Plant Growth and Development
Concept 26.1 Plants Develop in Response to the Environment

Factors involved in regulating plant growth and development:

1. *Environmental cues* (e.g., day length)
2. *Receptors* to sense environmental cues (e.g., photoreceptors)
3. *Hormones*—chemical signals
4. The plant’s *genome*, which encodes regulatory proteins and enzymes
Concept 26.1 Plants Develop in Response to the Environment

Seeds are **dormant**—development of the embryo is stopped.

Seeds maintain dormancy by:

1. Exclusion of water or oxygen by an impermeable seed coat
2. Mechanical restraint of the embryo by a tough seed coat
3. Chemical inhibition of germination
Advantages of dormancy:

1. Ensures survival during unfavorable conditions

2. Results in germination when conditions are most favorable

3. Helps seeds survive long-distance dispersal, allowing plants to colonize new territory.
**Germination**—seeds begin to grow, or sprout:

1. **Imbibition**—seeds take up water if seed coat is permeable (e.g., a germination inhibitor might be washed away by rain).

2. Enzymes are activated, RNA and proteins synthesized, cellular respiration increases, and other metabolic pathways start up.
3. Embryo grows using food stored in the *cotyledons* or *endosperm*.

4. Germination is completed when the radicle (embryonic root) emerges.

The plant is then called a **seedling**.
A shrub in your yard has produced some beautiful flowers, and you want to save some of its seeds and plant them later in the year. You take some seeds inside your house and store them inside a safe, dry, temperature-controlled closet for about six months. You leave the rest of the seeds on the plant.

Six months later you plant several dozen of the seeds that were in your closet, but not a single one of them germinates. However, you notice that the other seeds that you had left on the plant, which have since fallen to the ground, have germinated on their own.

Why didn’t the seeds from the closet germinate? List as many possibilities as you can think of.

What could you try to make the remaining seeds germinate?
The first step in germination is the uptake of water, which is known as _______.

List at least three metabolic changes that occur as seeds take up water.
Germination is complete and the plant is called a “seedling” when

a. the germination inhibitor is present.

b. at least 5–15 percent of the seed’s weight is water.

c. there is a negative water potential.

d. the radicle emerges from the seed coat.
Plants respond to internal and external cues during development.

Responses are initiated and maintained by *hormones* and *photoreceptors*.

These regulators act through signal transduction pathways.
Hormones—chemical signals that act at very low concentrations at sites often far from where they are produced.

Photoreceptors—pigments associated with proteins that absorb light.
Table 26.1  Comparison of Plant and Animal Hormones

<table>
<thead>
<tr>
<th>CHARACTERISTIC</th>
<th>PLANT HORMONES</th>
<th>ANIMAL HORMONES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size, chemistry</td>
<td>Small organic molecules</td>
<td>Peptides, proteins, small molecules</td>
</tr>
<tr>
<td>Site of synthesis</td>
<td>Throughout the plant</td>
<td>Specialized glands or cells</td>
</tr>
<tr>
<td>Site of action</td>
<td>Local or distant</td>
<td>Distant, transported</td>
</tr>
<tr>
<td>Effects</td>
<td>Diverse</td>
<td>Often specific</td>
</tr>
<tr>
<td>Regulation</td>
<td>Decentralized</td>
<td>By central nervous system</td>
</tr>
</tbody>
</table>

**TABLE 26.1**  Comparison of Plant and Animal Hormones

*PRINCIPLES OF LIFE, Table 26.1*

Arabidopsis thaliana (mustard) has been a major model organism for investigating signal transduction.

**Genetic screen**—technique to identify genes involved in a signal transduction pathway.

Mutated plants are created.

Phenotypes with characteristics influenced by the pathway of interest are selected and their genome compared with wild-type plants.
Figure 26.2 A Genetic Screen

RESEARCH TOOLS

No ethylene added

Ethylene added

Many seeds suspended in a mutagen solution in a test tube

Ethylene insensitive mutant

Ethylene sensitive (wild-type) plants

Gene required for ethylene response

PRINCIPLES OF LIFE, Figure 26.2
Two key plant hormones:

- Gibberellins
- Auxin

Mutants plants that don’t make these hormones display dwarfism; supplying them with the hormones results in normal growth.

Actions of plant hormones are not unique and specific.
Figure 26.3 Hormones Reverse a Mutant Phenotype (Part 1)
You’ve planted a garden full of fruits and vegetables, but they should be much taller than they are. You have watered them, provided the right amount of shade and sun, but they all seem extremely short—much shorter than other varieties of vegetables that your neighbor is growing next door.

