TWELFTH EDITION

CAMPBELL BIOLOGY URRY · CAIN · WASSERMAN MINORSKY · ORR



Chapter 30

Plant Diversity II: The Evolution of Seed Plants

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Fireweed seed

Figure 30.1c



What adaptations have enabled seed plants to make up the vast majority of plant biodiversity?

- A seed consists of an embryo and nutrients surrounded by a protective coat
- Seeds can disperse over long distances by wind or other means
 - For example, fireweed seeds were transported by wind to the Mount St. Helens blast zone a few years after the volcanic eruption

CONCEPT 30.1: Seeds and pollen grains are key adaptations for life on land

- In addition to seeds, all seed plants have reduced gametophytes, heterospory, ovules, and pollen
- These adaptations help plants cope with drought and exposure to ultraviolet (UV) radiation
- Water is not required for fertilization in seed plants

Advantages of Reduced Gametophytes

- Seed plant life cycles are sporophyte-dominated; gametophytes are microscopic and dependent
- Gametophytes develop from spores retained within the sporangia of the sporophyte
- They are protected from environmental stress and receive nutrients form the parent sporophyte

	Mosses and other nonvascular plants	Ferns and other seedless vascular plants	Seed plants (gymnosperms and angiosperms)
Gametophyte	Dominant	Reduced, independent (photosynthetic and free-living)	Reduced (usually microscopic), dependent on surrounding sporophyte tissue for nutrition
Sporophyte	Reduced, dependent on gametophyte for nutrition	Dominant	Dominant
Example	Sporophyte (2n) Gametophyte (n)	Sporophyte (2n) (2n) Gametophyte (n)	Gymnosperm Microscopic female gametophytes (n) inside ovulate cone Microscopic female gametophytes (n) inside these parts of flowers Microscopic male gametophytes (n) inside these parts of flowers (n) inside

Heterospory: The Rule Among Seed Plants

- Homosporous plants produce one kind of spore, and generally have bisexual gametophytes
- Heterosporous plants produce two types of spores, which form either male or female gametophytes
- Ferns and other close relatives of seed plants are homosporous; seed plants are heterosporous

- Spores develop within sporangia born on modified leaves called sporophylls
 - Megasporophylls bear megasporangia that produce megaspores, which form female gametophytes
 - Microsporophylls bear microsporangia that produce microspores, which form male gametophytes

Ovules and Production of Eggs

- An ovule consists of a megaspore within a megasporangium, surrounded by one or more protective coats called integuments
- Gymnosperms typically have one integument, whereas angiosperms generally have two



Pollen and Production of Sperm

- Each microspore develops into a male gametophyte enclosed within the pollen wall, a pollen grain
- Pollination is the transfer of pollen to the part of a seed plant containing the ovules
- Pollen can be transferred long distances by wind or animals, eliminating the reliance on water for sperm transfer

- Pollen grains germinate when they reach the female reproductive structure
- A germinated pollen grain produces a pollen tube
- The pollen tube grows into the ovule and discharges sperm into the female gametophyte

The Evolutionary Advantage of Seeds

- If a sperm fertilizes the egg of a seed plant, the zygote grows into a sporophyte embryo
- The ovule develops into a seed: an embryo, with a food supply, packaged in a protective coat

 Both seeds and spores provide protection from harsh conditions and facilitate dispersal

- Seeds provide evolutionary advantages over spores
 - Seeds are multicellular; spores are single cells
 - Seeds can remain dormant for years until conditions are favorable for germination, whereas spores are shorter-lived
 - Seeds have stored food to nourish growing seedlings; spores do not provide nourishment to gametophytes
 - Seeds can be transported longer distances by wind or animals, but spores usually drop closer to the parent plant

CONCEPT 30.2: Gymnosperms bear "naked" seeds, typically on cones

- Gymnosperms have "naked seeds" exposed on sporophylls that usually form cones
- Most gymnosperms are cone-bearing plants called conifers, such as pines, firs, and redwoods



