

## Plant Growth and Reproduction

### The Control of Patterning in Plant Root Development

Did you ever think of how a root grows? Down in the dark, with gravity its only cue, the very tip of the root elongates, periodically forming a node from which root branches will extend. How does the root determine the position of its branches, and the spacing between them? The serial organization of the root's branches is controlled by events that happen on a microscopic scale out at the very tip of the root, the so-called root apex. There, within a space of a millimeter or less, molecular events occur that orchestrate how the root will grow and what it will be like.

The problem of understanding how a plant's root apex controls the way a root develops is one example of a much larger issue, perhaps the most challenging research problem in modern botany: What mechanism mediates central pattern formation in the plant kingdom? Almost nothing was known of these mechanisms a decade ago, but intensive research is now rapidly painting in the blank canvas.

Much of the most exciting research on plant pattern formation is being performed on a small weedy relative of the mustard plant, the wall cress *Arabidopsis thaliana* (see photo above). With individual plants no taller than your thumb that grow quickly in laboratory test-tubes, *Arabidopsis* is an ideal model for studying plant development. Its genome, about the size of the fruit fly *Drosophila*, has been completely sequenced, greatly aiding research into the molecular events underlying pattern formation.

To gain some insight into the sort of research being done, we will focus on work being done by John Schiefelbein and colleagues at the University of Michigan. Schiefelbein has focused on one sharply defined aspect of plant root pattern formation in *Arabidopsis*, the formation of root hairs on the epidermis, the root's outer layer of cells. These root hairs constitute the principal absorbing surface of the root, and their position is under tight central control.

In a nutshell, the problem of properly positioning root hairs is one of balancing cell production and cell differentiation. Cells in the growth zone beneath the surface of the root—a sheath called a meristem—are constantly dividing. The cells that are produced by the meristem go on to differ-



*Arabidopsis thaliana*. An important plant for studying root development because it offers a simple pattern of cellular organization in the root.

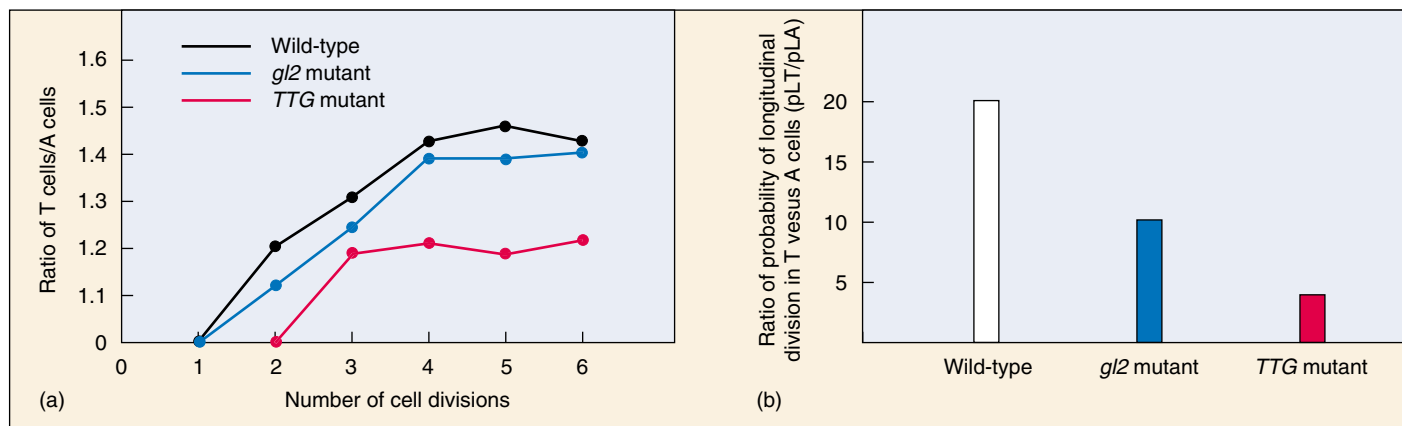
entiate into two kinds of cells: trichoblasts which form hair-bearing epidermal cells, and atrichoblasts which form hairless epidermal cells. The positioning of trichoblasts among atrichoblasts determines the pattern of root hairs on the developing root.

When researchers looked very carefully at the dividing root meristem, they found that the initial cells determined to be trichoblasts and atrichoblasts alternate with one another in a ring of 16 cells around the circumference of the root. As the cells divide, more and more cells are added, forming columns of cells extending out in 16 files. As the files extend farther and farther out, occasional side-ways divisions fill in the gaps that develop, forming new files.

Maintaining this simple architecture requires that the root maintain a tight control of the plane and rate to cell division. Because this rate is different for the two cell types, the root must also control the rate at which the cell types differentiate. Schiefelbein set out to learn how the root apex coordinates these two processes.

To get a handle on the process, Schiefelbein seized on a recently characterized root pattern mutant called *transparent testa glabra (TTG)*. This mutant changes the pattern of root hairs in *Arabidopsis*, and it has been proposed that it controls whether a cell becomes a trichoblast or an atrichoblast. But does it control the rate and orientation in the root meristem epidermis?

To answer this question, Schiefelbein's team used clonal analysis to microscopically identify individual cell types in the root epidermis, and set out to see if they indeed divide at different rates, and if the *TTG* mutation affects these rates differently. If so, there must be a link between cell differentiation and the control of cell division in plants.



**Comparing the differentiation and cell division of trichoblast (T) cells versus atrichoblast (A) cells in root epidermis.** (a) As cell divisions proceeded, T cells and A cells were identified in the root epidermis of wild-type plants and two mutants, *gl2* and *TTG*. Comparing the ratio of T cells to A cells, there is an increase in the number of A cells compared to T cells in the *TTG* mutant. (b) The rate of cell division was also examined by comparing the ratio of probabilities of longitudinal anticlinal cell division in T cells and A cells among the wild-type and mutant plants. This ratio was lowest in *TTG* mutants, indicating that this mutation affects cell division.

## The Experiment

Two developmental mutants of *A. thaliana* were compared to investigate whether the control of cell differentiation and the rate of cell division were linked. One, *TTG*, alters early events in root epidermal cell differentiation, while the other, *glabra2* (*gl2*) acts later.

The investigators first set out to map the surface of the roots of each mutant type, as well as those of nonmutant wild type. To avoid confusion in studying files of cells, it is necessary to clearly identify the starting point of each file of cells. To do this, roots were selected that contained clones of trichoblast and atrichoblast produced by longitudinal cell divisions perpendicular to the surface of the root. Called longitudinal anticlinal cell divisions, these clones are rare but easily recognized when stained with propidium iodide. Careful mapping of individual cells with a confocal microscope allowed investigators to determine the number and location of trichoblast and atrichoblast cells present in the epidermal tissue of each clone.

## The Results

The researchers made two important observations based on their visual identification of individual trichoblast and atrichoblast cells in the various plant types examined.

1. *The two cell types are produced at different rates.* Among plants that had been cultured for up to six cell divisions, they observed a significant difference in the ratio of trichoblast (T) versus atrichoblast (A) cells following two or more cell divisions. In their study you can readily see that the *TTG* mutant produces a significantly lower ratio of T cells to A cells compared to the wild-type plants or *gl2* mutants (see graph *a* above). This strongly suggests that *TTG* is involved in controlling the rate of cell division in the T cell file.