What might your plants have a deficiency in?

a. Auxin
b. Cytokinins
c. Gibberellins
d. Both a and b
e. Both a and c
### Table 26.2 Plant Growth Hormones (Part 1)

<table>
<thead>
<tr>
<th>HORMONE</th>
<th>STRUCTURE</th>
<th>TYPICAL ACTIVITIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abscisic acid</td>
<td><img src="image" alt="Abscisic acid Structure" /></td>
<td>Maintains seed dormancy; closes stomata</td>
</tr>
<tr>
<td>Auxin (indole-3-acetic acid)</td>
<td><img src="image" alt="Auxin Structure" /></td>
<td>Promotes stem elongation, lateral root initiation, and fruit development; inhibits axillary bud outgrowth, leaf abscission, and root elongation</td>
</tr>
<tr>
<td>Brassinosteroids</td>
<td><img src="image" alt="Brassinosteroids Structure" /></td>
<td>Promote stem and pollen tube elongation; promote vascular tissue differentiation</td>
</tr>
</tbody>
</table>

*PRINCIPLES OF LIFE, Table 26.2 (Part 1)*

**TABLE 26.2 Plant Growth Hormones**

<table>
<thead>
<tr>
<th>HORMONE</th>
<th>STRUCTURE</th>
<th>TYPICAL ACTIVITIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cytokinins</td>
<td><img src="image" alt="Cytokinins Structure" /></td>
<td>Inhibit leaf senescence; promote cell division and axillary bud outgrowth; affect root growth</td>
</tr>
<tr>
<td>Ethylene</td>
<td><img src="image" alt="Ethylene Structure" /></td>
<td>Promotes fruit ripening and leaf abscission; inhibits stem elongation</td>
</tr>
<tr>
<td>Gibberellins</td>
<td><img src="image" alt="Gibberellins Structure" /></td>
<td>Promote seed germination, stem growth, and fruit development; break winter dormancy; mobilize nutrient reserves in grass seeds</td>
</tr>
</tbody>
</table>

*PRINCIPLES OF LIFE, Table 26.2 (Part 2)*
Gibberellins have several roles in plant growth and development:

1. Stem elongation
   ex: (florists can control growth by spraying with gibberellin inhibitors)
2. Fruit Growth

*Gibberellins are sprayed on seedless grapes to get larger fruit.
3. Seed germination—trigger hydrolysis of stored food molecules
ex: gibberellins used to enhance malting (germination) of barley and breakdown of endosperm)
Auxin was discovered in the context of **phototropism**: response to light—stems bend toward a light source.

Auxin is made in shoot apex and diffuses down the shoot in one direction (polar transport) stimulating cell elongation.
Auxin can also be transported laterally in a stem; results in directional growth (e.g., bending towards a light).

Auxin concentration increases on the shaded side and cell elongation on that side causes the stem to bend.
Figure 26.6  Plants Respond to Light and Gravity (Part 1)
Concept 26.2 Gibberellins and Auxin Have Diverse Effects but a Similar Mechanism of Action
Auxins also have a role in **gravitropism**.

*Negative gravitropism*—upward gravitropic response of shoots

*Positive gravitropism*—downward gravitropic response of roots
(B) Negative gravitropism of shoot

PRINCIPLES OF LIFE, Figure 26.6 (Part 2)
Auxin has many roles in plant growth and development:

1. Root initiation—shoot cuttings of many species will develop roots if cut surface is dipped into an auxin solution.

2. Leaf **abscission** (detachment of old leaves from the stem) is inhibited.
3. Helps maintain apical dominance

Apical dominance: apical buds inhibit growth of axillary buds. Diffusion gradient results in more axillary bud growth and branching lower down the stem.
4. Fruit Development

- Treatment with auxin or gibberellin causes parthenocarpy (fruit formation without fertilization).


- Wall structure must change to allow expansion.

a. **Acid growth hypothesis**—protons are pumped into cell wall and activate *expansins*, which catalyze changes that loosen the cell wall.

b. Auxin increases synthesis of proton pumps and guides their insertion into the plasma membrane.
Figure 26.7 Auxin and Cell Expansion

The diagram illustrates the process of auxin and cell expansion. Auxin enters the cell and stimulates the proton pump, which produces ATP and expels protons (H+ ions) from the cell. This process leads to the expansion of the cell wall, facilitated by expansin and cellulose microfibrils, which are cross-linked by polymers.
Auxins and gibberellins work by similar mechanisms.