Nonvascular plants (bryophytes) Seedless vascular plants Gymnosperms Angiosperms

The Life Cycle of a Pine

- Seed plant evolution has included three key reproductive adaptations
 - Miniaturization of gametophytes
 - Production of the seed as a resistant, dispersible stage in the life cycle
 - Pollen, an airborne agent bringing gametes together

- A pine tree is an example of a sporophyte that produces sporangia in male and female cones
- Pollen cones are small and consist of microsporophylls that bear microsporangia
- Microsporocytes undergo meiosis to produce haploid microspores within the microsporangia
- Each microspore develops into a pollen grain containing a male gametophyte
- Cones release large amounts of wind-carried pollen

- Ovulate cones are larger and consist of modified stem tissue and megasporophylls bearing megasporangia
- Within each megasporangium, megasporocytes undergo meiosis to produce haploid megaspores
- Megaspores develop into female gametophytes, which are retained within the megasporangia

- In most pine species, each tree has both male and female cones
- It takes nearly three years from the time the cones first appear to produce mature seeds
- The scales of each ovulate cone separate at maturity and seeds are dispersed by wind
- At germination, the sporophyte embryo emerges as a seedling



Animation: Pine Life Cycle



Early Seed Plants and the Rise of Gymnosperms

- Characteristics found in living seed plants date back to the late Devonian period (380 million years ago)
 - For example, Archaeopteris was a heterosporous tree with a woody stem, but it did not bear seeds
- A 360-million-year-old fossil from the genus *Elkinsia* provides the earliest evidence of seed plants



- The oldest gymnosperm fossils are about 305 million years old
- Gymnosperms replaced seedless vascular plants in the drying climate of the late Carboniferous period
- Seeds, pollen, and adaptations for drought tolerance helped gymnosperms thrive into the Permian period

- Gymnosperms dominated terrestrial ecosystems during the Mesozoic era, 252 to 66 million years ago
- They served as food for herbivorous dinosaurs
- Recent fossil discoveries show that gymnosperms were pollinated by insects over 100 million years ago
- Angiosperms began to replace gymnosperms near the end of the Mesozoic era



Gymnosperm Diversity

- Today, angiosperms dominate most terrestrial ecosystems, but gymnosperms are still important
 - For example, vast regions in northern latitudes are covered by forests of conifers

- The gymnosperms consist of four phyla:
 - Cycadophyta
 - Ginkgophyta
 - Gnetophyta
 - Coniferophyta

Phylum Cycadophyta

- The 350 living species of cycads have large cones and palmlike leaves
- Unlike most seed plants, they have flagellated sperm
- Cycads thrived during the Mesozoic, but today are the most endangered of all plant groups

Figure 30.7

Phylum Cycadophyta



Cycas revoluta

Phylum Ginkgophyta

- Ginkgo biloba is the only living species in this group
- Like the cycads, ginkgos have flagellated sperm
- They are popular in cities because they tolerate air pollution well
- Fleshy seeds produced by female trees smell rancid as they decay

Phylum Ginkgophyta



Ginkgo biloba
Phylum Gnetophyta

- This phylum comprises three genera: *Gnetum*, *Ephedra*, and *Welwitschia*
- Some species are tropical; others live in deserts

Phylum Gnetophyta



Welwitschia Ovulate cones



Gnetum



Welwitschia



Ephedra

Welwitschia

- The only species in this genus, Welwitschia mirabilis, occurs only in deserts of Southwestern Africa
- Plants can live for thousands of years
- They have large straplike leaves and produce ovulate cones on stalks

Figure 30.7



Welwitschia

Ephedra

- The approximately 40 species in this genus inhabit arid regions worldwide
- They produce ephedrine, a compound used medicinally as a decongestant



