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Plant Diversity II: The Evolution of Seed Plants

KEY CONCEPTS

- **30.1** Seeds and pollen grains are key adaptations for life on land
- **30.2** Gymnosperms bear "naked" seeds, typically on cones
- **30.3** The reproductive adaptations of angiosperms include flowers and fruits
- **30.4** Human welfare depends greatly on seed plants

▲ **Figure 30.1 What human reproductive organ is functionally similar to this seed?**

OVERVIEW

Transforming the World

Continuing the saga of how plants have transformed Earth, this chapter follows the emergence and diversification of seed plants. Fossils and comparative studies of living plants offer clues about the origin of seed plants some 360 million years ago. As this new group of plants became established, they dramatically altered the course of plant evolution. We'll begin our exploration of how this occurred by looking at the innovation for which seed plants are named: seeds **(Figure 30.1)**.

A **seed** consists of an embryo and its food supply, surrounded by a protective coat. When mature, seeds are dispersed from their parent by wind or other means. Because it nourishes and protects the embryo—yet can move away from the mother plant—a seed is analogous to a detachable and mobile version of a pregnant woman's womb. As we'll see, seeds are a key adaptation that helped seed plants to become the dominant producers on land and to make up the vast majority of plant biodiversity today.

Seed plants have also had an enormous impact on human society. Starting about 13,000 years ago, humans began to cultivate wheat, figs, maize (commonly called corn in the United States), bananas, and other wild seed plants. This practice emerged independently in various parts of the world, including the Near East, East Asia, Africa, and the Americas. One piece of evidence, the well-preserved squash seed in Figure 30.1, was found in a cave in Mexico and dates from between 8,000 and 10,000 years ago. This seed differs from wild squash seeds, suggesting that squash was being domesticated by that time. The domestication of seed plants, particularly angiosperms, produced the most important cultural change in human history, transforming most human societies from roving bands of hunter-gatherers to permanent settlements anchored by agriculture.

In this chapter, we will first examine the general characteristics of seed plants. Then we will look at the distinguishing features and evolution of gymnosperms and angiosperms.

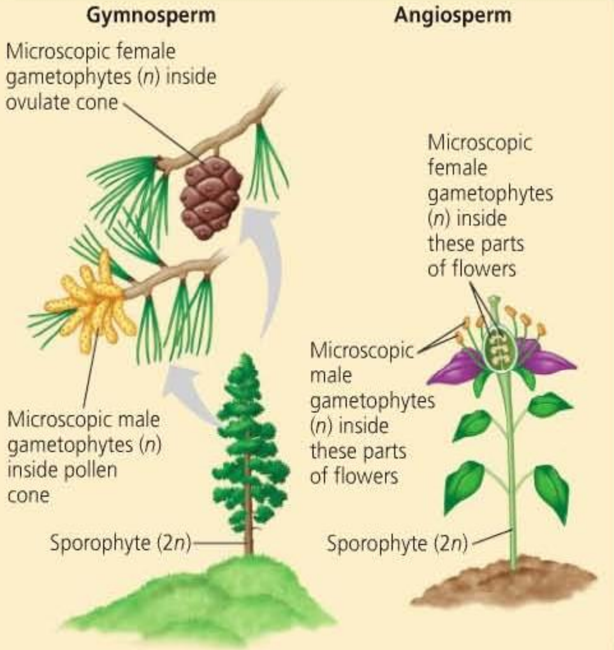
CONCEPT 30.1

Seeds and pollen grains are key adaptations for life on land

We begin with an overview of terrestrial adaptations that seed plants added to those already present in nonvascular plants (bryophytes) and seedless vascular plants (see Chapter 29). In addition to seeds, the following are common to all seed plants: reduced gametophytes, heterospory, ovules, and pollen. As you'll read, these adaptations provided new ways for seed plants to cope with terrestrial conditions such as drought and exposure to the ultraviolet (UV) radiation in sunlight. Novel adaptations also freed seed plants from requiring water for fertilization, enabling reproduction to occur under a broader range of conditions than in seedless plants.