2. *TTG controls the rate of longitudinal cell division.* The re-

search team went on to examine longitudinal cell divisions that fill in the gaps as cell division causes files of cells to extend outward from the meristem. The researchers set out to determine the probability of such longitudinal anticlinal cell division occurring in the three types of plants shown in graph *a*. The more rapidly cell files are produced, the more often longitudinal divisions would be required to fill in gaps between files. For proper root hair position to be maintained, the rate of this longitudinal division would have to be tightly coordinated with the rate of vertical division within the file.

The investigators found that longitudinal cell division, always rare, was usually seen, when it did occur, in T cell files. Did the *TTG* mutation affect this process as well as file-extending cell divisions? This was determined by examining the ratio of the probability of longitudinal anticlinal divisions in T cells versus A cells (pLT/pLA).

Researchers compared the ratio in wild-type plants with that in the two mutants, *TTG* and *gl2*. Did the *TTG* mutation alter longitudinal division? Yes! Their results indicate at least a 60% reduction in the pLT/pLA ratio of the *TTG* mutant compared to wild type and *gl2* plants (see graph *b* above). The percent of clones in the A file of the *TTG* mutants exhibiting this type of cell division was twice that seen in the wild-type or *gl2* mutants.

This observation directly supports the hypothesis that the *TTG* gene is not only required for cell division in the T cell file, but also controls longitudinal cell divisions which are characteristically more frequent in trichoblasts.

The research team concluded from these studies that *TTG* is probably the earliest point of control of root epidermis cell fate specification, and that this control most likely acts by negatively controlling trichoblast cell fate.



To explore this experiment further, go to the Virtual Lab at [www.mhhe.com/raven6/vlab11.mhtml](http://www.mhhe.com/raven6/vlab11.mhtml)

# 40

## Early Plant Development

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### Concept Outline

#### 40.1 Plant embryo development establishes a basic body plan.

**Establishing the Root-Shoot Axis.** Asymmetric cell division starts patterning the embryo. Early in embryogenesis the root-shoot axis is established.

**Establishing Three Tissue Systems.** Three tissue systems are established without any cell movement. While the embryo is still a round ball, the root-shoot axis is established. The shape of the plant is determined by planes of cell division and direction of cell elongation. Nutrients are used during embryogenesis, but proteins, lipids, and carbohydrates are also set aside to support the plant during germination before it becomes photosynthetic.

#### 40.2 Seed formation protects the dormant embryo from water loss.

**How Seeds Form.** Seeds allow plants to survive unfavorable conditions and invade new habitats.

#### 40.3 Fruit formation enhances the dispersal of seeds.

**How Fruits Form.** Seed-containing fruits are carried far by animals, wind and water, allowing angiosperms to colonize large areas.

#### 40.4 Germination initiates post-seed development.

**Mechanisms of Germination.** External signals including water, light, abrasion, and temperature can trigger germination. Rupturing the seed coat and adequate oxygen are essential. Stored reserves in the endosperm or cotyledon are made available to the embryo during germination.



**FIGURE 40.1**

**This plant has recently emerged from its seed.** It is extending its shoot and leaves up into the air, toward light.

In chapter 37 we emphasized evolutionary changes in reproduction and physiology that gave rise to the highly successful flowering plants (angiosperms). Chapters 38 and 39 explored the morphological and anatomical development of the angiosperm sporophyte, where most of these innovations occurred. In the next few chapters, we continue our focus on the sporophyte generation of the angiosperms. In many cases, we will use the model plant *Arabidopsis*, a weedy member of the mustard family. Its very small genome has allowed plant biologists to study how genes regulate plant growth and development. In this chapter, we will follow the development of the embryo through seed germination (figure 40.1). The next few chapters will also continue to emphasize the roles of gene expression, hormones, and environmental signals in regulating plant development and function.

## 40.1 Plant embryo development establishes a basic body plan.

### Establishing the Root-Shoot Axis

In plants, three-dimensional shape and form arises by regulating the amount and pattern of cell division. Even the very first cell division is asymmetric resulting in two different cell types. Early in embryo development most cells can give rise to a wide range of cell and organ types, including leaves. As development proceeds, the cells with multiple potentials are restricted to regions called meristems. Many meristems are established by the time embryogenesis ends and the seed becomes dormant. Apical meristems will continue adding cells to the growing root and shoot tips after germination. These generate the large numbers of cells needed to form leaves, flowers, and all other components of the mature plant. Apical meristem cells of corn, for example, divide every 12 hours, producing half a million cells a day in an actively growing corn plant. Lateral meristems can cause an increase in the girth of some plants, while intercalary meristems within the stems allow for elongation.

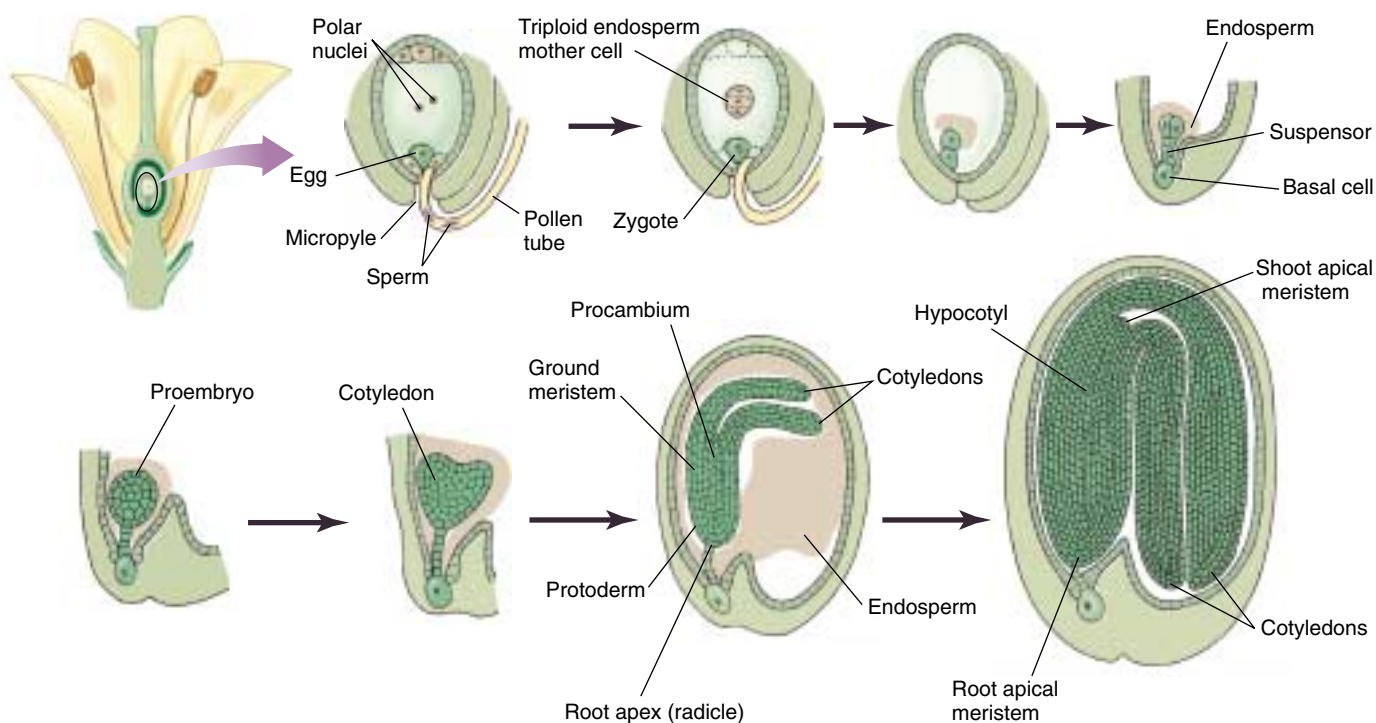
In addition to developing the root-shoot axis in embryogenesis, cell differentiation occurs and three basic tissue systems are established. These are the dermal, ground, and vascular tissue systems and they are radially patterned. These tissue systems contain various cell types that can be highly differentiated for specific functions.