Ephedra

Gnetum

- This genus includes about 35 species of tropical trees, shrubs, and vines, mainly in Africa and Asia
- The leaves look similar to flowering plants, and seeds look somewhat like fruits

Figure 30.7



Gnetum

Phylum Coniferophyta

- With about 600 species, this is the largest phylum of the gymnosperms
- Most have woody cones and some have fleshy cones
- Leaves are needlelike in some and scalelike in others
- Most are evergreens and retain leaves year round; some deciduous species drop their leaves in autumn

Phylum Coniferophyta



Common juniper

Phylum Coniferophyta



Douglas fir



Wollemi pine





European larch



Sequoia

CONCEPT 30.3: The reproductive adaptations of angiosperms include flowers and fruits

- Angiosperms are seed plants with reproductive structures called flowers and fruits
- With more than 290,000 species (90% of all plants), they are the most diverse and widespread plants



Nonvascular plants (bryophytes) Seedless vascular plants Gymnosperms Angiosperms

Characteristics of Angiosperms

- All angiosperms belong to the phylum Anthophyta
- Angiosperms have two key adaptations: flowers and fruit

Flowers

- The flower is an angiosperm structure specialized for sexual reproduction
- In many species, insects or other animals transfer pollen from one flower to the sex organs of another
- Some angiosperms are wind pollinated, particularly those that occur in dense populations, such as grass

- A flower is a specialized shoot with up to four types of modified leaves called floral organs:
 - Sepals are usually green and enclose the flower bud
 - Petals are often brightly colored to attract pollinators; wind-pollinated flowers are not usually brightly colored
 - Stamens are microsporophylls, male reproductive organs
 - Carpels are megasporophylls, female reproductive organs



Video: Flower Blooming



- A stamen consists of a stalk called a filament, with a terminal sac called an anther
- Microspores are produced within the anthers and develop into pollen grains which contain the male gametophytes

- A carpel consists of an ovary at the base of a style leading up to a sticky stigma that receives pollen
- The ovary contains the female gametophyte(s) within the ovule(s)
- Fertilized ovules develop into seeds
- The term **pistil** can be used to refer to a single carpel or two or more fused carpels

- Flowers are variable in shape, size, color, and odor
 - For example, some flowers have radial symmetry, while others have bilateral symmetry
 - In radial symmetry, any imaginary line through the central axis divides the flower into two equal parts
 - In bilateral symmetry, a flower can only be divided into two equal parts by a single imaginary line





Fruits

- As seeds develop, the ovary wall thickens and the ovary matures into a **fruit**
 - For example, a pea pod is a fruit with seeds (mature ovules, peas) encased in a ripened ovary (the pod)
- Fruits protect seeds and aid in their dispersal

- Mature fruits can be either fleshy or dry
 - For example, tomatoes, plums, and grapes are fleshy fruits with a soft ovary wall (pericarp)
 - Dry fruits include beans, nuts, and grains; some split open and release mature seeds, others remain closed



- Various adaptations of fruits and seeds help to disperse seeds
 - Some fruits, such as dandelions, function like parachutes for wind dispersal
 - Some, such as coconuts, are adapted to float for dispersal by water
 - Fruits modified as burrs cling to animal fur
 - Sweet tasting, vividly colored fruits are eaten by animals and dispersed in their feces

Figure 30.11



Animation: Fruit Structure and Seed Dispersal



The Angiosperm Life Cycle

- Male gametophytes are contained within pollen grains produced by the microsporangia of anthers
- Each ovule develops within the ovary and contains a female gametophyte, also called an **embryo sac**
- The egg is contained within the embryo sac

- Pollen is released from the anther and carried to the sticky stigma at the tip of a carpel
- Some flowers can self-pollinate, but most have mechanisms to ensure cross-pollination, transfer of pollen from a different individual
 - For example, the stamens and carpels of a single flower may mature at different times

