

Undergraduate Level Course of ZHIYUAN College Life—The Science of Biology

Plant Development and Reproduction

Wen-Hui Lin
Shanghai Jiao Tong University
2017-11

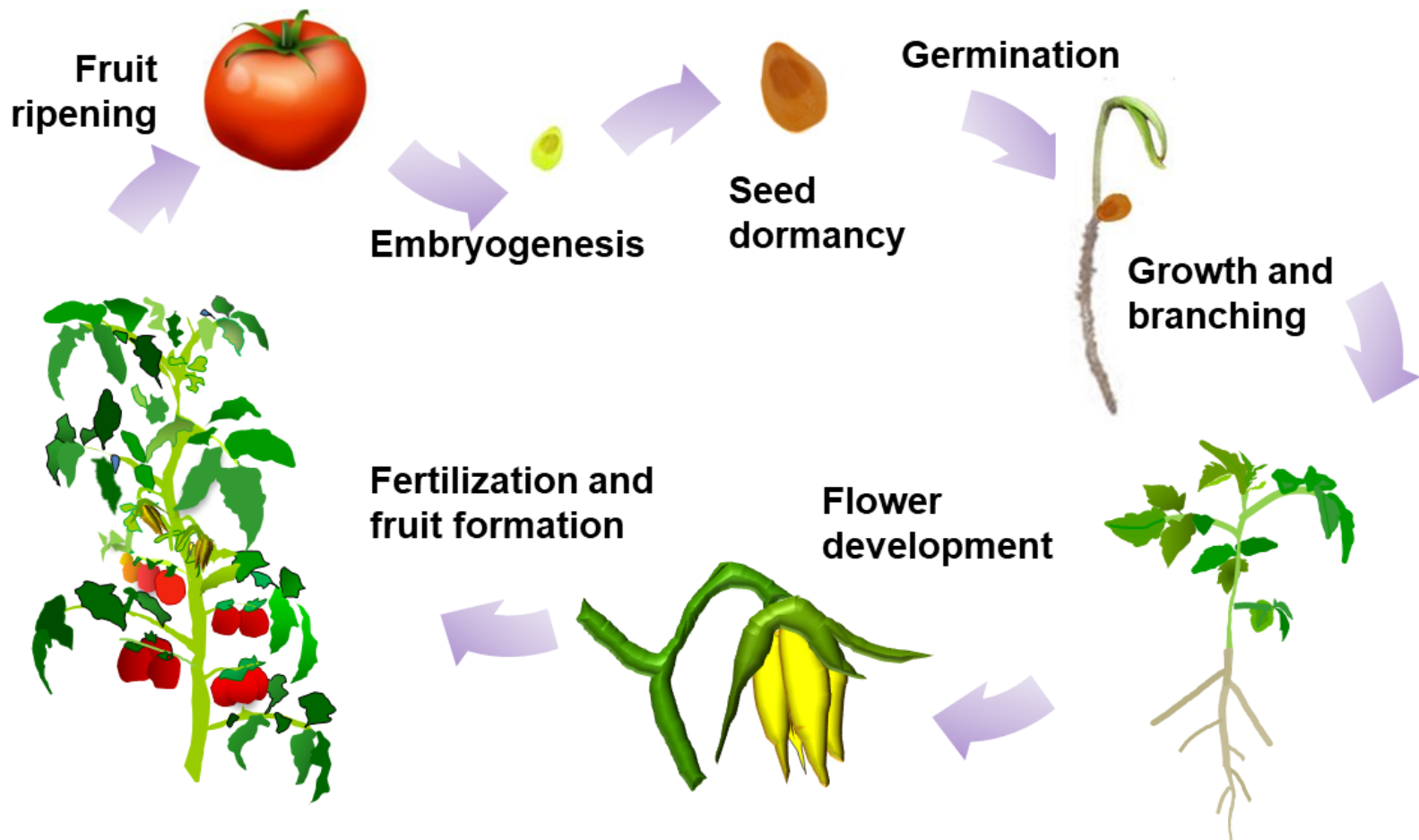


36.1 Plants Develop in Response to the Environment

36.2 Gibberellins and Auxin Have Diverse Effects but a Similar Mechanism of Action

36.3 Other Plant Hormones Have Diverse Effects

36.4 Photoreceptors Initiate Developmental Responses to Light



Features that maximize the ability of plants to obtain resources:

- *Meristems* allow growth throughout the plant's life.
- *Post-embryonic organ formation*—new organs can develop throughout life.
- *Differential growth*—they can grow the organs most needed (e.g., more leaves).

Key factors that regulate plant growth and development:

- *Hormones*
- *Environmental cues*
- *Receptors* such as photoreceptors
- *Regulatory proteins and enzymes*

From seed to seedling—Germination

In seeds, development of the embryo can be halted for long periods of time.

If development stops even when conditions would be adequate for development, seed is said to be **dormant**.

Seed dormancy may last weeks, months, or years.

Mechanisms to maintain dormancy:

- *Exclusion of water or oxygen* by an impermeable seed coat.
- *Mechanical restraint* of embryo by a tough seed coat.
- *Chemical inhibition* of germination by growth regulators.
- *Photodormancy*—some seeds need a period of light or dark before they can germinate.
- *Thermodormancy*—some seeds need high or low temperatures to germinate.

Dormancy can be broken by factors that overcome these mechanisms.

Rain can wash away chemical inhibitors, or the seed coat may be damaged by passage through an animal's digestive system.

Compounds in smoke break dormancy in some seeds that germinate after forest fires.

Advantages of seed dormancy and quiescence:

Ensures seed will germinate at a suitable time in the plant's life cycle

Helps seeds survive droughts or long-distance dispersal, allowing plants to colonize new territory



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Germination

1. **Imbibition**, or uptake of water

Seeds have negative water potential and will take up water if the seed coat is permeable.

Seeds contain polar macromolecules, such as cellulose and starch, which attract and bind polar water molecules.

As the seed takes up water, enzymes are activated, RNA and proteins are synthesized, cellular respiration increases, and other metabolic pathways are activated.

In many seeds, growth results from the expansion of small, preformed cells.

Starch, proteins, and lipids stored in cotyledons or endosperm are hydrolyzed to provide energy and building blocks for the growing embryo.

Germination is complete when the **radicle** (embryonic root) emerges. The plant is now a **seedling**.

If the seedling germinates underground, it must elongate rapidly in the right direction and cope with darkness for a time.

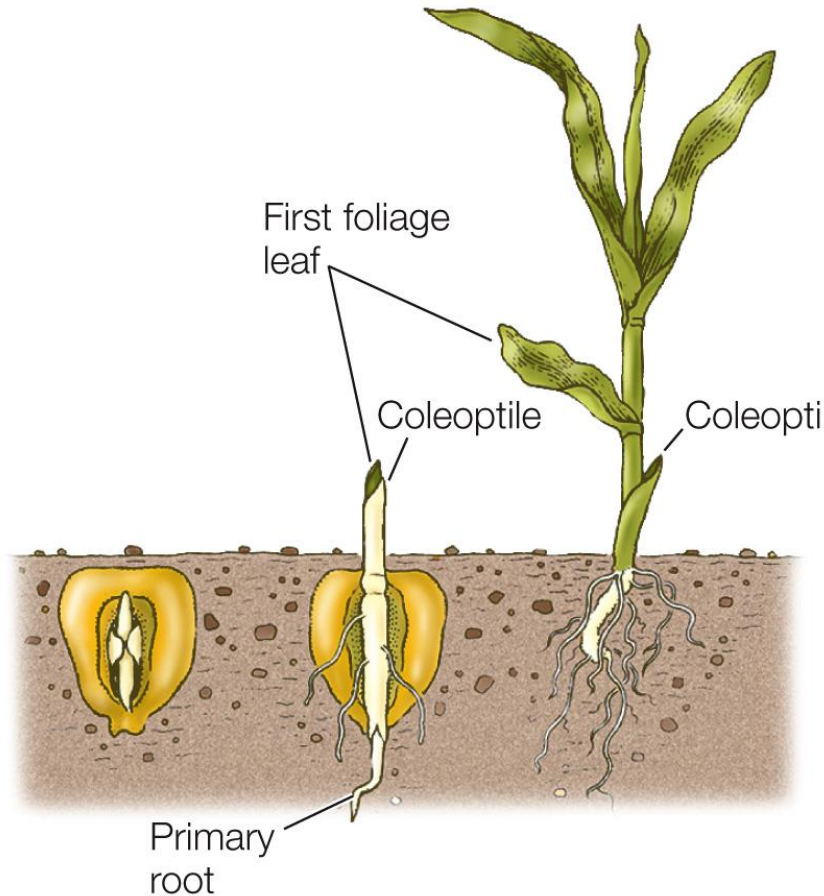
A series of photoreceptors directs this stage of development.

The pattern of early shoot development varies among monocots and eudicots.