Advantages of Reduced Gametophytes

Mosses and other bryophytes have life cycles dominated by gametophytes, whereas ferns and other seedless vascular plants have sporophyte-dominated life cycles. The evolutionary trend

	PLANT GROUP		
	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			

▲ Figure 30.2 **Gametophyte-sporophyte relationships in different plant groups.**

of gametophyte reduction continued further in the vascular plant lineage that led to seed plants. While the gametophytes of seedless vascular plants are visible to the naked eye, the gametophytes of seed plants are mostly microscopic.

This miniaturization allowed for an important evolutionary innovation in seed plants: Their tiny gametophytes can develop from spores retained within the sporangia of the parental sporophyte. This arrangement protects the delicate female (egg-containing) gametophytes from environmental stresses. The moist reproductive tissues of the sporophyte shield the gametophytes from UV radiation and protect against drying out. This relationship also enables the dependent gametophytes to obtain nutrients from the sporophyte. In contrast, the free-living gametophytes of seedless plants must fend for themselves. **Figure 30.2** contrasts the gametophyte-sporophyte relationships in nonvascular plants, seedless vascular plants, and seed plants.

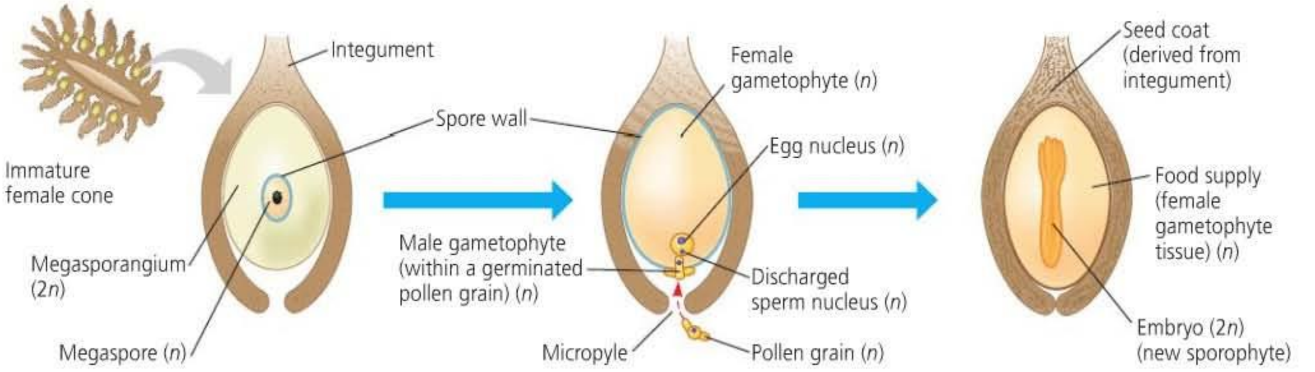
Heterospory: The Rule Among Seed Plants

You read in Chapter 29 that nearly all seedless plants are homosporous—they produce one kind of spore, which usually gives rise to a bisexual gametophyte. The closest relatives of seed plants are all homosporous, suggesting that seed plants had homosporous ancestors. At some point, seed plants or their ancestors became heterosporous: Megasporangia produce megaspores that give rise to female gametophytes, and microsporangia produce microspores that give rise to male gametophytes. Each megasporangium has a single functional megaspore, whereas each microsporangium contains vast numbers of microspores.

As we noted previously, the miniaturization of seed plant gametophytes likely contributed to the great success of this clade. Next we will look at the development of the female gametophyte within an ovule and the development of the male gametophyte in a pollen grain. Then we will follow the transformation of a fertilized ovule into a seed.

Ovules and Production of Eggs

Although a few species of seedless plants are heterosporous, seed plants are unique in retaining the megasporangium and megaspore within the parent sporophyte. A layer of sporophyte tissue called **integument** envelops and protects the megasporangium.