These tissue systems are organized radially around the root-shoot axis.

While the embryo is developing, two other critical events are occurring. A food supply is established that will support the embryo during germination while it gains photosynthetic capacity. This starts with the second fertilization event that produces endosperm in angiosperms. Secondly, ovule tissue (from the parental sporophyte) differentiates to form a hard, protective covering around the embryo. The seed (ovule containing the embryo) then enters a dormant phase, signaling the end of embryogenesis. Environmental signals (for example, water, temperature, and light) can break dormancy and trigger a cascade of internal events resulting in germination.

### Early Cell Division and Patterning

The first division of the fertilized egg in a flowering plant is asymmetric and generates cells with two different fates (figure 40.2). One daughter cell is small, with dense cytoplasm. That cell, which will become the embryo, begins to divide repeatedly in different planes, forming a ball of cells. The other daughter cell divides repeatedly, forming an elongated structure called a *suspensor*, which links the embryo to the nutrient tissue of the seed. The suspensor also



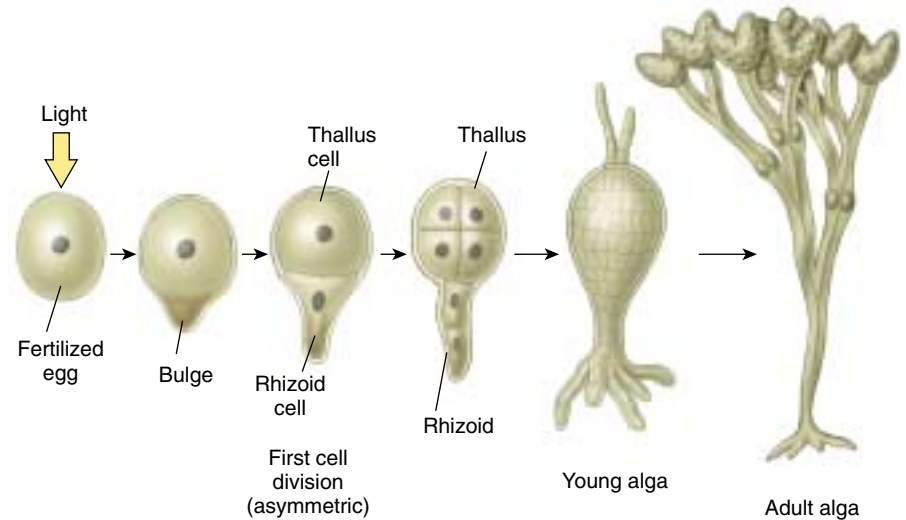
**FIGURE 40.2**

**Stages of development in an angiosperm embryo.** The very first cell division is asymmetric. Differentiation begins almost immediately after fertilization.

**FIGURE 40.3**

**Asymmetric cell division in a *Fucus* zygote.**

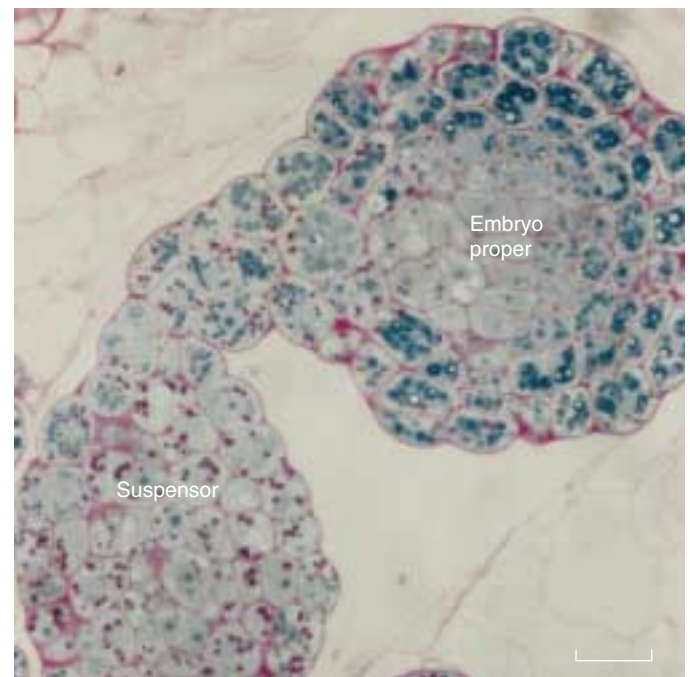
An unequal distribution of material in the fertilized egg leads to a bulge where the first cell division will occur. This division results in a smaller cell that will go on to divide and produce the rhizoid that anchors the plant; the larger cell divides to form the thallus or main plant body. The point of sperm entry determines where the smaller rhizoid cell will form, but light and gravity can modify this to ensure that the rhizoid will point downward where it can anchor this brown alga. Calcium-mediated currents set up an internal gradient of charged molecules which lead to a weakening of the cell wall where the rhizoid will form. The fate of the two resulting cells is held in memory by cell wall components.



provides a route for nutrients to reach the developing embryo. The root-shoot axis also forms at this time. Cells near the suspensor are destined to form a root, while those at the other end of the axis ultimately become a shoot.

Investigating the asymmetry of the first cell division is difficult because the fertilized egg is embedded within the gametophyte, which is surrounded by sporophyte tissue (ovule and carpel tissue). One approach has been to use the brown alga *Fucus* as a model system. Although there is a huge evolutionary difference between brown algae and the angiosperms, there are similarities in early embryogenesis which may have ancient origins. The egg is released prior to fertilization so there are no extra tissues surrounding the zygote (fertilized egg). One side of the zygote begins to bulge establishing the vertical axis. Cell division occurs and the original bulge becomes the smaller of the two cells. It develops into a rhizoid that anchors the alga and the other cell develops into the main body, or thallus, of the sporophyte. This axis is first established by the point of sperm entry, but can be changed by environmental signals, especially light and gravity which ensure that the rhizoid is down and the thallus is up. Internal gradients are established that specify where the rhizoid will form in response to environmental signals (figure 40.3). The ability to “remember” where the rhizoid will form depends on the cell wall. Enzymatic removal of the cell wall in *Fucus* cells specified to form either rhizoids or plant body, resulted in cells that could give rise to both. Cell walls contain a wide variety of carbohydrates and proteins attached to the wall’s structural fibers. Attempting to pin down the identities of these suspected developmental signals is an area of active research.