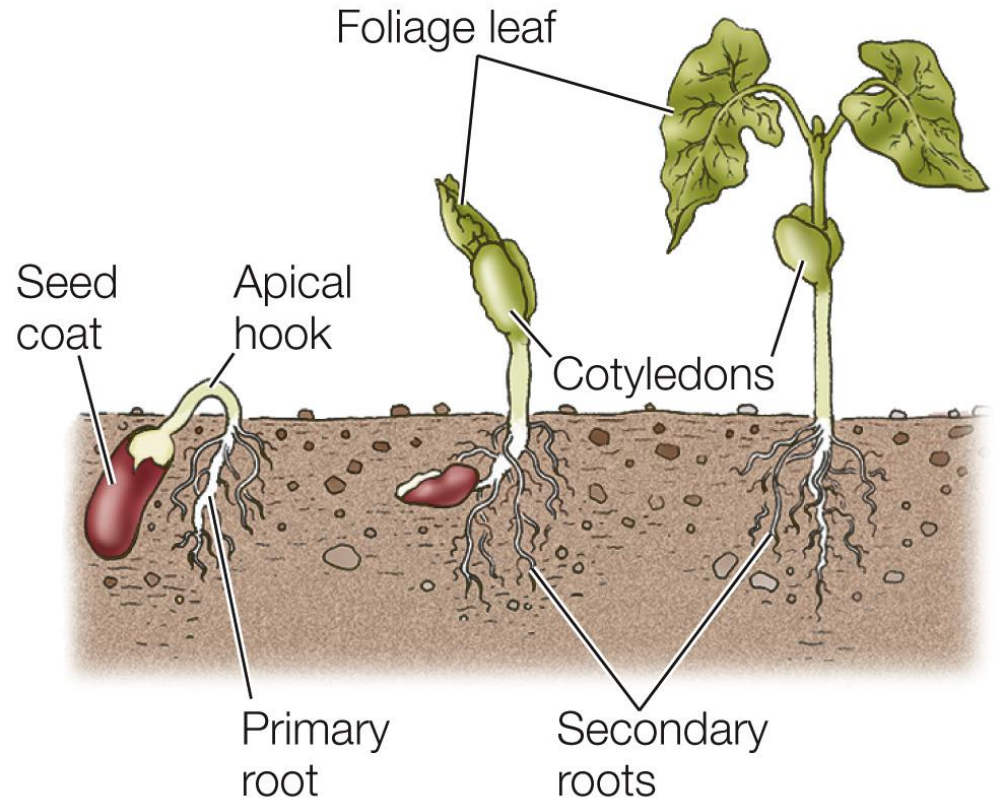
In monocots, the shoot is protected by a sheath of cells called the **coleoptile**.

In dicots, the shoot is protected by the cotyledons.

(A) Monocot shoot development (corn)



(B) Eudicot shoot development (bean)



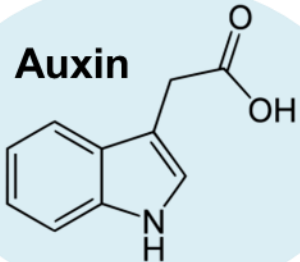
Hormones: Chemical signals that act at low concentrations, often at sites distant from where they were produced.

Plant hormones are very different from their counterparts in animals.

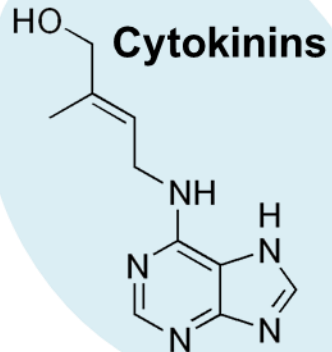
Each plant hormone has multiple regulatory roles. Interactions can be complex.

table 36.1 Comparison of Plant and Animal Hormones		
Characteristic	Plant hormones	Animal hormones
Size, chemistry	Peptides, small organic molecules	Peptides, proteins, small molecules
Site of synthesis	Usually at many locations	Specialized glands or cells
Site of action	Local or distant	Usually distant, transported
Effects	Often diverse	Often specific
Regulation	By biochemical feedback	By central nervous system, ions, or feedback

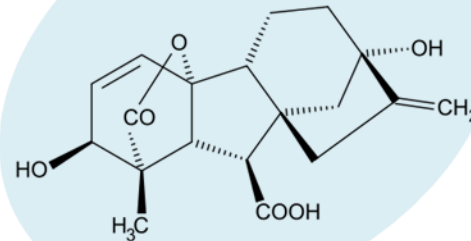
What are phytohormones?



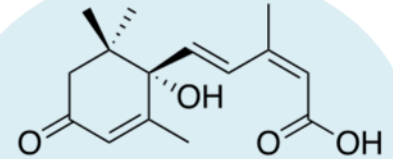
Auxin



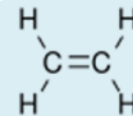
Cytokinins



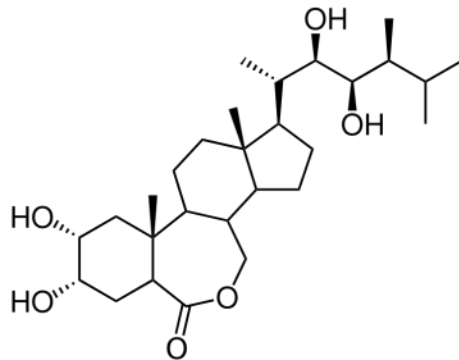
Gibberellins



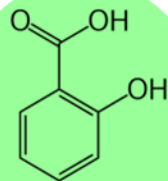
Abscisic Acid



Ethylene



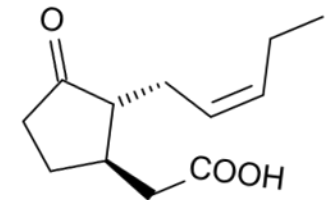
Brassinosteroids



Salicylates



Strigolactones



Jasmonates

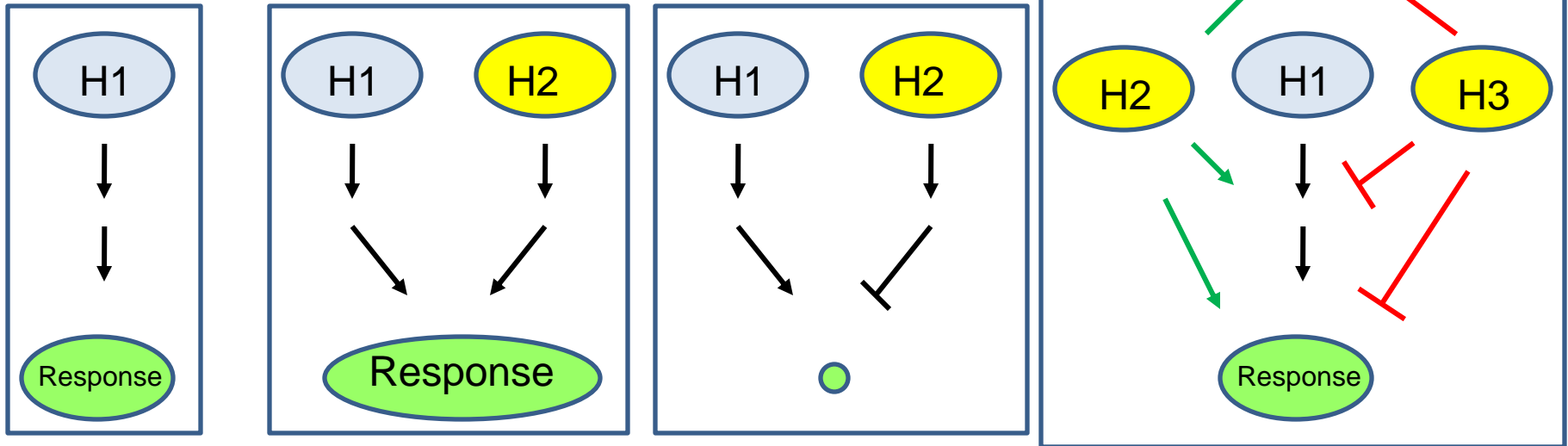
growth substance; very low quantity and concentration; transduction; receptors; signaling molecules.

A Survey of Plant Hormones

Table 39.1 An Overview of Plant Hormones

Hormone	Where Produced or Found in Plant	Major Functions
Auxin (IAA)	Embryo of seed, meristems of apical buds, young leaves	Stimulates stem elongation (low concentration only), root growth, cell differentiation, and branching; regulates development of fruit; enhances apical dominance; functions in phototropism and gravitropism; promotes xylem differentiation; retards leaf abscission
Cytokinins	Synthesized in roots and transported to other organs	Affect root growth and differentiation; stimulate cell division and growth; stimulate germination; delay senescence
Gibberellins	Meristems of apical buds and roots, young leaves, embryo	Promote seed and bud germination, stem elongation, and leaf growth; stimulate flowering and development of fruit; affect root growth and differentiation
Brassinosteroids	Seeds, fruit, shoots, leaves, and floral buds	Inhibit root growth; retard leaf abscission; promote xylem differentiation
Absciscic acid	Leaves, stems, roots, green fruit	Inhibits growth; closes stomata during water stress; promotes seed dormancy
Ethylene	Tissues of ripening fruit, nodes of stems, aging leaves and flowers	Promotes fruit ripening, opposes some auxin effects; promotes or inhibits growth and development of roots, leaves, and flowers, depending on species

Crosstalk between hormone signaling pathways



Crosstalk (or cross-regulation) occurs when two pathways are not independent. It can be positive and additive or synergistic (协同的), or negative and antagonistic (拮抗的).

