producing two different types of sporangia that produce two types of spores.
 - Megaspangia on megasporophylls produce megaspores, which give rise to female (egg-containing) gametophytes.
 - Microspangia on microsporophylls produce microspores, which give rise to male (sperm-containing) gametophytes.

Seed plants produce ovules.

- In contrast to the few species of heterosporous seedless vascular plants, seed plants are unique in retaining the megasporangium and megaspores within the parent sporophyte.
- Layers of sporophyte tissue, **integuments**, envelop and protect the megasporangium.
 - Gymnosperm megasporangia are surrounded by one integument.
 - Angiosperm megasporangia are surrounded by two integuments.
- An **ovule** consists of the megasporangium, megaspores, and integuments.
- A female gametophyte develops from a megaspore and produces one or more egg cells.

Pollen eliminates the liquid water requirement for fertilization.

- A microspore develops into a **pollen grain**, consisting of a male gametophyte enclosed within a pollen wall.
 - Pollen grains are covered with a tough coat containing sporopollenin, which protects them as they are transported by wind or animals.
- The transfer of pollen to the vicinity of the ovule is called **pollination**.
- The pollen grain germinates and grows as a pollen tube into the ovule, where it delivers two sperm into the female gametophyte.
- Bryophytes and seedless vascular plants have flagellated sperm cells that swim a few centimeters through a film of water to reach the egg cells within the archegonium.
- The sperm of most seed plants lack flagella and do not require a film of water because they rely on the pollen tube to reach the egg cell of the female gametophyte within the ovule.
 - The sperm of some gymnosperm species, such as ginkgos and cycads, retain the ancestral flagellated condition, providing evidence of this evolutionary transition.
 - Flagella have been lost in the sperm of most gymnosperms and all angiosperms.

Seeds are an important means of dispersing offspring.

- What is a seed?
 - When a sperm fertilizes an egg of a seed plant, the zygote grows into a sporophyte embryo.
 - The ovule develops into a **seed**, consisting of the embryo and its food supply within a protective coat derived from the integuments.
- The evolution of the seed enabled plants to resist harsh environments and disperse offspring more widely.
 - For bryophytes and seedless vascular plants, single-celled spores are the only protective and

- dispersal stage in the life cycle.
- Moss spores can survive even if the local environment is too cold, too hot, or too dry for the moss plants themselves to survive.
- Because of their tiny size, the spores themselves can be dispersed in a dormant state to a new area.
- Spores were the main way that plants spread over Earth for the first 100 million years of life on land.
- The seed represents one solution to resisting harsh environments and dispersing offspring.
 - In contrast to a single-celled spore, a multicellular seed is a much more complex, resistant structure.
 - Unlike spores, seeds have a supply of stored food.
 - After being released from the parent plant, a seed may remain dormant for days or years.
 - Under favorable conditions, a seed germinates and the sporophyte embryo emerges as a seedling.
 - Some seeds drop close to the parent plant, while others are transported long distances by wind or animals.

Concept 30.2 Gymnosperms bear “naked” seeds, typically on cones.

- Gymnosperms have “naked seeds” that are not enclosed in ovaries.
- The seeds of gymnosperms are exposed on modified leaves (sporophylls) that usually form cones (strobili).
- In contrast, the ovules and seeds of angiosperms develop in enclosed chambers called ovaries.

The Mesozoic era was the age of gymnosperms.