Another approach to investigating the initial asymmetry in embryos has been to study mutants with abnormal suspenders. By understanding what is going wrong, it is often possible to infer normal developmental mechanisms. For example, the *suspensor* mutant in *Arabidopsis* has aberrant



**FIGURE 40.4**

**The embryo suppresses development of the suspensor as a second embryo.** This *suspensor* mutant of *Arabidopsis* has a defect appear in embryo development followed by embryo-like development of the suspensor.

development in the embryo followed by embryo-like development of the suspensor (figure 40.4). From this, one can conclude that the embryo normally prevents the suspensor from developing into a second embryo.

**Early in embryogenesis the root-shoot axis is established.**

## Establishing Three Tissue Systems

Three basic tissues differentiate while the plant embryo is still a ball of cells, the globular stage (figure 40.5), but no cell movements are involved. The *protoderm* consists of the outermost cells in a plant embryo and will become *dermal tissue*. These cells almost always divide with their cell plate perpendicular to the surface. This perpetuates a single outer layer of cells. Dermal tissue produces cells that protect the plant from desiccation, including the stomata that open and close to facilitate gas exchange and minimize water loss. The bulk of the embryonic interior consists of *ground tissue* cells that eventually function in food and water storage. Lastly, *procambium* at the core of the embryo is destined to form the future *vascular tissue* responsible for water and nutrient transport.

### Root and Shoot Formation

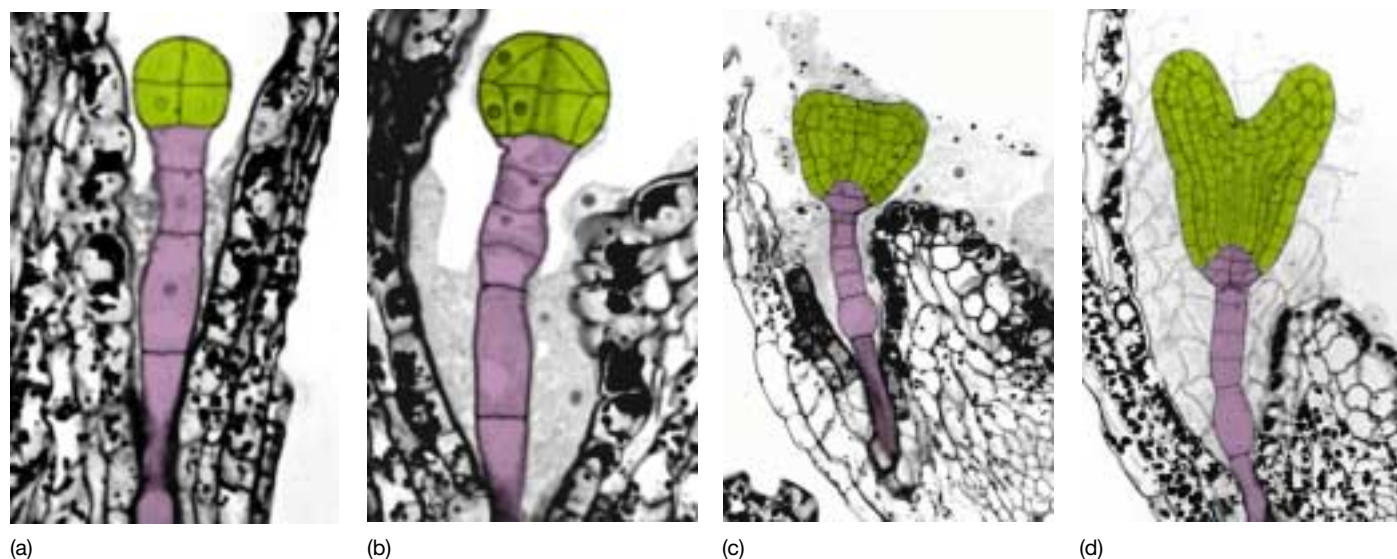
The root-shoot axis is established during the globular stage of development. The shoot apical meristem will later give rise to leaves and eventually reproductive structures. While both the shoot and root meristems are apical meristems, their formation is controlled independently. This conclusion is supported by mutant analysis in *Arabidopsis* where the *shootmeristemless* (*stm*) mutant fails to produce a viable shoot, but does produce a root (figure 40.6). Similarly, root meristem-specific genes have been identified. For example, monopterous mutants of *Arabidopsis* lack roots. The hormone auxin may play a role in root-shoot axis formation. Auxin is one of six classes of hormones that



**FIGURE 40.6** Shoot-specific genes specify formation of the shoot apical meristem. The *shootmeristemless* mutant of *Arabidopsis* has a normal root meristem, but fails to produce a shoot meristem.

regulate plant development and function that we will explore in more detail later in this unit.

As you study the development of roots and shoots after germination, you will notice that many of the same patterns of tissue differentiation seen in the embryo are reiterated in the apical meristems. Remember that there are also many events discussed earlier in this chapter that are unique to embryogenesis. For example, the *LEAFY COTYLEDON*



**FIGURE 40.5** Early developmental stages of *Arabidopsis thaliana*. (a) Early cell division has produced the embryo and suspensor. (b) Globular stage. (c,d) Heart-shaped stage.

gene in *Arabidopsis* is active in early and late embryo development and may be responsible for maintaining an embryonic environment. It is possible to turn this gene on later in development using recombinant DNA techniques (see chapter 43). In that case, embryos can form on leaves!

## Morphogenesis

The globular stage gives rise to a heart-shaped embryo in one group of angiosperms (the dicots, see figure 40.5) and a ball with a bulge on a single side in another group (the monocots). The bulges are cotyledons (“first leaves”) and are produced by the embryonic cells, not the shoot apical meristem that begins forming during the globular stage. This process, called *morphogenesis* (generation of form), results from changes in planes and rates of cell division. Because plant cells cannot move, the form of a plant body is largely determined by the plane in which cells divide and by controlled changes in cell shape as they expand osmotically after they form. Both microtubules and actin play a role in establishing the position of the cell plate which determines the direction of division. Plant growth-regulators and other factors influence the orientation of bundles of microtubules on the interior of the plasma membrane. These microtubules also guide cellulose deposition as the cell wall forms around the outside of a new cell, determining its final shape. For example, if you start with a box and reinforce four of the six sides more heavily with cellulose, the cell will expand and grow in the direction of the two sides with less reinforcement. Much is being learned at the cell biological level about morphogenesis from mutants that divide, but cannot control their plane of cell division or the direction of cell expansion.