Crosstalk can affect the synthesis, transport or signaling pathway of another hormone.

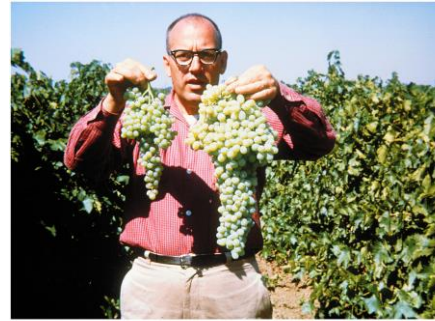
Hormones function in plant growth and development

(B) Treatment with auxin



From W. M. Gray, 2004. *PLoS Biol.* 2(9): e311.

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Courtesy of Eugenia Russinova, VIB Department of Plant Systems Biology, Ghent University, Belgium



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(A) Treatment with gibberellin



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Courtesy of J. A. D. Zeevaert, Michigan State U.



David McIntyre

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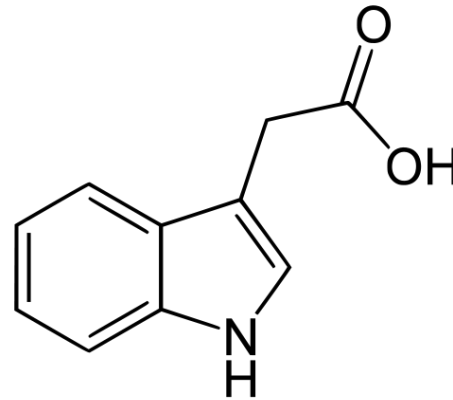


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Courtesy of Adel A. Kader

Auxin (生长素)

- Growth
- Phototropism and gravitropism
- Branching
- Embryonic patterning
- Stem cell maintenance
- Organ initiation

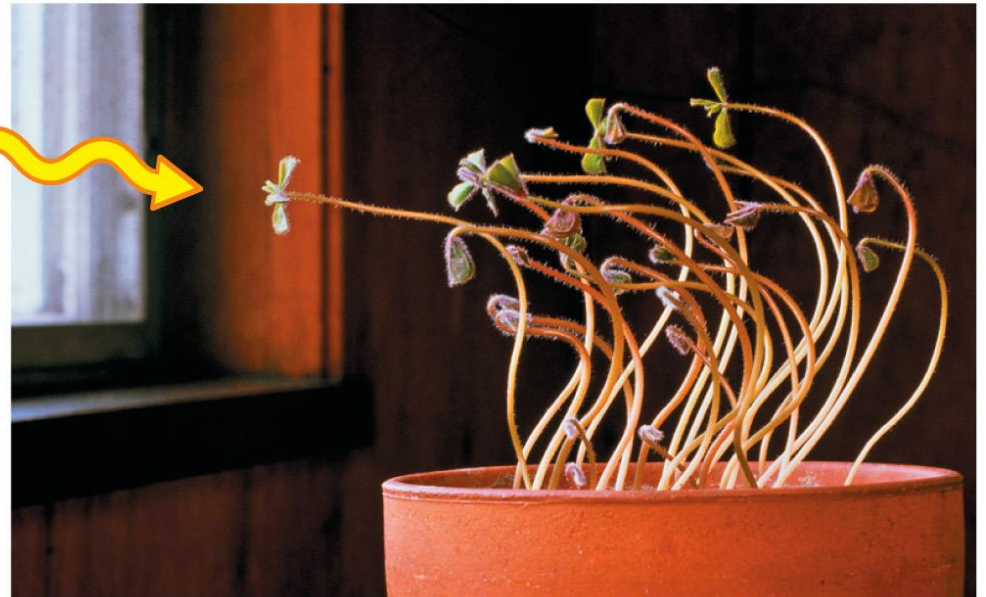


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Light

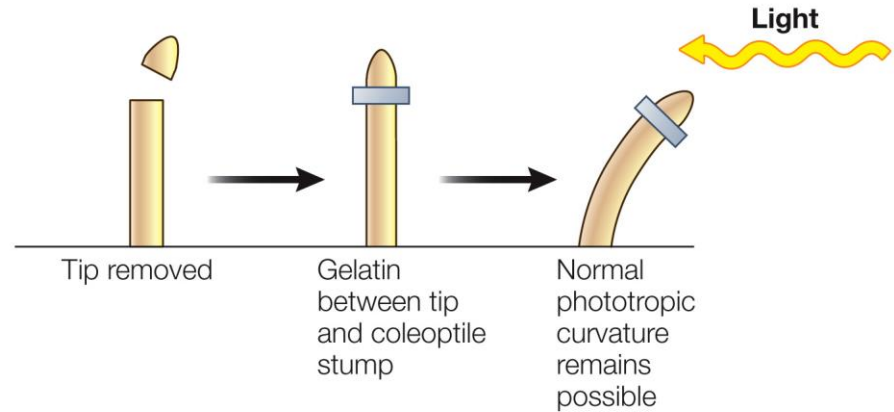
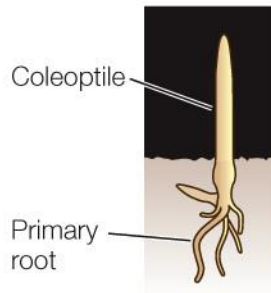


Auxin was discovered in the context of **phototropism**—plants bend toward a light source.

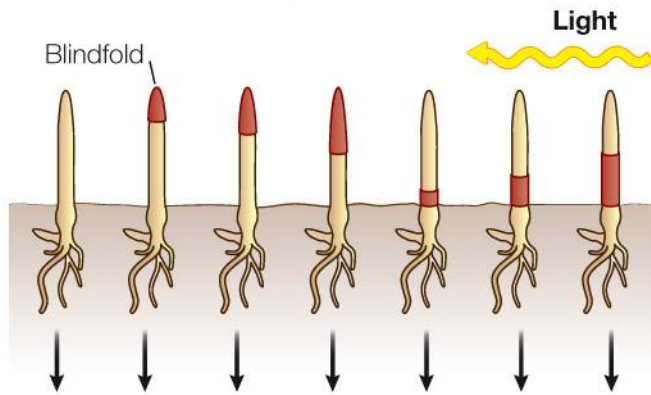


HYPOTHESIS ▶ Only part of the coleoptile senses the light that triggers phototropism.

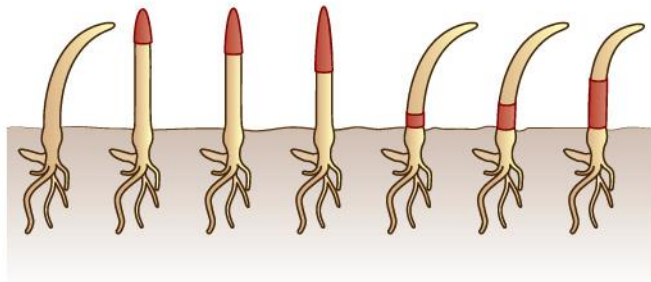
METHOD



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RESULTS



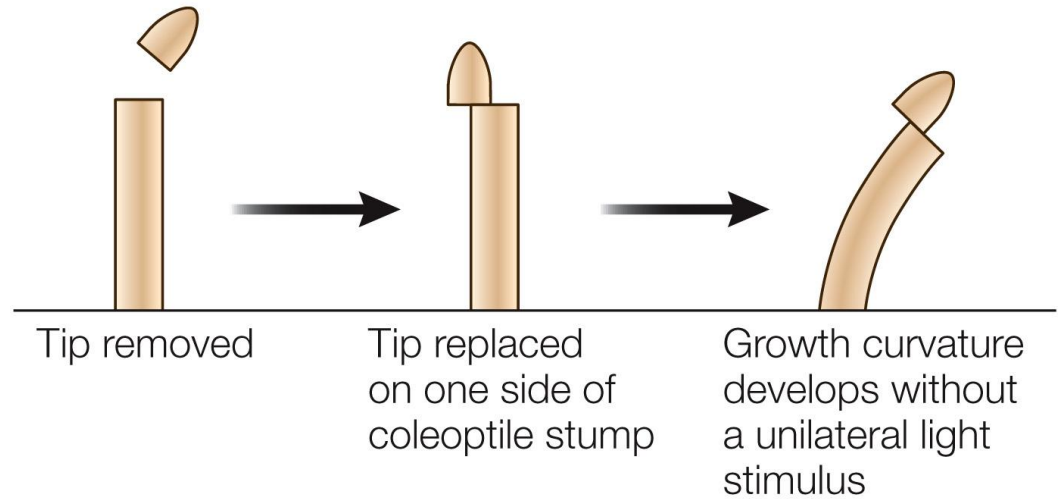
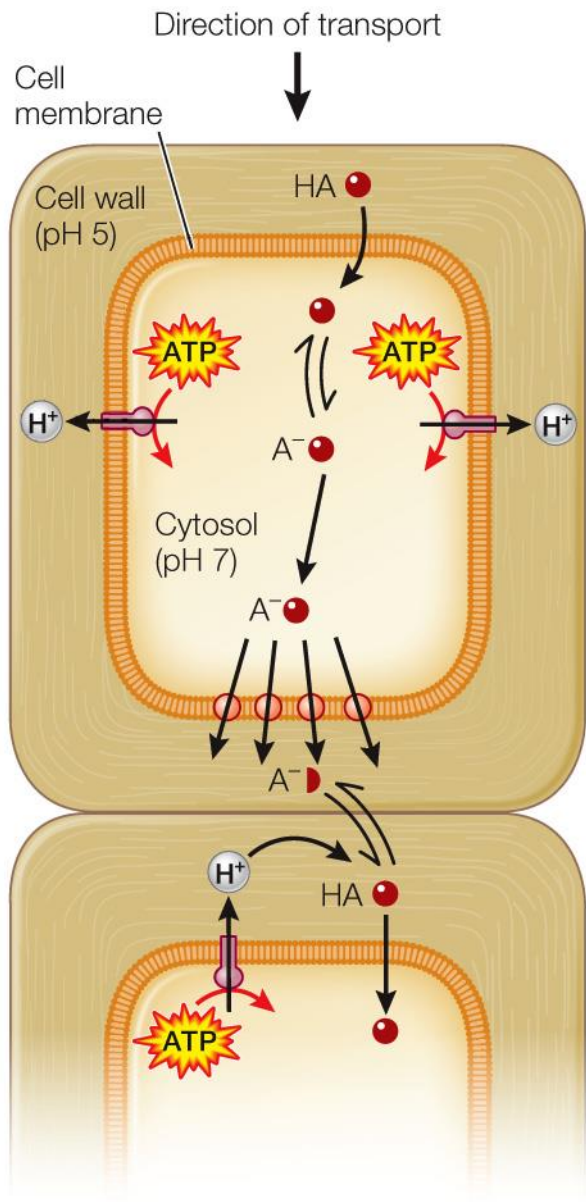
CONCLUSION ▶ The coleoptile tip senses light and then transmits a growth signal to the tissue away from the light source.