- Morphological and molecular evidence places the surviving lineages of seed plants into two monophyletic sister clades: gymnosperms and angiosperms.
- Gymnosperms probably descended from **progymnosperms**, a group of Devonian plants, including *Archaeopteris*, that were heterosporous but lacked seeds.
- The first seed-bearing plants appeared in the fossil record about 360 million years ago.
- Angiosperms arose more than 200 million years later.
- The earliest fossils of gymnosperms are about 305 million years old.
- These early gymnosperms lived in Carboniferous ecosystems dominated by seedless vascular plants.
- The flora and fauna of Earth changed dramatically during the formation of the supercontinent Pangaea in the Permian.
- The climate became warmer and drier, favoring the spread of gymnosperms.
- Many groups of organisms disappeared, while others emerged.
 - Amphibians decreased in diversity and were replaced by reptiles, which were better adapted to arid conditions.
 - The lycophytes, horsetails, and ferns that had dominated in Carboniferous swamps were largely replaced by gymnosperms.
- Gymnosperms have a number of key terrestrial adaptations.
 - Some of these adaptations are found in all seed plants, such as seeds and pollen.

- Pines and firs are well suited to arid conditions because of their needle-shaped leaves, which have thick cuticles and relatively small surface areas.
- Because the change in organisms was so dramatic at the end of the Permian, 251 million years ago, geologists use this time as the boundary between the Paleozoic (“old life”) and Mesozoic (“new life”) eras.
- The terrestrial animals of the Mesozoic, including dinosaurs, were supported by vegetation consisting of mostly gymnosperms.
- The dinosaurs did not survive the mass extinction at the end of the Mesozoic, but many gymnosperms persisted and are still an important part of Earth’s flora.

The four phyla of extant gymnosperms are Ginkgophyta, Cycadophyta, Gnetophyta, and Coniferophyta.

- **Phylum Ginkgophyta** consists of only a single extant species, *Ginkgo biloba*.
 - This popular ornamental species has fanlike leaves that turn gold before they fall off in the autumn.
 - Landscapers usually plant only male trees because the coats of seeds produced by female plants produce a repulsive odor as they decay.
- Cycads (**phylum Cycadophyta**) have large cones and palmlike leaves.
 - Cycads flourished in the Mesozoic era, which was known as the “Age of Cycads.”
 - Today, 130 species of cycads survive.
- **Phylum Gnetophyta** consists of three very different genera.
 - *Welwitschia* plants, from deserts in southwestern Africa, have straplike leaves that are among the largest known leaves.
 - *Gentium* species are tropical trees or vines.
 - *Ephedra* (Mormon tea) is a shrub of the American deserts.
- The conifers belong to the largest gymnosperm phylum, the **phylum Coniferophyta**.
 - The term **conifer** comes from the reproductive structure, the cone, which is a cluster of scalelike sporophylls.
- Although there are only about 600 species of conifers, a few species dominate vast forested regions in the Northern Hemisphere where the growing season is short.
- Conifers include pines, firs, spruces, larches, yews, junipers, cedars, cypresses, and redwoods.
- Most conifers are evergreen, retaining their leaves and photosynthesizing throughout the year.
 - Some conifers, like the dawn redwood and tamarack, are deciduous, dropping their leaves in autumn.
- The needle-shaped leaves of some conifers, such as pines and firs, are adapted for dry conditions.
 - A thick cuticle covering the leaf and the placement of stomata in pits further reduce water loss.
- Much of our lumber and paper comes from the wood (actually xylem tissue, which gives the tree structural support) of conifers.
- Coniferous trees are among the largest and oldest organisms of Earth.
 - Redwoods from northern California can grow to heights of over 100 m.
 - One bristlecone pine, also from California, is more than 4,600 years old and may be the

world's oldest living organism.