## Food Storage

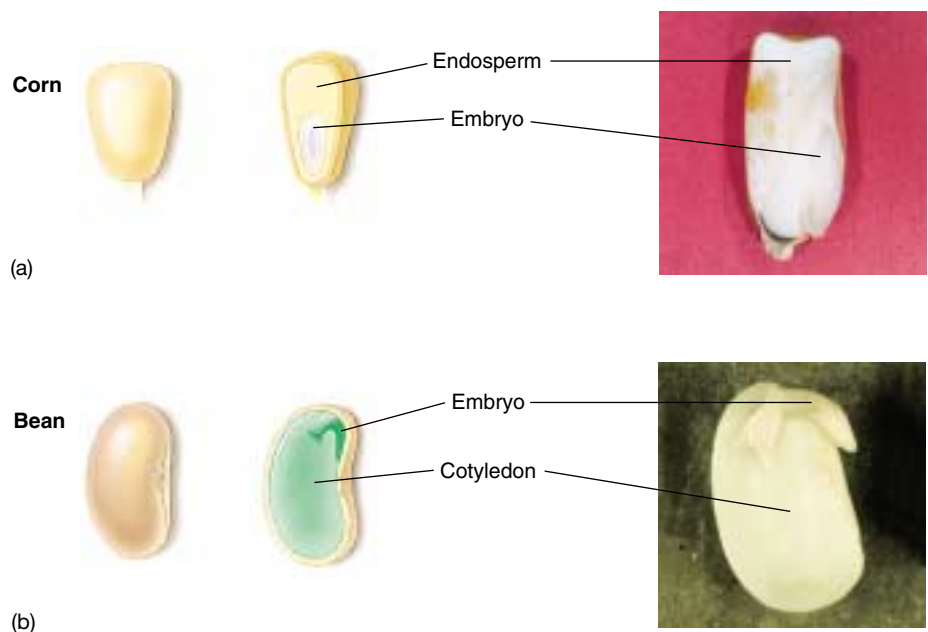
Throughout embryogenesis there is the production of starch, lipids, and proteins. The seed storage proteins are so abundant that the genes coding for them were the first cloning targets for plant molecular biologists. As noted in chapter 37, the evolutionary trend in the plants has been toward increased protection of the embryo. One way this is accomplished is through parental sporophyte input transferred by the suspensor in angiosperms (in gymnosperms the suspensor serves only to push the embryo closer to the gametophytic nutrient source produced by multiple nuclear divisions without cell division). This happens concurrently with the development of the endosperm (present only in angiosperms, although double fertilization has been observed in the gymnosperm *Ephedra*) which may be extensive or minimal. Endosperm in coconut is the “milk” and is in liquid form. In corn the endosperm is solid and in popping corn expands with heat to form the edible part of popcorn. In peas and beans, the endosperm is used up during embryo development and nutrients are stored in thick, fleshy cotyledons (figure 40.7). The photosynthetic machinery is built in response to light. So, it is critical that seeds have stored nutrients to aid in germination until the growing sporophyte can photosynthesize. A seed buried too deeply will use up all its reserves before reaching the surface and sunlight.

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After the root-shoot axis is established, a radial, three-tissue system, and a stored food supply, are formed through controlled cell division and expansion.

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**FIGURE 40.7**  
**Endosperm in corn and bean.** The corn kernel has endosperm that is still present at maturity, while the endosperm in the bean has disappeared; the bean embryo’s cotyledons take over food storage functions.



## 40.2 Seed formation protects the dormant embryo from water loss.

### How Seeds Form

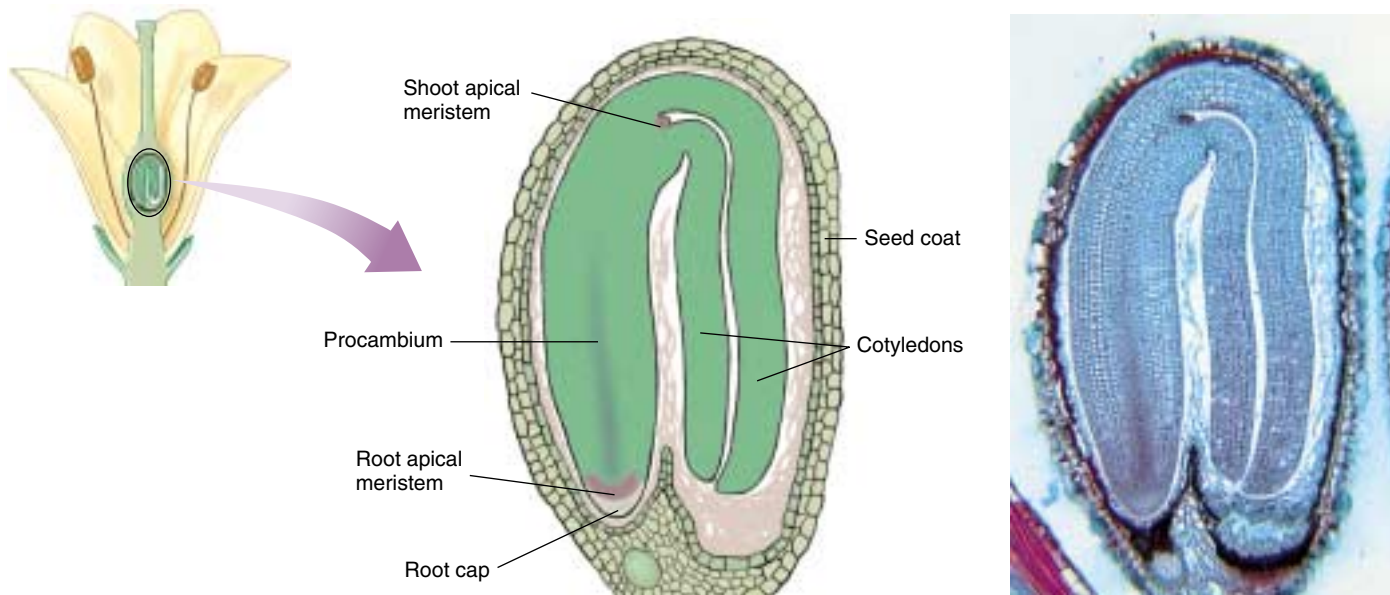
A protective seed coat forms from the outer layers of ovule cells, and the embryo within is now either surrounded by nutritive tissue or has amassed stored food in its cotyledons. The resulting package, known as a *seed*, is resistant to drought and other unfavorable conditions; in its dormant state, it is a vehicle for dispersing the embryo to distant sites and allows a plant embryo to survive in environments that might kill a mature plant. In some embryos, the cotyledons are bent over to fit within the constraints of the hardening ovule wall with the inward cotyledon being slightly smaller for efficient packing (figure 40.8). Remember that the ovule wall is actually tissue from the previous sporophyte generation.

### Adaptive Importance of Seeds

Early in the development of an angiosperm embryo, a profoundly significant event occurs: the embryo stops developing. In many plants, development of the embryo is arrested soon after the meristems and cotyledons differentiate. The *integuments*—the outer cell layers of the ovule—develop into a relatively impermeable seed coat, which encloses the seed with its dormant embryo and stored food. Seeds are important adaptively in at least four ways:

1. They maintain dormancy under unfavorable conditions and postpone development until better conditions arise. If conditions are marginal, a plant can “afford” to have some seeds germinate, because others will remain dormant.
2. The seed affords maximum protection to the young plant at its most vulnerable stage of development.
3. The seed contains stored food that permits development of a young plant prior to the availability of an adequate food supply from photosynthetic activity.
4. Perhaps most important, the dispersal of seeds facilitates the migration and dispersal of plant genotypes into new habitats.