Charles Darwin and his son Francis studied this using canarygrass seedlings grown in the dark.

They covered different regions of the coleoptiles, then exposed them to light.

Hypothesis: Only part of the coleoptile senses the light that triggers phototropism.

Placing a coleoptile tip on a decapitated coleoptile led to bending, even if a block of gelatin separated tip and coleoptile.



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Lateral redistribution of auxin causes directional plant growth.

If a coleoptile tip is placed to the side, the plant bends. The carrier proteins move from the base of the cell to one side; auxin exits only on that side and moves sideways.

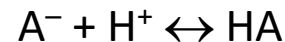
When light strikes a coleoptile on one side, auxin at the tip moves toward the shaded side.

The asymmetry is maintained as polar transport moves auxin down the coleoptile.

The movement of auxin is polar—unidirectional from apex to base.

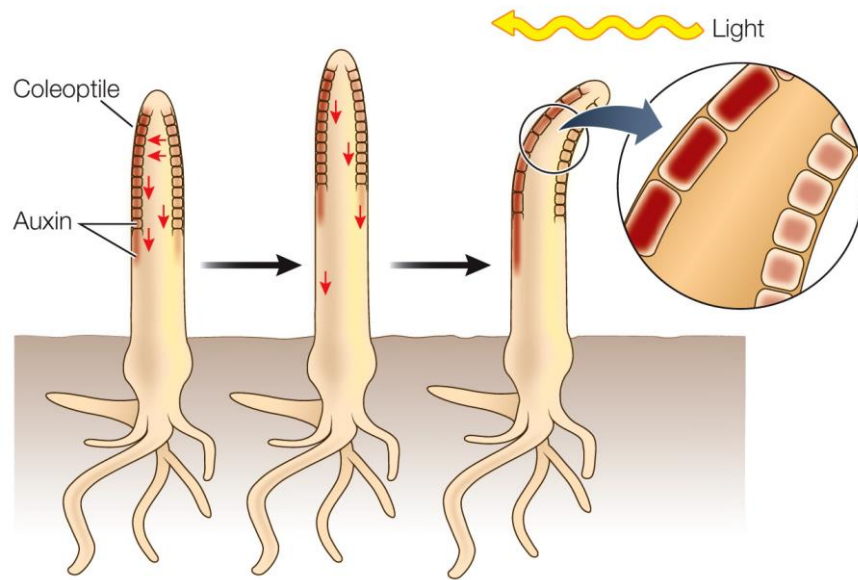
It depends on 4 processes:

1. *Diffusion across a cell membrane*: Polar molecules diffuse less readily than nonpolar.
2. *Membrane protein asymmetry*: Active transport carriers for auxin are in the basal end of the cell.
3. *Proton pumping/chemiosmosis*: H^+ is pumped out of the cell, decreasing pH in the cell wall. The resulting electrochemical gradient provides energy to drive transport of auxin.
4. *Ionization of a weak acid*: Indole-3-acetic acid is a weak acid.



pH levels drive the reaction to the right or left and determine which form is dominant.

(A) Phototropism

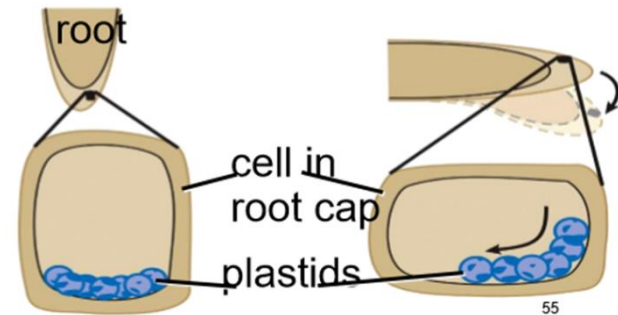


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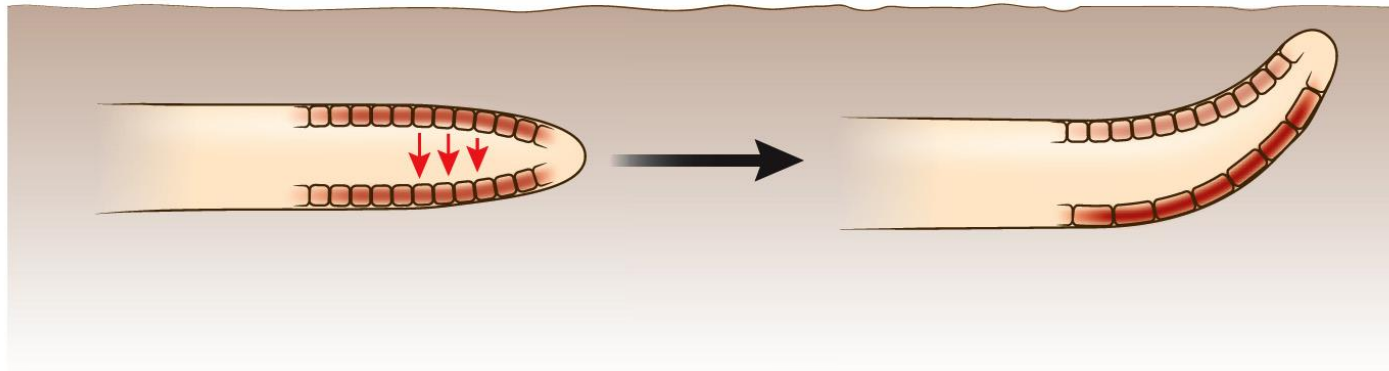
If a shoot is tipped over, auxin will move to the lower side—cell growth results in bending of the shoot so that it grows up (**gravitropism**).

Upward gravitropic response of shoots is negative gravitropism.

The downward response of roots is positive gravitropism.



(B) Negative gravitropism of shoot



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Auxin has many roles in plant development:

Root initiation

Shoot cuttings from some plants can form roots and develop a new plant.

Undifferentiated parenchyma cells in the stem must dedifferentiate to form a root meristem. This can be stimulated by dipping the shoot into an auxin solution.

Abscission: Detachment of old leaves from the stem.

Results from breakdown of cells in the abscission zone of the petiole; inhibited by auxin.

Timing of leaf fall is determined in part by a decrease in movement of auxin from the blade through the petiole.

Apical dominance: Apical buds inhibit growth of axillary buds, resulting in minimal branching.

A diffusion gradient of auxin from the apical tip down the stem results in lower branches receiving less auxin and therefore branching more.