Genetic screens were used to study the mechanisms using insensitive mutants (not affected by added hormones):

• *Excessively tall plants*—the hormone response is always “on”

• *Dwarf plants*—the hormone response is always “off”
Mutations in both types affect the same protein—a *repressor* of a transcription factor that stimulates expression of growth-promoting genes.
The repressor has 2 domains:

1. One region binds to the transcription complex to inhibit transcription.

   In excessively tall mutants the repressor does not bind to the transcription complex.

2. Another region causes it to be removed from the transcription complex.

   In dwarf mutants the repressor is always bound to the complex.
Figure 26.8  Gibberellins and Auxin Have Similar Signal Transduction Pathways
Gibberellins and Seed Germination

Working with a partner, fill in the blanks below:

1. The embryo _______ water and swells.

2. The embryo secretes _______ that diffuse into the _______ layer, where they trigger the synthesis of digestive enzymes.

3. The digestive enzymes from the _______ layer move into the _______.

4. The enzymes digest the _______ and _______ in the endosperm, releasing monomers from which the embryo synthesizes new cells.
Review:

1. Why are seedless grapes usually smaller than grapes that have seeds? What can grape growers spray on the grapes to make them bigger, and how does the spray work?

2. Why do plants tend to bend toward the light? That is, what exactly causes the bending, and how?

3. Why are Christmas trees conical, with large branches on the bottom, and progressively smaller branches higher up the tree?
Concept 26.3 Other Plant Hormones Have Diverse Effects on Plant Development

**Ethylene** gas—promotes leaf abscission and senescence; speeds ripening of fruit

Ethylene also causes an increase in its own production. Once fruit ripening begins, more and more ethylene forms.
Concept 26.3 Other Plant Hormones Have Diverse Effects on Plant Development

Ethylene gas is used to ripen stored fruit quickly.
The **apical hook** of eudicot seedlings is maintained by asymmetrical production of ethylene, which inhibits elongation of cells on the inner surface.

After seedling breaks through soil, ethylene production stops, cells on inner surface elongate, and the hook unfolds.
Figure 26.1 Patterns of Early Shoot Development (Part 2)

(B) Eudicot (bean)

- Foliage leaf
- Apical hook
- Seed coat
- Cotyledons
- Primary root
- Secondary roots
A stunted growth habit occurs when plants are treated with ethylene, due to the *triple response*:

- Stem elongation is inhibited
- Lateral swelling of stems is promoted
- Sensitivity of stems to gravitropic stimulation decreases
Cytokinins have several effects, often interacting with auxin:

- Induce proliferation of cultured plant cells
- In cell cultures, high cytokinin-to-auxin ratio promotes formation of shoots; low ratio promotes formation of roots.
- Cause some light-requiring seeds to germinate even if kept in darkness.
• Usually inhibit elongation of stems, but also cause lateral swelling of stems and roots (e.g., radishes).

• Stimulate axillary buds to grow into branches; auxin-to-cytokininin ratio controls extent of branching
Concept 26.3 Other Plant Hormones Have Diverse Effects on Plant Development

• Cytokinins delay senescence of leaves
Cytokinin signaling pathway includes proteins similar to those in *two-component systems* in bacteria:

- *Receptor*—acts as a protein kinase, phosphorylating itself and a target protein

- *Target protein*—acts as a transcription factor to regulate the response
Figure 26.9  The Cytokinin Signal Transduction Pathway (Part 1)
Figure 26.9 The Cytokinin Signal Transduction Pathway (Part 2)
Brassinosteroids also have diverse effects:

- Enhance cell elongation and cell division in shoots
- Promote xylem differentiation
- Promote growth of pollen tubes
- Promote seed germination
- Promote apical dominance and leaf senescence
A defect in the brassinosteroid signaling pathway results in stunted growth *Arabidopsis* mutants.
Abscisic acid—actions involve inhibition of other hormones:

• Prevents seed germination when seeds are still on parent plant

• Promotes seed dormancy; inhibits initiation of germination events

• Mediates responses to environmental stresses and pathogens (e.g., closure of stomata to prevent water loss)
**Photomorphogenesis**—physiological and developmental events that are controlled by light

Plants respond to light *quality* (wavelengths) and *quantity* (intensity and duration of exposure).
In the action spectrum for phototropism of coleoptiles, blue light was found to be the most effective at inducing the coleoptile to curve.

A blue light receptor called phototropin was identified using blue-light-insensitive *Arabidopsis* mutants.
Figure 26.10  Action Spectrum for Phototropism (Part 1)
Figure 26.10  Action Spectrum for Phototropism (Part 2)

Light

Time = 0 minutes

Time = 90 minutes

PRINCIPLES OF LIFE, Figure 26.10 (Part 2)
Light absorption by phototropin starts a signal transduction cascade that results in stimulation of cell elongation by auxin.