(a) Unfertilized ovule. In this longitudinal section through the ovule of a pine (a gymnosperm), a fleshy megasporangium is surrounded by a protective layer of tissue called an integument. (Angiosperms have two integuments.)

(b) Fertilized ovule. A megaspore develops into a multicellular female gametophyte. The micropyle, the only opening through the integument, allows entry of a pollen grain. The pollen grain contains a male gametophyte, which develops a pollen tube that discharges sperm, thereby fertilizing the egg.

(c) Gymnosperm seed. Fertilization initiates the transformation of the ovule into a seed, which consists of a sporophyte embryo, a food supply, and a protective seed coat derived from the integument.

▲ **Figure 30.3 From ovule to seed in a gymnosperm.**

? *A gymnosperm seed contains cells from how many different plant generations? Identify the cells and whether each is haploid or diploid.*

Gymnosperm megasporangia are surrounded by one integument, whereas those in angiosperms usually have two integuments. The whole structure—megasporangium, megaspore, and their integument(s)—is called an **ovule** (**Figure 30.3a**). Inside each ovule (from the Latin *ovulum*, little egg), a female gametophyte develops from a megaspore and produces one or more eggs.

Pollen and Production of Sperm

A microspore develops into a **pollen grain** that consists of a male gametophyte enclosed within the pollen wall. The tough pollen wall, which contains the polymer sporopollenin, protects a pollen grain as it is transported from the parent plant by wind, for example, or by hitchhiking on the body of an animal. The transfer of pollen to the part of a seed plant that contains the ovules is called **pollination**. If a pollen grain germinates (begins growing), it gives rise to a pollen tube that discharges sperm into the female gametophyte within the ovule, as shown in **Figure 30.3b**.

Recall that in nonvascular plants and seedless vascular plants such as ferns, free-living gametophytes release flagellated sperm that must swim through a film of water to reach eggs. The distance for this sperm transport rarely exceeds a few centimeters. By contrast, in seed plants a sperm-producing male gametophyte inside a pollen grain can be carried long distances by wind or by animals, eliminating the dependence on water for sperm transport. The sperm of seed plants also do not require motility because sperm are carried directly to the eggs by pollen tubes. Living gymnosperms provide evidence of the evolutionary transition to nonmotile sperm. The sperm of some gymnosperm species (such as ginkgos and cycads, depicted a little later in Figure 30.5) retain the ancient flagellated condition, but flagella have been lost in the sperm of most gymnosperms and all angiosperms.

The Evolutionary Advantage of Seeds

If a sperm fertilizes an egg of a seed plant, the zygote grows into a sporophyte embryo. As shown in **Figure 30.3c**, the whole ovule develops into a seed: the embryo, along with a food supply, packaged within a protective coat derived from the integument(s).

Until the advent of seeds, the spore was the only protective stage in any plant life cycle. Moss spores, for example, may survive even if the local environment becomes too cold, too hot, or too dry for the mosses themselves to live. Their tiny size enables the moss spores to be dispersed in a dormant state to a new area, where they can germinate and give rise to new moss gametophytes if and when conditions are favorable enough for them to break dormancy. Spores were the main way that mosses and other seedless plants spread over Earth for the first 100 million years of plant life on land.

Although mosses and other seedless plants continue to be very successful today, seeds represent a major evolutionary innovation that contributed to the opening of new ways of life for seed plants. What advantages do seeds provide over spores? Spores are usually single-celled, whereas seeds have a multicellular layer of tissue, the seed coat, that provides extra protection to the embryo. Unlike spores, seeds also have a supply of stored food. This enables a seed to remain dormant for days, months, or even years after being released from the parent plant. (Most spores have much shorter lifetimes.) Under favorable conditions, the seed can then germinate, with its stored food providing critical support for growth as the sporophyte embryo emerges as a