Fruit development

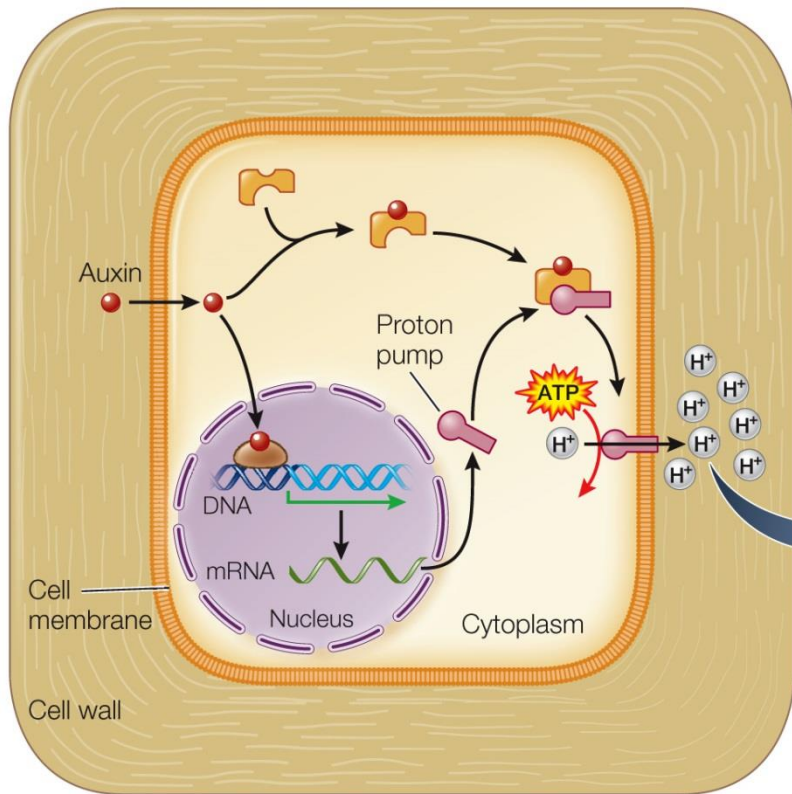
Normally depends on fertilization of the ovule, but if unfertilized ovaries are treated with auxin or gibberellins it causes **parthenocarpy** (单性结实) —fruit formation without fertilization.

Some plants spontaneously form parthenocarpic fruits (e.g., seedless grapes, bananas, some cucumbers).

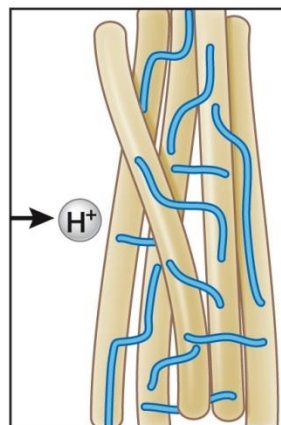
Cell expansion

Auxin acts on cell walls to regulate cell expansion and growth.

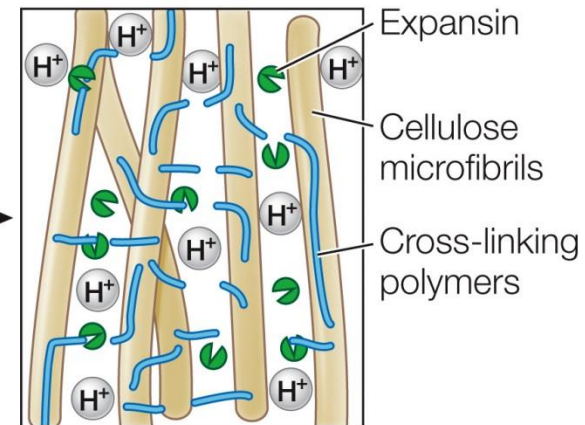
Expansion of plant cells is driven primarily by water uptake. For the cell to expand, the wall structure must loosen.



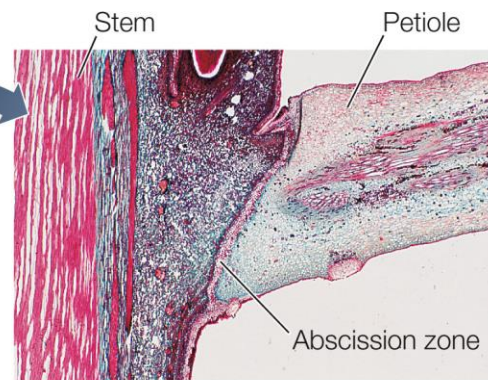
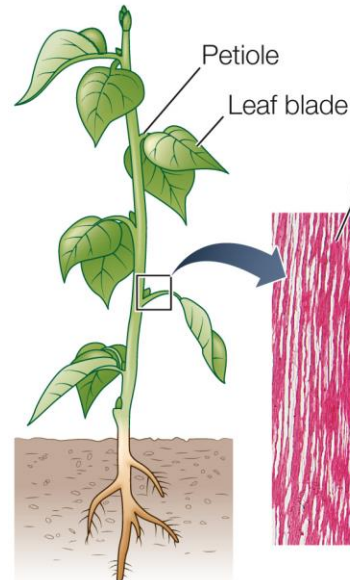
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Acid growth hypothesis



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Detachment of old leaves from the stem

Gibberellins have multiple roles in plant growth and development.

A rice disease caused by the fungus *Gibberella fujikori* results in plants that grow overly tall and spindly. Chemicals were then isolated that Gibberellic acid made by *G. fujikori* caused rice plants to overgrow.

Stem elongation—inhibitors of gibberellin synthesis reduce stem elongation. Flower growers use inhibitors to control plant height.

Fruit growth

Seedless grape varieties have smaller fruit than seeded varieties. Experimental removal of seeds resulted in small fruits, suggesting seeds were the source of a growth regulator. Spraying young seedless grapes with gibberellins causes them to grow as large as seeded varieties.

Mobilization of seed reserves

In germinating cereal seeds, gibberellins diffuse through the endosperm to surrounding tissue called the **aleurone layer** underneath the seed coat. A cascade of events is triggered, causing this layer to secrete enzymes to digest the endosperm.

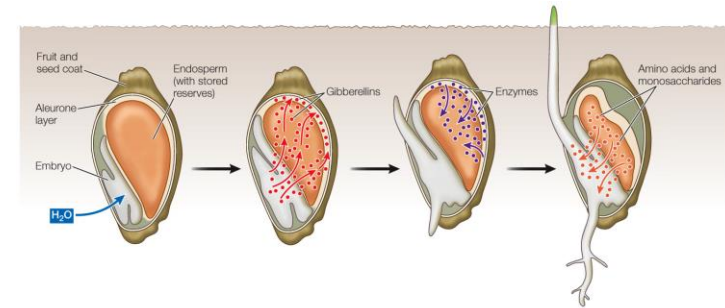
In the beer brewing industry, gibberellins are used to enhance “malting” (germination) of barley. Breakdown of the endosperm produces sugar that is fermented to alcohol.

Genes controlling GA synthesis are important “green revolution” genes



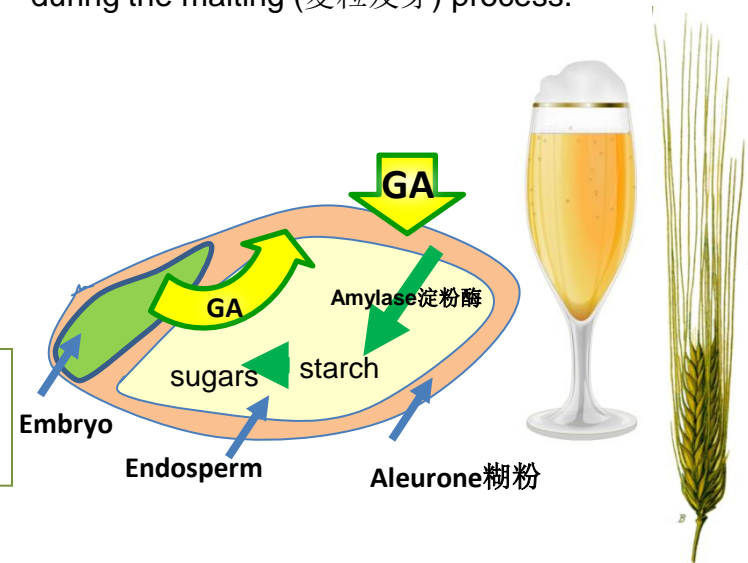
Distinguished plant breeder and Nobel Laureate
[Norman Borlaug](#) 1914-2009

Photos courtesy of S. Harrison, [LSU Ag center](#) and [The World Food Prize](#).