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

- The life cycle of a pine illustrates the three key adaptations to terrestrial life in seed plants:
 1. Increasing dominance of the sporophyte generation
 2. The advent of the seed as a resistant, dispersible stage in the life cycle
 3. The evolution of pollen as an airborne agent bringing gametes together
- The pine tree is the sporophyte. It produces its sporangia on scalelike structures that are packed densely in cones.
- Conifers, like all seed plants, are heterosporous.
- Male and female gametophytes develop from different types of spores produced by separate cones: small pollen cones and large ovulate cones.
 - In most pine species, each tree produces both types of cones.
- Each pollen cone produces microsporocytes (microspore mother cells) that undergo meiosis to produce haploid microspores.
 - Each microspore develops into a pollen grain containing a male gametophyte.
 - In pines and other conifers, yellow pollen is released in large amounts and carried by wind.
- In larger ovulate cones, megasporocytes (megaspore mother cells) undergo meiosis to produce haploid megaspores inside the ovule.
 - Surviving megaspores develop into female gametophytes, which are retained within the sporangia.
- It takes nearly three years for male and female gametophytes to be produced in growing cones and brought together, and for mature seeds to form from the fertilized ovules.
- The scales of each ovulate cones separate, and the seeds are typically dispersed by the wind.
- A seed that lands in a habitable location germinates, and its embryo emerges as a pine seedling.

Concept 30.3 The reproductive adaptations of angiosperms include flowers and fruits.

- Angiosperms, commonly known as flowering plants, are seed plants that produce flowers and fruits.
- The name *angiosperm* refers to the seeds contained in fruits, the mature ovaries.
- Angiosperms are the most diverse and geographically widespread of all plants, including more than 90% of plant species.
 - There are more than 250,000 known species of angiosperms.
- All angiosperms are placed in a single phylum, Anthophyta.

The flower is the defining reproductive adaptation of angiosperms.

- The **flower** is an angiosperm structure specialized for sexual reproduction.
 - In many species of angiosperms, insects or other animals transfer pollen from one flower to the female sex organs of another.
 - ♣ This makes pollination more directed than the wind-dependent pollination of

gymnosperms.

- Some species that occur in dense populations, like grasses and temperate trees, *are* wind-pollinated.
- A flower is a specialized shoot with up to four rings of modified leaves (sporophylls) called floral organs: sepals, petals, stamens, and carpals.
- The **sepals** at the base of the flower are modified leaves that are usually green and enclose the flower before it opens.
- The **petals** lie inside the ring of sepals.
 - Petals are often brightly colored in plant species that are pollinated by animals, helping to attract pollinators.
 - Petals typically lack bright coloration in wind-pollinated plant species.
 - Sepals and petals are sterile floral parts, not directly involved in reproduction.
- **Stamens** produce microspores that develop into pollen grains containing male gametophytes.
 - A stamen consists of a stalk (the **filament**) and a terminal sac (the **anther**) where pollen is produced.
- **Carpals** produce megaspores and their products, female gametophytes.
 - At the tip of the carpal is a sticky **stigma** that receives pollen.
 - A **style** leads to the **ovary** at the base of the carpal.
 - If fertilized, an ovule develops into a seed.

Fruits help disperse the seeds of angiosperms.

- A **fruit** usually consists of a mature ovary, although it may include other flower parts as well.
 - As seeds develop from ovules after fertilization, the wall of the ovary thickens to form the fruit.
- Fruits protect dormant seeds and aid in their dispersal.
- Mature fruits can be fleshy or dry.
 - Oranges, plums, and grapes are fleshy fruits, in which the ovary wall softens during ripening.
 - Dry fruits include beans, nuts, and grains.
 - The dry, wind-dispersed fruits of grasses are major food staples for humans.
 - The cereal grains of wheat, rice, and maize are fruits with a dry outer covering (the former ovary wall), which adheres to the seed coat of the seed.
- Fruits are adapted to disperse seeds.
 - Dandelion and maple seeds are contained within fruits that function as kites or propellers to assist in wind dispersal.
 - Coconuts are specialized for water dispersal.
 - Some fruits are modified as burrs that cling to animal fur.
 - Many fruits are edible, nutritious, sweet-tasting, and colorful. Animals eat these fleshy fruits and deposit the seeds, along with a supply of fertilizer, some distance from the parent plant.

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

- All angiosperms are heterosporous, producing microspores that form male gametophytes and megaspores that form female gametophytes.