Phototropin also participates with another blue-light receptor, zeaxanthin, in the light-induced opening of stomata.
Cryptochromes—blue-light receptors located in the nucleus; affect seedling development and flowering.

Mechanism of action is unknown.
Phytochromes—red-light (650–680 nm) receptors

Lettuce seedlings germinate only in response to red light.

Red light responses are reversible by far-red light (710–740 nm).
INVESTIGATION

HYPOTHESIS
The effects of red and far-red light on lettuce seed germination are mutually reversible.

METHOD
Expose lettuce seeds to alternating periods of red light $R$ for 1 minute and far-red light $FR$ for 4 minutes.

```
R    R FR   ...   R FR R FR R FR R   R FR R FR R FR R FR R FR
```

RESULTS

- Most germinate
- Few germinate
- Most germinate
- Few germinate

PRINCIPLES OF LIFE, Figure 26.11 (Part 1) © 2012 Sinauer Associates, Inc.
**INVESTIGATION**

**CONCLUSION**

Red light and far-red light reverse each other's effects.

**ANALYZE THE DATA**

Seven groups of 200 lettuce seeds each were incubated in water for 16 hours in the dark. One group was then exposed to white light for 1 min. A second group (controls) remained in the dark. Five other groups were exposed to red (R) and/or far-red (FR) light. All the seeds were then returned to darkness for 2 more days. Germination was then observed.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Seeds germinated</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. White light</td>
<td>199</td>
</tr>
<tr>
<td>2. Dark</td>
<td>17</td>
</tr>
<tr>
<td>3. R</td>
<td>196</td>
</tr>
<tr>
<td>4. R then FR</td>
<td>108</td>
</tr>
<tr>
<td>5. R then FR then R</td>
<td>200</td>
</tr>
<tr>
<td>6. R then FR then R then FR</td>
<td>86</td>
</tr>
<tr>
<td>7. R then FR then R then FR then R</td>
<td>198</td>
</tr>
</tbody>
</table>

A. Calculate the percentage of seeds that germinated in each case.

B. What can you conclude about the photoreceptors involved?
Phytochrome exists in two interconvertible *isoforms*, or states.
Ratio of red to far-red light determines phytochrome-mediated responses.

During daylight, ratio is about 1.2:1; the $P_{fr}$ isoform predominates.

In shade, ratio may be as low as 0.13:1; $P_r$ isoform predominates.

Shade-intolerant species respond by stimulating stem cell elongation, thus growing taller to escape the shade.
Phytochrome is a protein with two subunits, each contains a pigment called a *chromophore*.

When $P_r$ absorbs red light, the chromophore changes shape, leading to the $P_{fr}$ form.

This exposes two regions of the phytochrome, which both affect transcriptional activity.
Exposure of a *nuclear localization signal sequence* results in movement of $P_{fr}$ from cytosol to nucleus, where it binds to transcription factors and stimulates expression of genes involved in photomorphogenesis.

Exposure of a *protein kinase* domain causes $P_{fr}$ to phosphorylate itself and other proteins, which changes the activity of other transcription factors.
Figure 26.12  Phytochrome Stimulates Gene Transcription
In *Arabidopsis*, phytochrome affects 2,500 genes (10% of the genome) by increasing or decreasing their expression.
Timing and duration of biological activities in living organisms are governed by a “biological clock”—an oscillator that alternates between two states at roughly 12-hour intervals.

This results in **circadian rhythms** (e.g., the opening of stomata during the day and closing at night).
Circadian rhythms can be reset, or *entrained* by changing light–dark cycles.

Phytochrome is likely involved: at sundown phytochrome is mostly $P_{fr}$. Through the night, $P_{fr}$ is converted to $P_r$. At daylight, it rapidly converts to $P_{fr}$.

However long the night, the clock is reset at dawn every day; the clock adjusts to changes in day length over the course of the year.
In semi-dwarf wheat, the mutant allele (Rht “reduced height”) is involved in signal transduction in response to gibberellin.

Rht mutants also put a greater proportion of their photosynthate into making seeds than wild-type plants do (higher harvest index).

In the mutant plants, the repressor is always bound to the transcription factor, keeping the gibberellin response “off.”
In semi-dwarf rice, the mutant allele is involved with gibberellin synthesis.

The gene *sd-1* ("semi-dwarf") encodes an enzyme that catalyzes one of the last steps in gibberellin synthesis.
Figure 26.13  Semi-dwarf Rice