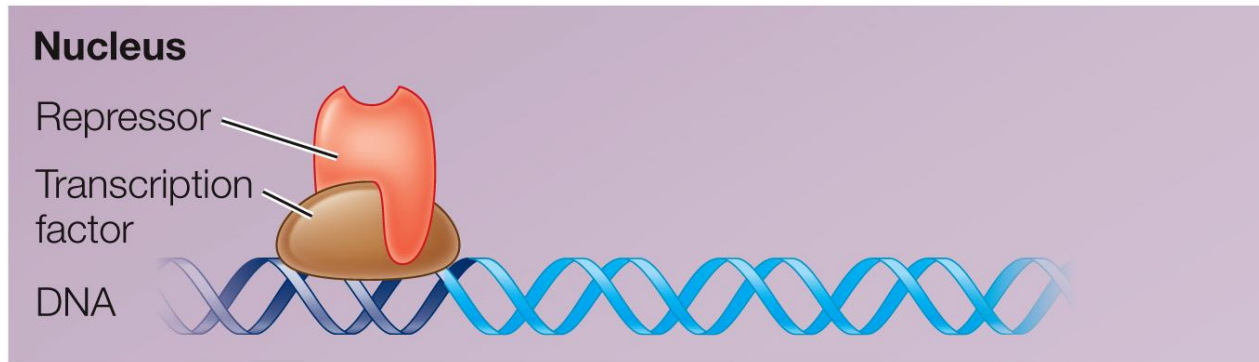


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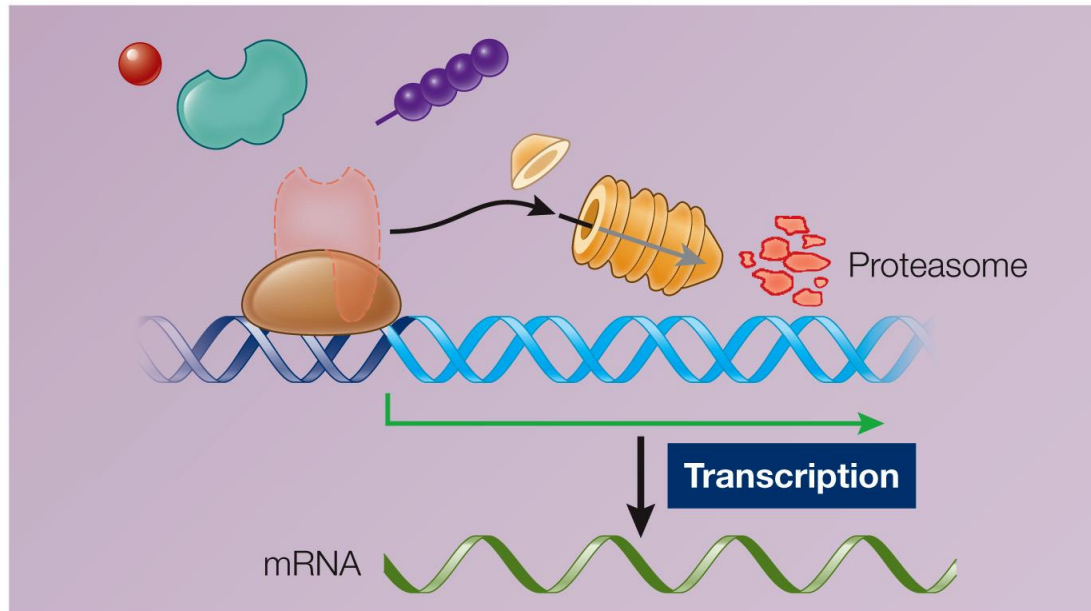
Breakdown of starch in the endosperm is initiated by GA produced by the endosperm or added during the malting (麦粒发芽) process.



Auxin signal transduction pathway (similar to GA)



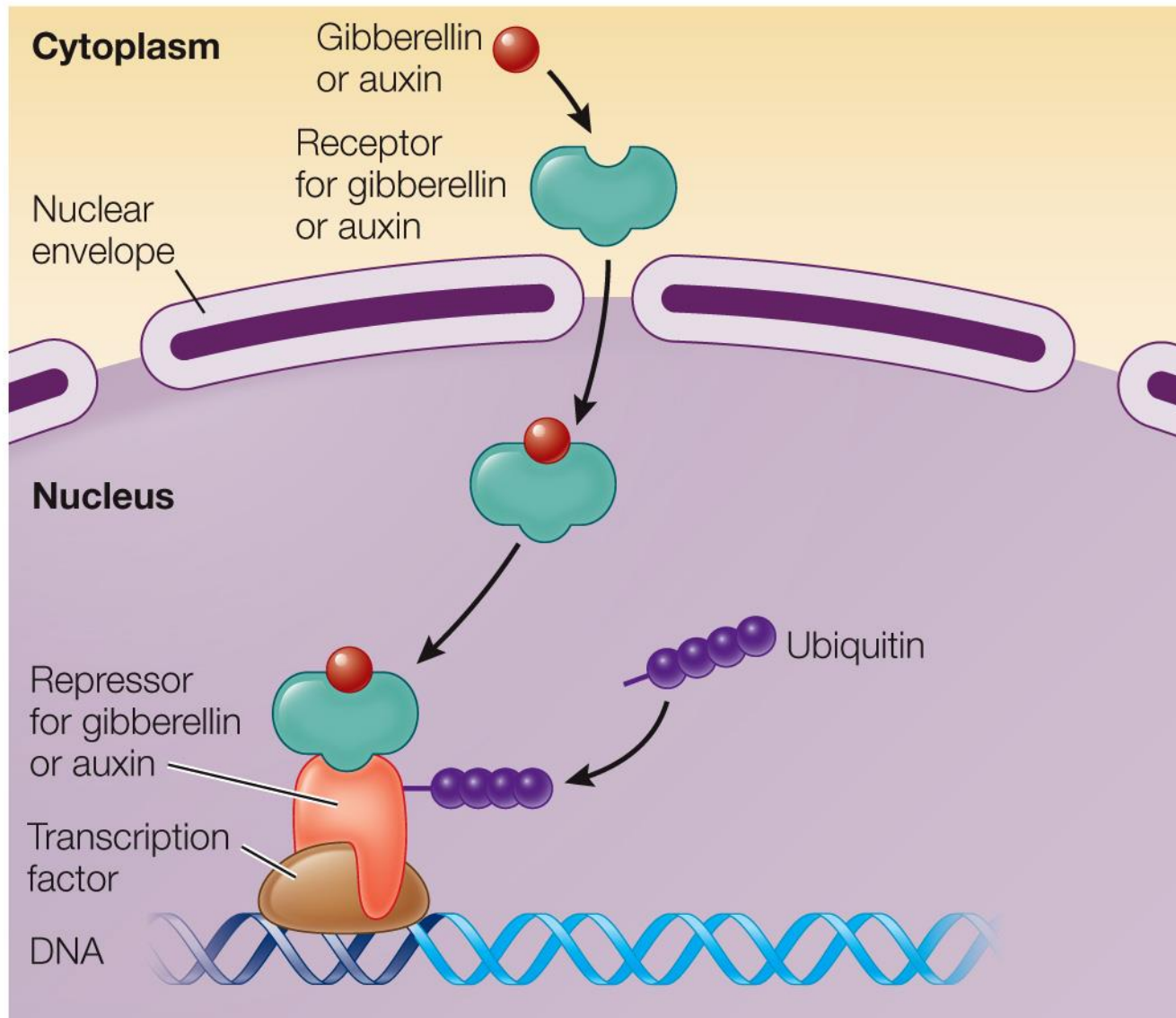
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The auxin binds to a receptor, which binds to the repressor. Poly-ubiquitination of the repressor targets it for breakdown in a proteasome.

The receptors contain a region called an F-box that facilitates protein–protein interactions necessary for protein breakdown.



Other phytohormones

- **Cytokinins** are plant hormones that affect many growth functions related to cell division, growth, and senescence.

With auxin, stimulate rapid cell division in tissue cultures and regeneration. In cell cultures, high cytokinin-to-auxin ratio promotes formation of shoots; low ratio promotes formation of roots. Inhibit stem elongation but cause lateral swelling of stems and roots. Stimulate axillary buds to grow; Cause light-requiring seeds to germinate in darkness; auxin-to-cytokinin ratio controls extent of branching; delay senescence of leaves.

- The gaseous hormone **ethylene** has several functions related to senescence, including fruit ripening; it also affects auxin gradients during shoot development.

Promotes leaf abscission and speeds ripening of fruit; also causes an increase in its own production; involved in other stages of plant development. The **apical hook** of eudicots protects the shoot while the stem grows through the soil. The hook results from asymmetrical production of auxin, controlled by ethylene.

- **Brassinosteroids**, or plant steroid hormones, have a variety of functions that vary among plants.

Promote xylem differentiation, growth of pollen tubes, seed germination, apical dominance and leaf senescence, enhance cell elongation and cell division in shoots.



Plants respond to two aspects of light:

Quality—the wavelengths of light that can be absorbed by molecules in the plant.

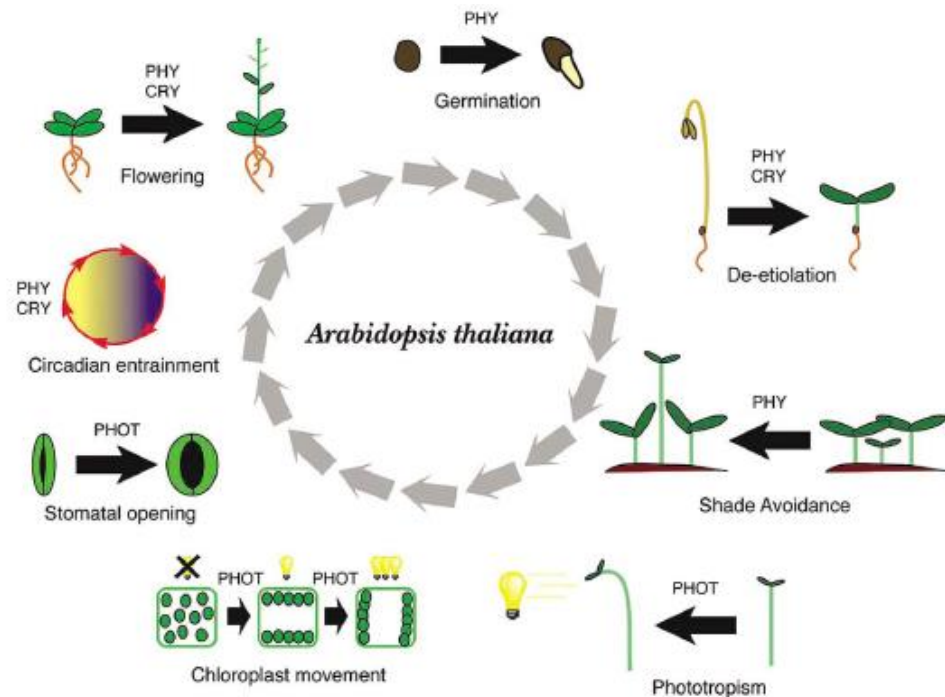
Quantity—the intensity and duration of light exposure.