- The male gametophytes are in the pollen grains, which develop within microsporangia in the anthers.
 - Each male gametophyte has two haploid cells: a *generative cell* that divides to form two sperm and a *tube cell* that produces a pollen tube.
- The ovule, which develops in the ovary, contains the female gametophyte, the **embryo sac**.
 - The embryo sac consists of only a few cells, one of which is the egg.
- The pollen is released from the anther and carried to the sticky stigma at the tip of the carpel.
 - Most flowers have mechanisms to ensure **cross-pollination**, thus enhancing genetic variability.
 - In some cases, the stamens and carpels of a single flower may mature at different times, or they may be arranged so that self-pollination is unlikely.
- The pollen grain germinates, and the male gametophyte extends a pollen tube that grows down within the style of the carpel.
- After reaching the ovary, the pollen tube penetrates the **micropyle**, a pore in the integuments of the ovule.
- Two sperm are discharged into the female gametophyte.
 - One fertilizes the egg to form a diploid zygote.
 - The other fuses with two polar nuclei in the large central cell of the female gametophyte to form the triploid cell.
- **Double fertilization** in which one fertilization event produces a zygote and the other produces a triploid cell is unique to angiosperms.
- After double fertilization, the ovule matures into a seed.
- The zygote develops into a sporophyte embryo that is packaged with food in the seed.
 - The embryo has a rudimentary root and one or two seed leaves, or **cotyledons**.
 - The fertilized nucleus of the central cell of the female gametophyte develops into **endosperm**, food-rich tissue that nourishes the developing embryo.
- One hypothesis for the function of double fertilization is that it synchronizes development of food storage in the seed with development of the embryo.
 - Double fertilization may prevent flowers from squandering nutrients on infertile ovules.
- Another type of double fertilization, in which two embryos are formed, has evolved independently in gymnosperms of the phylum Gnetophyta.
- The seed consists of the embryo, endosperm, and a seed coat derived from the integuments.
- As the ovules develop into seeds, the ovary develops into a fruit.
- After dispersal by wind or animals, a seed germinates if environmental conditions are favorable.
- During germination, the seed coat ruptures and the embryo emerges as a seedling.
- The seedling initially uses the food stored in the endosperm and cotyledons to support development.

The origin and evolution of angiosperms are complex.

- The oldest angiosperm fossils are about 140 million years old.

- During the late Mesozoic, the major branches of the clade diverged from their common ancestor.
- By the mid-Cretaceous period, 100 million years ago, angiosperms began to dominate many terrestrial ecosystems.
 - Earth's landscape changed dramatically as conifers, cycads, and other gymnosperms were replaced by flowering plants in many habitats.
- With flowers and fruits, angiosperms are very different from living gymnosperms.
- To understand how the angiosperm body plan emerged, scientists are studying newly discovered fossils, refining phylogeny, and seeking to understand the developmental patterns that underlie flowers and other angiosperm innovations.
- In the late 1990s, scientists in China discovered fossils of 125-million-year-old angiosperms named *Archaeofructus liaoningensis* and *Archaeofructus sinensis*.
 - These fossils display both derived and primitive traits.
 - *A. sinensis* has anthers and has seeds inside closed carpels but lacks petals and sepals.
- In 2002, scientists completed a phylogenetic comparison of *A. sinensis* with 173 living plants.
 - The researchers concluded that among all known plant fossils, *Archaeofructus* is the most closely related to all living angiosperms.
 - This species may be a “proto-angiosperm,” suggesting that the ancestors of flowering plants were herbaceous rather than woody.
- *Archaeofructus* was found along with fish fossils and may be aquatic.
 - The paleobotanists who discovered *Archaeofructus* suggest that angiosperms originated as aquatic plants.
 - Fast-growing herbaceous plants could have returned to water and thrived there, escaping competition with other seed plants and then later returning to—and dominating—terrestrial ecosystems.
 - Others dispute this idea, pointing out that more derived lineages of angiosperms that have become aquatic tend to evolve simpler flowers similar to the “primitive” flowers of *Archaeofructus*.