Once a seed coat forms, most of the embryo’s metabolic activities cease. A mature seed contains only about 5% to 20% water. Under these conditions, the seed and the young plant within it are very stable; it is primarily the progressive and severe desiccation of the embryo and the associated reduction in metabolic activity that are responsible for its arrested growth. Germination cannot take place until water and oxygen reach the embryo, a process that sometimes involves cracking the seed coat through abrasion or alternate freezing and thawing. Seeds of some plants have been known to remain viable for hundreds and, in rare instances, thousands of years (figure 40.9).



**FIGURE 40.8**

**A mature angiosperm embryo.** Note that two cotyledons have grown in a bent shape to accommodate the tight confines of the seed. In some embryos, the shoot apical meristem will have already initiated a few leaf primordia as well.





**FIGURE 40.9**

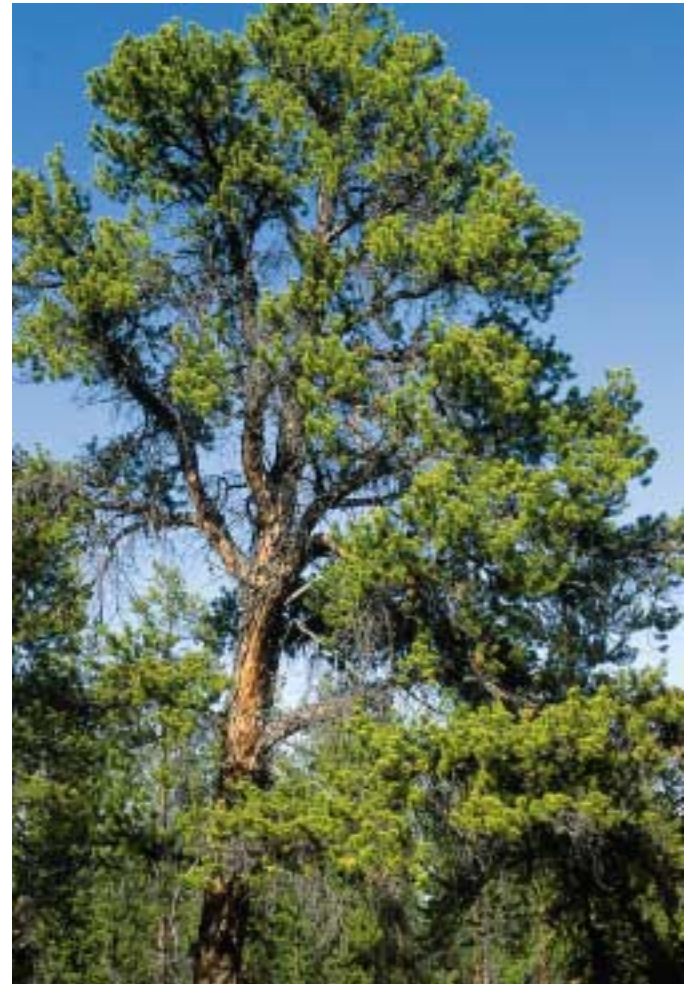
**Seeds can remain dormant for long periods.** This seedling was grown from a lotus seed recovered from the mud of a dry lake bed in Manchuria, northern China. The radiocarbon age of this seed indicates that it was formed around A.D. 1515. The coin is included in the photo to give some idea of the size.

Specific adaptations often help ensure that the plant will germinate only under appropriate conditions. Sometimes, seeds lie within tough cones that do not open until they are exposed to the heat of a fire (figure 40.10). This causes the plant to germinate in an open, fire-cleared habitat; nutrients will be relatively abundant, having been released from plants burned in the fire. Seeds of other plants will germinate only when inhibitory chemicals have been leached from their seed coats, thus guaranteeing their germination when sufficient water is available. Still other plants will germinate only after they pass through the intestines of birds or mammals or are regurgitated by them, which both weakens the seed coats and ensures the dispersal of the plants involved. Sometimes seeds of plants thought to be extinct in a particular area may germinate under unique or improved environmental circumstances, and the plants may then reappear.

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**Seed dormancy is an important evolutionary factor in plants, ensuring their survival in unfavorable conditions and allowing them to germinate when the chances of survival for the young plants are the greatest.**

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(a)



(b)



(c)

**FIGURE 40.10**

**Fire induces seed germination in some pines.** (a) Fire will destroy these adult jack pines, but stimulate growth of the next generation. (b) Cones of a jack pine are tightly sealed and cannot release the seeds protected by the scales. (c) High temperatures lead to the release of the seeds.

## 40.3 Fruit formation enhances the dispersal of seeds.

### How Fruits Form

Paralleling the evolution of angiosperm flowers, and nearly as spectacular, has been the evolution of their **fruits**, which are defined simply as mature ovaries (carpels). During seed formation, the flower ovary begins to develop into fruit. Fruits form in many ways and exhibit a wide array of spe-

cializations in relation to their dispersal. The differences among some of the fruit types seen today are shown in figure 40.11. Three layers of ovary wall can have distinct fates which accounts for the diversity of fruit types from fleshy to dry and hard. An array of mechanisms allow for the release of the seed(s) within the fruits. Developmentally, fruits are fascinating organs that contain three generations



#### Follicles

Split along one carpel edge only; milkweed, larkspur.



#### Legumes

Split along two carpel edges with seeds attached to carpel edges; peas, beans.



#### Samaras

Not split and with a wing formed from the outer tissues; maples, elms, ashes.



#### Drupes

Single seed enclosed in a hard pit; peaches, plums, cherries.



#### True berries

More than one seed and a thin skin; blueberries, tomatoes, grapes, peppers.



#### Hesperidiums

More than one seed and a leathery skin; oranges, lemons, limes.



#### Aggregate fruits

Derived from many ovaries of a single flower; strawberries, blackberries.



#### FIGURE 40.11

**Examples of some kinds of fruits.** Distinguishing features of each of these fruit types are listed below each photo. Follicles, legumes, and samaras are examples of dry fruits. Drupes, true berries, and hesperidiums are simple fleshy fruits; they develop from a flower with a single pistil. Aggregate and multiple fruits are compound fleshy fruits; they develop from flowers with more than one ovary or from more than one flower.

#### Multiple fruits

Develop from a cluster of flowers; mulberries, pineapples.

in one package. The fruit and seed coat are from the prior sporophyte generation. Within the seed are remnants of the gametophyte generation that produced the egg that was fertilized to give rise to the next sporophyte generation, the embryo.

### The Dispersal of Fruits

Aside from the many ways fruits can form, they also exhibit a wide array of specialized dispersal methods. Fruits with fleshy coverings, often shiny black or bright blue or red, normally are dispersed by birds or other vertebrates (figure 40.12*a*). Like red flowers, red fruits signal an abundant food supply. By feeding on these fruits, birds and other animals may carry seeds from place to place and thus transfer plants from one suitable habitat to another.