Light influences seed germination, shoot elongation, flowering, and many other aspects of plant development.

Photoreceptors detect changes in quality and direction of light and day length.

They are often proteins associated with pigments.

Light acts directly on them; they regulate developmental processes that need to be responsive to light.



Photomorphogenesis—physiological and developmental events that are controlled by light:

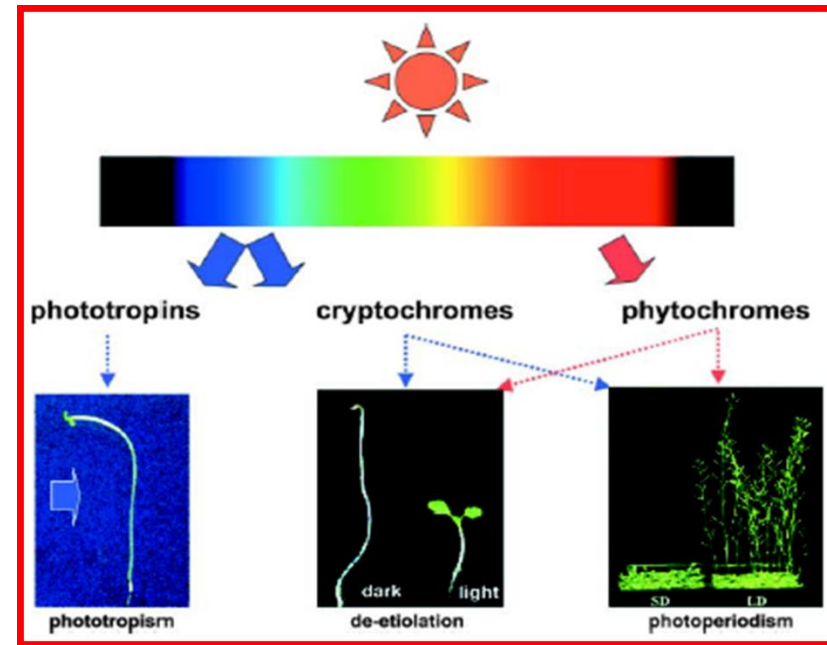
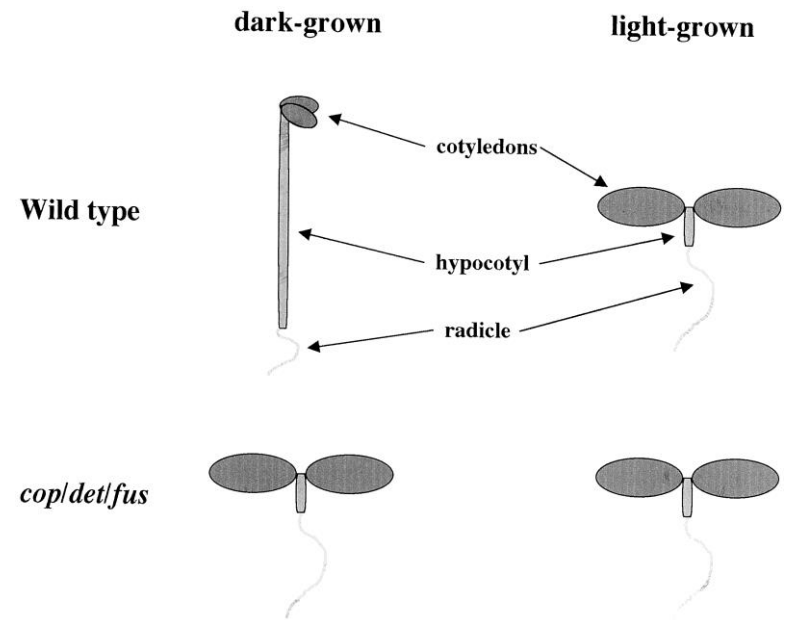
A bean seedling that is underground is elongate and pale (**etiolated**); when it emerges, light-induced changes occur—apical hook straightens, the leaf unfolds, and chlorophyll is made.

Lettuce seeds will germinate only in response to light. Even a flash of dim light will suffice. Cocklebur plants flower when exposed to long nights. If there is a brief light flash in the middle of the night, they do not flower.

Action spectra of the above processes show they are induced by red light (650–680 nm).

The processes can be reversed by far-red light (710–740 nm).

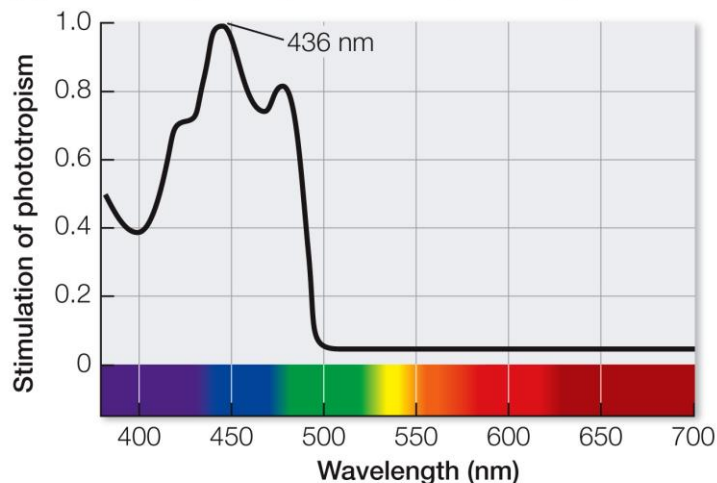
If lettuce seeds are exposed to brief, alternating periods of red and far-red light, they respond only to the final exposure.



- Inhibit hypocotyl/stem elongation
- Enhance cotyledon/leaf expansion
- Enhance anthocyanin production
- Promote floral initiation
- Entrain the circadian clock
- Mediate blue-light-induced stomatal opening and development
- Mediate shade avoidance response
- affect plant resistance to pathogen
- Sense magnetic fields in insects and mammals

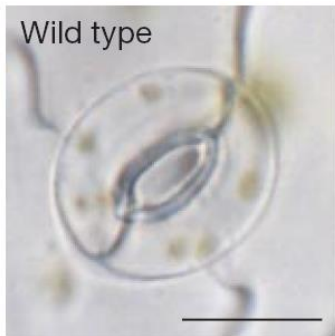
Blue light receptor: Cryptochrome (CRY)

(A) The absorption spectrum for phototropin

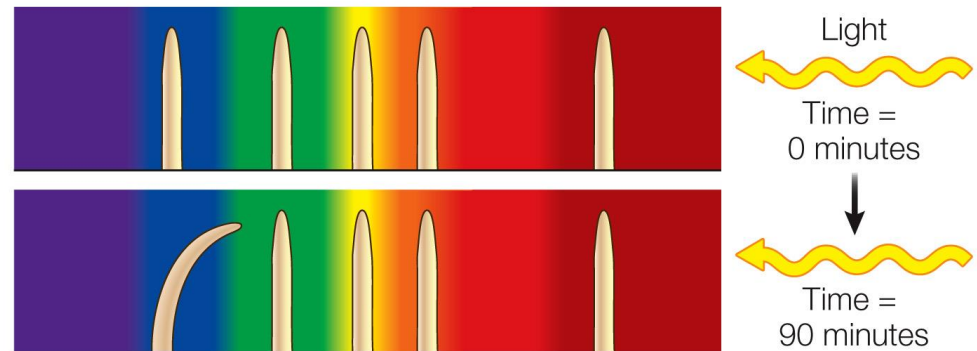


Blue light receptor: Phototropins (PHOT)