- Pollen grains germinate on the stigma and produce a pollen tube that grows down to the ovary
- The pollen tube penetrates the **micropyle**, a pore in the integuments, and discharges two sperm cells

- Both sperm cells are used in a process called double fertilization
 - One sperm fertilizes the egg, forming a diploid zygote
 - The other sperm fuses with two nuclei in the embryo sac, forming a triploid cell (3n)

- The fertilized ovule matures into a seed
- The zygote forms a sporophyte embryo with a simple root and one or two cotyledons (seed leaves)
- The triploid cell forms the **endosperm**, tissue rich in starch and other food for the developing embryo

- In favorable conditions, the seed may germinate
- The seed coat ruptures and the embryo emerges as a seedling
- Food stored in the endosperm and cotyledons is used until the seedling can start photosynthesis



Video: Angiosperm Life Cycle

Angiosperm Life Cycle



Animation: Plant Fertilization


Animation: Seed Development



Angiosperm Evolution

- Angiosperms appear suddenly and widely in the fossil record from about 100 million years ago
- We currently do not understand how angiosperms arose from earlier seed plants

Fossil Angiosperms

- Angiosperms originated in the early Cretaceous period, about 140 million years ago
- They dominated some terrestrial ecosystems by the mid-Cretaceous, about 100 million years ago
- They diversified through the mass extinctions at the end of the Cretaceous, 66 million years ago

- The earliest pollen fossils with angiosperm characteristics are 130 million years old
- The earliest fossils of larger flowering plant structures are more recent
 - For example, Archaefructus and Leefructus were discovered in 125 million year old rocks in China

- Archaefructus, an herbaceous and likely aquatic plant, is not thought to be the common ancestor
- Fossils of other seed plants closely related to angiosperms indicate the ancestor was probably woody and not aquatic





Angiosperm Phylogeny

- Extant gymnosperms diverged from the lineage leading to angiosperms about 305 million years ago
- Angiosperms may be more closely related to Bennettitales, extinct seed plants with flowerlike structures



(a) A close relative of the angiosperms?

(b) Angiosperm phylogeny

- Amborella trichopoda, water lilies, and star anise are representatives of lineages that diverged early in the history of angiosperms
- Based on the features of these groups, early angiosperms were likely small-flowered, woody shrubs with simple water-conducting cells

Evolutionary Links with Animals

- Animals and plants have influenced each other's evolutionary histories
 - For example, animal herbivory selects for plant defenses and plants select for herbivores that can overcome their defenses

- Plant-pollinator interactions may have affected the rate of new species formation
 - For example, bilaterally symmetrical flowers force pollinators into a specific position to receive pollen
 - This ensures that pollen will contact the stigma when the pollinator visits another flower of the same species
 - Reduced crosses between morphologically diverging populations may increase the speciation rate



Video: Bee Pollinating



- The hypothesis can be tested by comparing the number of species in closely related "bilateral" and "radial" clades
- In a study comparing 19 species pairs, on average, the "bilateral" clade had 2,400 more species than the "radial" clade



Angiosperm Diversity

- Angiosperms comprise more than 290,000 species
- They have been historically divided into two groups
 - Monocots (one cotyledon)
 - **Dicots** (two cotyledons)
- **Eudicots** ("true" dicots) form a clade that includes most of the species once categorized as dicots



- The remaining dicots form several small lineages
 - Basal angiosperms include the flowering plants belonging to the oldest lineages, *Amborella*, water lilies, star anise and relatives
 - Magnoliids share some traits with basal angiosperms but evolved later

Basal Angiosperms

- About 100 species composing three small lineages constitute the basal angiosperms
- These include Amborella trichopoda, water lilies, and star anise

Basal Angiosperms



Water lily (Nymphaea "Rene Gerard")



Star anise (Illicium)



Amborella trichopoda

Magnoliids

- Magnoliids consist of about 8,500 species, including both woody and herbaceous plants
- They share some traits with basal angiosperms, such as spirally arranged floral organs
- They are genetically more closely related to monocots and eudicots than basal angiosperms