Fruits with hooked spines, like those of burgrass (figure 40.12*b*), are typical of several genera of plants that occur in the northern deciduous woods. Such fruits are often disseminated by mammals, including humans. Squirrels and similar mammals disperse and bury fruits such as acorns and other nuts. Other fruits, such as those of maples, elms, and ashes, have wings which aid in their distribution by the wind. The dandelion provides another familiar example of a fruit type that is dispersed by wind (figure 40.13), and the dispersal of seeds from plants such as milkweeds, willows, and cottonwoods is similar. Orchids have minute, dustlike seeds, which are likewise blown away by the wind.

Coconuts and other plants that characteristically occur on or near beaches are regularly spread throughout a region by water (figure 40.14). This sort of dispersal is especially important in the colonization of distant island groups, such as the Hawaiian Islands. It has been calculated that seeds of about 175 original angiosperms, nearly a third from North America, must have reached Hawaii to have evolved into the roughly 970 species found there today. Some of these seeds blew through the air, others were transported on the feathers or in the guts of birds, and still others drifted across the Pacific. Although the distances are rarely as great as the distance between Hawaii and the mainland, dispersal is just as important for mainland plant species that have discontinuous habitats, such as mountaintops, marshes, or north-facing cliffs.

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**Fruits, which are characteristic of angiosperms, are extremely diverse. The evolution of specialized structures allows fruits to be dispersed by animals, wind, and water.**

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(a)



(b)

**FIGURE 40.12**

**Animal-dispersed fruits.** (a) The bright red berries of this honeysuckle, *Lonicera hispidula*, are highly attractive to birds, just as are red flowers. After eating the fruits, birds may carry the seeds they contain for great distances either internally or, because of their sticky pulp, stuck to their feet or other body parts. (b) The spiny fruits of this burgrass, *Cenchrus incertus*, adhere readily to any passing animal, as you will know if you have ever stepped on them.



**FIGURE 40.13**

**Wind-dispersed fruits.** False dandelion, *Pyrrhopappus carolinanus*. The “parachutes” disperse the fruits of both false and true dandelions widely in the wind, much to the gardener’s despair.



**FIGURE 40.14**

**A water-dispersed fruit.** This fruit of the coconut, *Cocos nucifera*, is sprouting on a sandy beach. Coconuts, one of the most useful plants for humans in the tropics, have become established on even the most distant islands by drifting on the waves.

## 40.4 Germination initiates post-seed development.

When conditions are satisfactory, the embryo emerges from its desiccated state, utilizes food reserves, and resumes growth. As the sporophyte pushes through the seed coat it orients with the environment so the root grows down and the shoot grows up. New growth comes from delicate meristems that are protected from environmental rigors. The shoot becomes photosynthetic and the post-embryonic phase of growth and development is underway.

### Mechanisms of Germination

Germination is the first step in the development of the plant outside of its seed coat. Germination occurs when a seed absorbs water and its metabolism resumes. The amount of water a seed can absorb is phenomenal and creates a force strong enough to break the seed coat. At this point, it is important that oxygen be available to the developing embryo because plants, like animals, require oxygen for cellular respiration. Few plants produce seeds that germinate successfully under water, although some, such as rice, have evolved a tolerance to anaerobic conditions.

A dormant seed, although it may have imbibed a full supply of water and may be respiring, synthesizing proteins and RNA, and apparently carrying on normal metabolism, may nonetheless fail to germinate without an additional signal from the environment. This signal may be light of the correct wavelengths and intensity, a series of cold days, or simply the passage of time at temperatures appropriate for germination. Seeds of many plants will not germinate unless they have been **stratified**—held for periods of time at low temperatures. This phenomenon prevents seeds of plants that grow in cold areas from germinating until they have passed the winter, thus protecting their seedlings from cold conditions.

Germination can occur over a wide temperature range (5° to 30°C), although certain species and specific habitats may have relatively narrow optimum ranges. Some seeds will not germinate even under the best conditions. In some species, a significant fraction of a season's seeds remain dormant, providing a gene pool of great evolutionary significance to the future plant population.

### The Utilization of Reserves

Germination occurs when all internal and external requirements are met. Germination and early seedling

growth require the utilization of metabolic reserves; these reserves are stored in the starch grains of **amyloplasts** (colorless plastids that store starch) and protein bodies. Fats and oils also are important food reserves in some kinds of seeds. They can readily be digested during germination, producing glycerol and fatty acids, which yield energy through cellular respiration; they can also be converted to glucose. Depending on the kind of plant, any of these reserves may be stored in the embryo itself or in the endosperm.

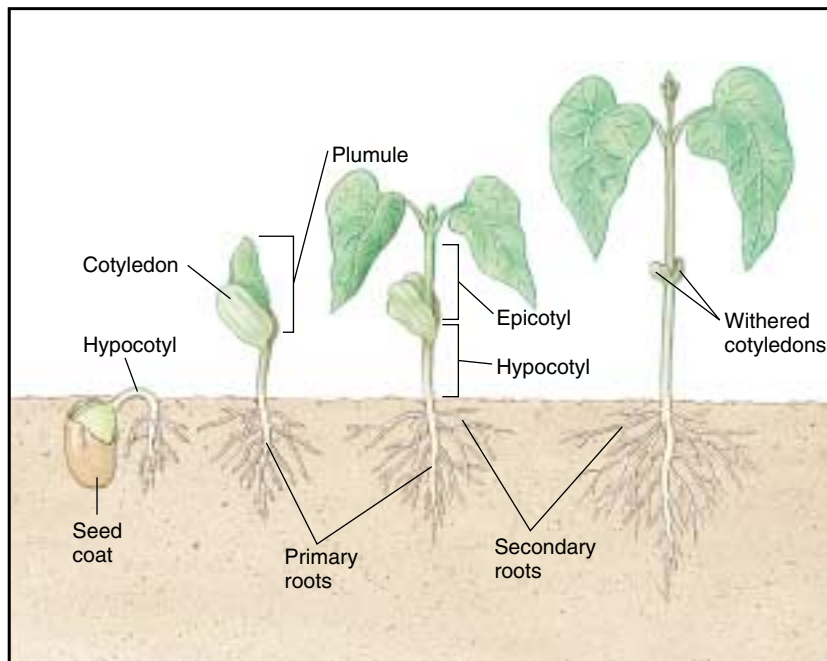
In the kernels of cereal grains, the single cotyledon is modified into a relatively massive structure called the **scutellum** (figure 40.15), from the Latin word meaning “shield.” The abundant food stored in the scutellum is used up first because these plants do not need to use the endosperm during germination. Later, while the seedling is becoming established, the scutellum serves as a nutrient conduit from the endosperm to the embryo. This is one of the best examples of how plant growth regulators modulate development in plants (40.16). The embryo produces gibberellic acid which signals the outer layer of the endosperm called the **aleurone** to produce  $\alpha$ -amylase. This enzyme is responsible for breaking the starch in the endosperm down into sugars that are passed by the scutellum to the embryo. Abscisic acid, another plant growth regulator, which is important in establishing dormancy, can inhibit this process. Abscisic acid levels may be reduced further when a seed absorbs water.