Angiosperm phylogeny may shed light on the evolution of the angiosperm body plan.

- Molecular and morphological evidence suggests that living gymnosperms are a monophyletic group whose earliest lineages diverged from the ancestors of angiosperms about 305 million years ago.
 - This does not mean that angiosperms originated 305 million years ago, but it does indicate that ancestors of angiosperms must have lived at that time.
- Angiosperms may, in fact, be most closely related to extinct seed plants such as the Bennettitales, which had flower-like structures that may have been pollinated by insects.
- Paleobotanists have made great progress in understanding the order in which angiosperm clades diverged from one another over time.
 - Molecular and morphological evidence suggests that *Amborella* and water lilies are living representatives of two of the most ancient angiosperm lineages.
- Additional clues about the origin of flowering plants are emerging from studies of plant development.

- A 2006 study demonstrated that egg cells in *Amborella* are formed from precursor cells that differ from the egg precursor cells of most living angiosperms but are similar to those of gymnosperms, a possible link to the ancient common ancestor of gymnosperms and angiosperms.
 - Other studies suggest that in a variety of early angiosperms (including *Amborella*), the outer integument (one of two protective layers that make up the seed coat) appears to be a modified leaf that originates separately from the inner integument.
 - Gymnosperms have only one integument, so scientists are seeking to understand exactly how the second integument originated in angiosperms.
- Finally, in work that holds great promise for deepening our understanding of the origin of flowering plants, researchers are currently studying how genes that control flower development are expressed in a range of gymnosperm and angiosperm species.

Angiosperms are very diverse.

- Angiosperms have diversified into more than 250,000 species that dominate most terrestrial ecosystems.
- Until the late 1990s, flowering plants were divided into **monocots** and **dicots** on the basis of the number of cotyledons, or seed leaves.
- Recent DNA studies support the view that monocots form a clade but reveal that dicots are paraphyletic.
- The majority of plants traditionally called “dicots” form a clade now known as **eudicots** or “true” dicots.
- The remaining plants are divided into several small lineages.
- Three of these lineages are called **basal angiosperms** because they include the oldest known lineages of flowering plants.
 - *Amborella* is a basal angiosperm that lacks vessels that are found in more derived angiosperms.
- Another lineage is the **magnoliids**.
 - Magnoliids encompass 8,000 species, including magnolias.
 - These angiosperms share primitive traits such as spiral arrangement of floral parts with the basal angiosperms.
- One-quarter of angiosperms are monocots.
 - Monocot traits include single cotyledons, parallel venation, scattered vascular bundles, fibrous root systems, pollen grains with a single opening, and floral parts in multiples of three.
- More than two-thirds of angiosperms—170,000 species—are eudicots.
 - Eudicot traits include two cotyledons, netlike venation, vascular bundles arranged as a ring, a taproot, pollen grains with three openings, and floral parts in multiples of four or five.

Animals and angiosperms share evolutionary links.

- Ever since they colonized the land, animals have influenced the evolution of terrestrial plants, and vice versa.

- Plants and animals have been important selective agents for each other.
- Herbivores can reduce a plant's reproductive success by eating its roots, leaves, or seeds.
- If a novel and effective defense against herbivores originates in a group of plants, those plants may be favored by natural selection—as will any herbivores that can overcome this new defense.
- Pollinator-plant relationships and other mutually beneficial interactions may also play a role in natural selection.
- Consider the evolutionary impact of flower petal arrangement.
- Flower petals can be symmetrical in one direction only (bilateral symmetry), or they can be symmetrical in all directions (radial symmetry).
- On a flower with bilateral symmetry, an insect pollinator may be able to obtain nectar only when it approaches the flower from a certain direction.
- Such constraints can make it more likely that as an insect moves from flower to flower, pollen is placed on a part of the insect's body that will come into contact with the stigma of a flower of the same species.
- Because of this specificity of pollen transfer, gene flow may be reduced more easily in diverging populations with bilateral symmetry than in populations with radial symmetry.
- Researchers have hypothesized that speciation should occur more rapidly in flowers with bilateral symmetry than in flowers with radial symmetry.
 - Risa Sargent of the University of British Columbia tested this hypothesis and found that clades with bilaterally symmetrical flowers do indeed have more species than do closely related clades with radially symmetrical flowers.
- Overall, such effects of plant-pollinator interactions are thought to have contributed to the increasing dominance of flowering plants in the Cretaceous period, helping to make angiosperms of central importance in ecological communities and human societies.