Magnoliids



Southern magnolia (*Magnolia grandiflora*)

Monocots

- About one-quarter of angiosperms are monocots about 72,000 species
- The largest groups are the orchids, grasses, and palms
- Grasses include some of the most agriculturally important crops, such as maize, rice, and wheat

Monocots





Orchid (Paphiopedilum callosum)

Barley (*Hordeum vulgare*), a grass



Pygmy date palm (*Phoenix roebelenii*)

Eudicots

- More than two-thirds of angiosperms are eudicots—roughly 210,000 species
- The largest group is the legume family including crops such as peas and beans
- The economically important rose family includes species with ornamental flowers and edible fruits
- Most familiar flowering trees are eudicots, such as oak, maple, walnut, willow, and birch

Eudicots



Snow pea (*Pisum* sativum), a legume



Dog rose (*Rosa canina*), a wild rose



CONCEPT 30.4: Human welfare depends on seed plants

- Seed plants are key sources of food, fuel, wood products, and medicine
- Our reliance on seed plants makes preservation of plant diversity critical

Products from Seed Plants

- Most of our food comes from angiosperms
- Six crops (wheat, rice, maize, potatoes, cassava, and sweet potatoes) yield 80% of the calories consumed by humans
- Angiosperms also feed livestock: 5–7 kg of grain are needed to produce 1 kg of grain-fed beef

- Modern crops are products of relatively recent genetic change resulting from artificial selection
- The number and size of seeds are greater in domesticated plants compared to wild relatives

- Flowering plants provide edible products including tea, coffee, chocolate, and spices
- Many seed plants are sources of wood used for fuel, paper production, and construction
- Medicinally active compounds in seed plants are used directly or synthesized to produce medicines

Table 30.1 Examples of Plant-Derived Medicines

Compound	Source	Use
Atropine	Belladonna plant	Eye pupil dilator
Digitalin	Foxglove	Heart medication
Menthol	Eucalyptus tree	Throat soother
Quinine	Cinchona tree	Malaria preventive
Taxol	Pacific yew	Ovarian cancer drug
Tubocurarine	Curare tree	Muscle relaxant
Vinblastine	Periwinkle	Leukemia drug

Threats to Plant Diversity

- Habitat destruction is threatening plants species worldwide
- In the tropics, 63,000 km² are cleared each year
- At this rate, the remaining tropical forests will be eliminated in 175 years
- Loss of forests reduces the absorption of CO₂ by photosynthesis, contributing to global warming



- The loss of plant species is often accompanied by the loss of insects and other animals they support
- At the current rate of habitat loss, 50% or more of Earth's species will be extinct within a few centuries
- This causes practical, as well as ethical concerns
 - For example, tropical rain forests likely contain undiscovered plants with useful medicinal compounds

Data from the Experiment

	Fraction of Carbon-14 Remaining
Seed 1 (not planted)	0.7656
Seed 2 (not planted)	0.7752
Seed 3 (germinated)	0.7977

Data from S. Sallon et al, *Germination, Genetics, and Growth of an Ancient Date Seed.* Science 320:1464 (2008).

Figure 30.UN04


Figure 30.UN05

Five Derived Traits of Seed Plants	
Reduced gametophytes	Microscopic male and female gametophytes (<i>n</i>) are nourished and protected by the sporophyte (2 <i>n</i>) Male gametophyte Female gametophyte
Heterospory	Microspore (gives rise to a male gametophyte) Megaspore (gives rise to a female gametophyte)
Ovules	Ovule (gymnosperm) Integument (2 <i>n</i>) Megaspore (<i>n</i>) Megasporangium (2 <i>n</i>)
Pollen	Pollen grains make water unnecessary for fertilization
Seeds	Seeds: survive better than unprotected spores, can be transported long distances



Figure 30.UN07