The emergence of the embryonic root and shoot from the seed during germination varies widely from species to species. In most plants, the root emerges before the shoot appears and anchors the young seedling in the soil (see figure 40.15). In plants such as peas and corn, the cotyledons may be held below ground; in other plants, such as beans, radishes, and sunflowers, the cotyledons are held above ground. The cotyledons may or may not become green and contribute to the nutrition of the seedling as it becomes established. The period from the germination of the seed to the establishment of the young plant is a very critical one for the plant's survival; the seedling is unusually susceptible to disease and drought during this period.

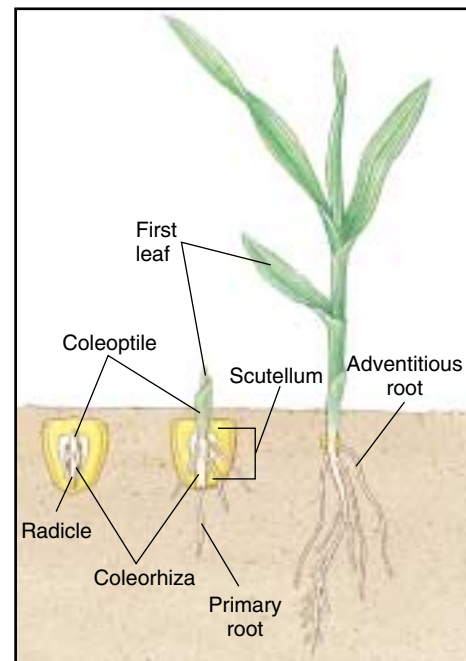
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**During germination and early seedling establishment, the utilization of food reserves stored in the embryo or the endosperm is mediated by hormones, which, in some cases, are gibberellins.**

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(a)



(b)

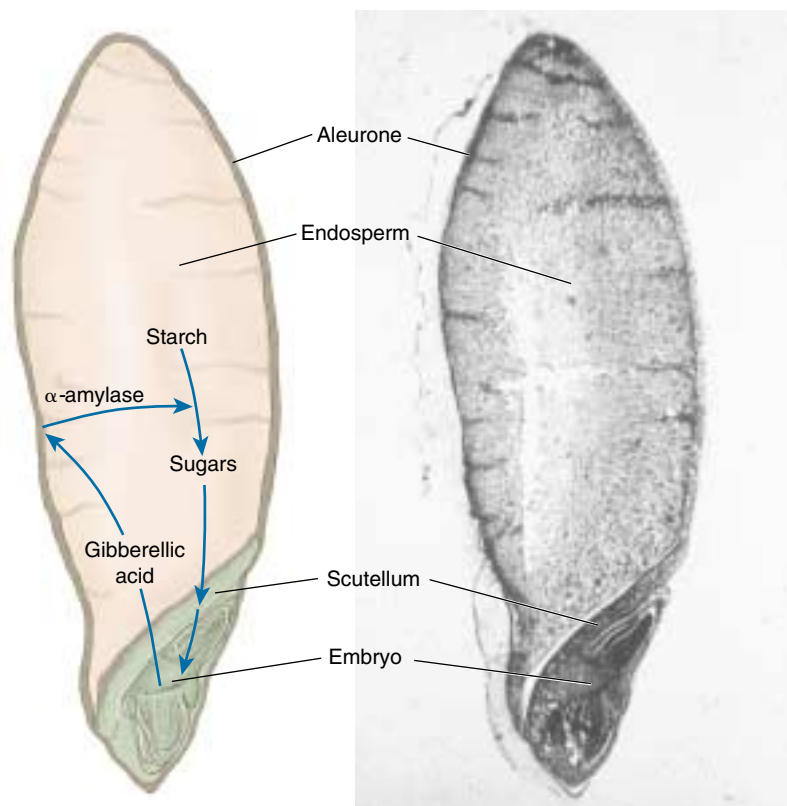
**FIGURE 40.15**

**Shoot development.** The stages shown are for a dicot, the common bean, (a) *Phaseolus vulgaris*, and a monocot, corn, (b) *Zea mays*.

**FIGURE 40.16**

**Hormonal regulation of seedling growth.**

The germinating barley embryos utilize the starch stored in the endosperm by releasing the hormone gibberellic acid (GA) that triggers the outer layers of the endosperm (aleurone layers) to produce the starch-digesting enzyme  $\alpha$ -amylase. The  $\alpha$ -amylase breaks down starch into sugar which moves through the scutellum (cotyledon) into the embryo where it provides energy for growth. A second hormone, abscisic acid (ABA), is important in establishing dormancy and becomes diluted as seeds imbibe water. When there is excess ABA, the GA-triggered production of alpha-amylase is inhibited.





## Summary

## Questions

## Media Resources

**40.1 Plant embryo development establishes a basic body plan.**

- Plant shape is determined by the direction of cell division and expansion.
- Three tissue systems form radially through regulated cell division and differentiation.
- Shoot and root apical meristems are established to continuously produce new tissues, which then differentiate into body parts.
- Carbohydrates, lipids, and proteins are stored for germination in the endosperm or cotyledons.

1. The pattern of cell division regulates the shape of an embryo. Describe the cell division pattern that results in the single, outer layer of protoderm in the globular stage embryo.
2. What evidence supports the claim that the shoot meristem is genetically specified separately from the root?



- Art Activity: Corn Grain Structure
- Art Activity: Garden Bean Seed Structure

**40.2 Seed formation protects the dormant embryo from water loss.**

- The ovule wall (integuments) around the embryo hardens to protect the embryo as embryogenesis ends.
- Seed formation allows the embryo to enter a dormant state and continue growth under more optimal conditions.

3. Why are seeds adaptively important? Why may a seed showing proper respiration and synthesis of proteins and nucleic acids and all other normal metabolic activities still fail to germinate?



- Embryos and Seeds

**40.3 Fruit formation enhances seed dispersal.**

- Fruits are an angiosperm innovation that develop from the ovary wall (a modified leaf) that surrounds the ovule(s).
- Fruits are highly diverse in terms of their dispersal mechanisms, often displaying wings, barbs, or other structures that aid in their transport from place to place. Fruit dispersal methods are especially important in the colonization of islands or other distant patches of suitable habitat.

4. Why is it advantageous for a plant to produce fruit? How does the genotype of the fruit compare with the genotype of the embryo? How does the genotype of the seed wall compare with the fruit wall?



- Activity: Fruits
- Fruits

**40.4 Germination initiates post-seed development.**

- In a seed, the embryo with its food supply is encased within a sometimes rigid, relatively impermeable seed coat that may need to be abraded before germination can occur. Weather or passage through an animal's digestive tract may be necessary for germination to begin.
- When temperature, light, and water conditions are appropriate, germination can begin. In some cases, a period of chilling is required prior to germination. This adaptation protects seeds from germinating during the cold season.
- At germination, the mobilization of the food reserves is critical. Hormones control this process.

5. Explain how the embryo signals the endosperm to obtain sugars for growth during germination.
6. Why does the root (actually the radicle) of the embryo emerge first?



- Germination