Concept 30.4 Human welfare depends greatly on seed plants.

- Humans depend greatly on seed plants as key sources of food, fuel, wood products, and medicine.
- Angiosperms provide nearly all our food.
- Just six crops—wheat, rice, maize, potatoes, cassava, and sweet potatoes—yield 80% of all calories consumed by humans.
- We also feed angiosperms to our livestock, using 5–7 kg of grain to produce a kilogram of beef.
- Modern crops are the products of a relatively recent burst of genetic change, resulting from artificial selection after the domestication of plants 13,000 years ago.
 - In maize, key changes such as increased cob size and removal of the hard coating of the kernels may have been initiated by as few as five gene mutations.
- How did wild plants change so dramatically and so quickly?
 - The answer is likely a combination of deliberate and unconscious selection for plants with desirable traits, such as large fruits and lack of toxins.

- Angiosperms also provide important nonstaple foods, such as tea, coffee, chocolate, and spices.
- Gymnosperms and angiosperms are sources of wood, which is absent in all living seedless plants and consists of an accumulation of tough-walled xylem cells.
 - Wood is the primary source of fuel for much of the world.
 - Wood pulp, typically derived from conifers, is used to make paper.
 - Wood is the world's most widely used construction material.
- Humans depend on seed plants for medicines.
 - Most cultures have a tradition of herbal medicine.
 - Scientific research has identified the relevant secondary compounds in many of these plants, leading to the synthesis of many modern medicines.
 - In the United States, about 25% of prescription drugs contain active ingredients extracted or derived from plants.

Plant diversity is a nonrenewable resource.

- Although plants are a renewable resource, plant diversity is not.
- The demand for space and natural resources resulting from the exploding human population is extinguishing plant species at an extremely rapid rate.
- This extinction is especially acute in the tropics, where more than half the human population lives and where population growth rates are highest.
 - Thirty-five million acres of tropical rain forest, an area nearly the size of the state of Iowa, are cleared each year, a rate that would completely eliminate Earth's tropical forests within 100–150 years.
 - The most common cause of this destruction is the slash-and-burn clearing of forests for agricultural use.
- The loss of plant species is often accompanied by the loss of insects and other rain forest animals.
 - Habitat destruction in rain forests and other ecosystems may be pushing hundreds of species toward extinction each year.
 - If current rates of loss in the tropics and elsewhere continue, scientists estimate that within the next 100–200 years, 50% or more of Earth's species will become extinct.
 - Such losses would constitute a global mass extinction, rivaling the Permian and Cretaceous mass extinctions and forever changing the evolutionary history of land plants (and many other organisms).
- In addition to the ethical concerns that many people have about the extinction of living forms, there are practical reasons to be concerned about the loss of plant diversity.
 - We have explored the potential uses for only a tiny fraction of the 290,000 known plant species.
 - Almost all of our food is based on the cultivation of only about two dozen species of seed plants
 - Researchers have investigated fewer than 5,000 plant species as potential sources of medicines.
 - The tropical rain forests and other plant communities may be a medicine chest of healing plants that could be extinct before we even know they exist.
- We need to view rain forests and other ecosystems as living treasures that we can harvest only at

sustainable rates.