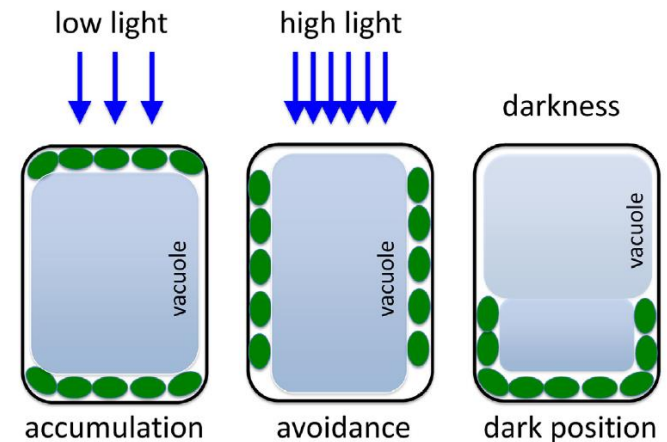
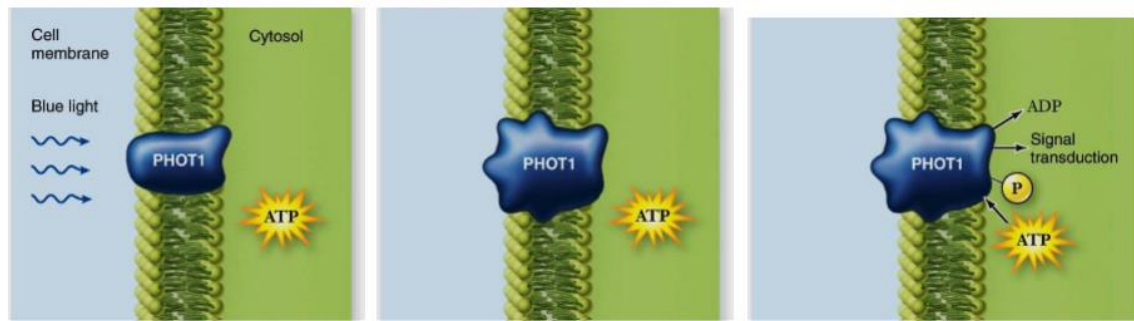
1. Phototropism
2. Chloroplast movement
3. Stomatal opening



(B) Effect of blue light on coleoptiles

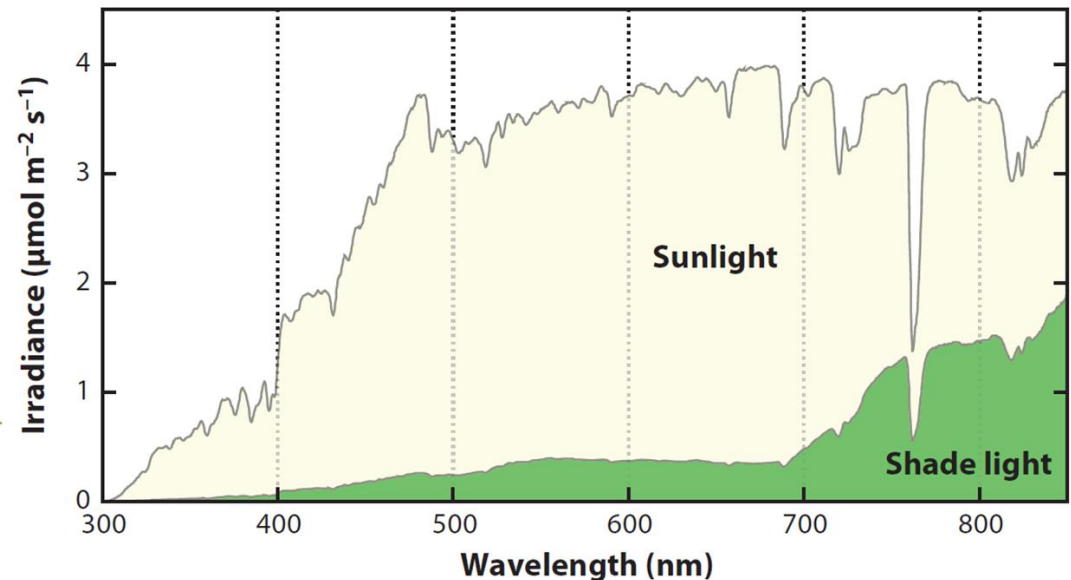
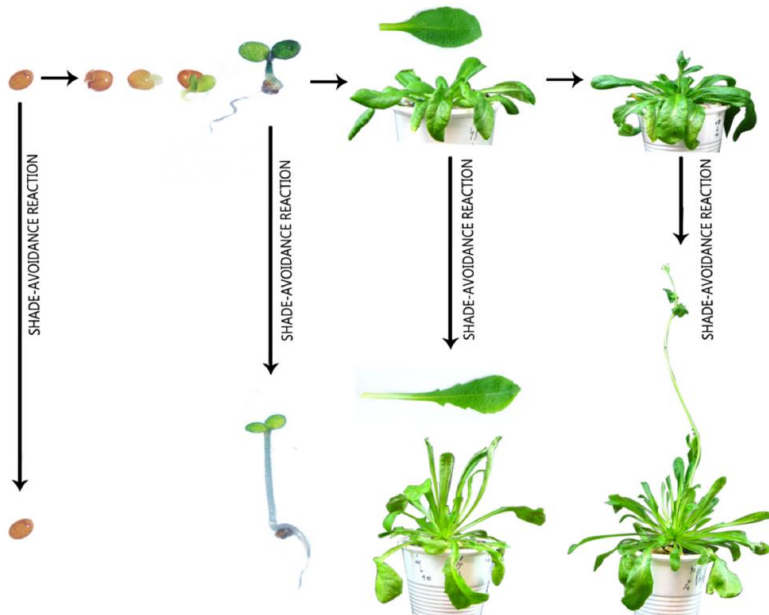
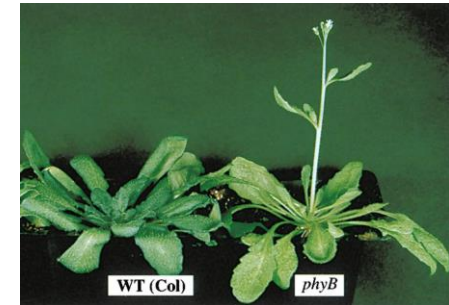
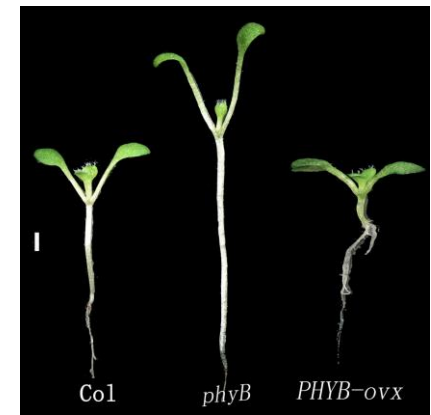


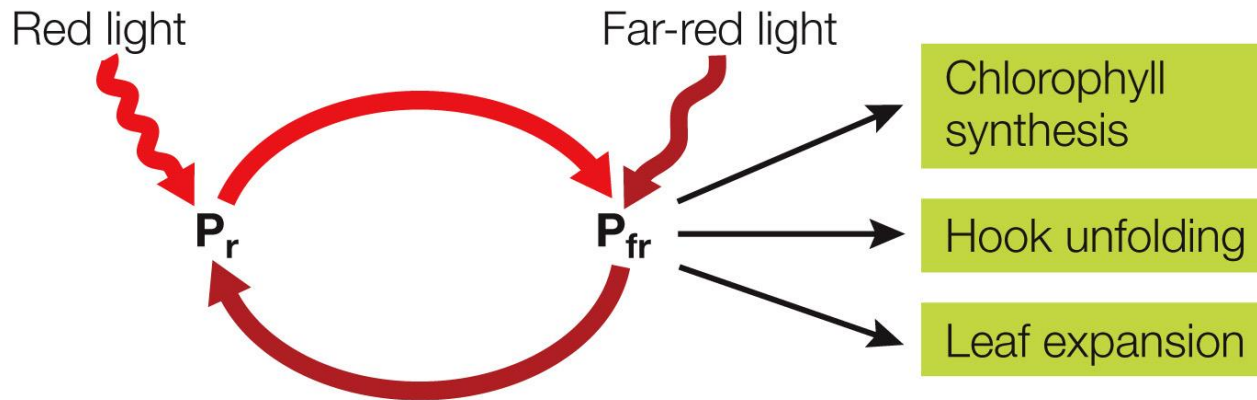
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Red light receptor: Phytochrome (PHY)

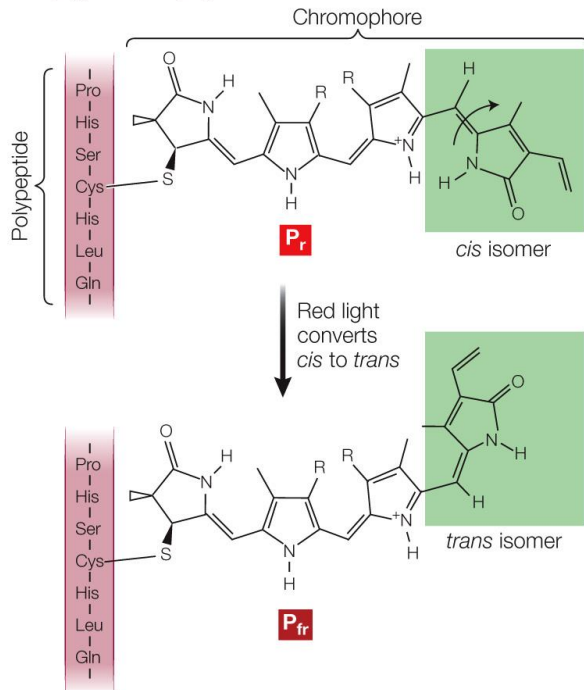
- Inhibit hypocotyl elongation
- Repress floral initiation
- Entrain the circadian clock
- Mediate red/far-red-light-induced stomatal opening and development
- Mediate shade avoidance response



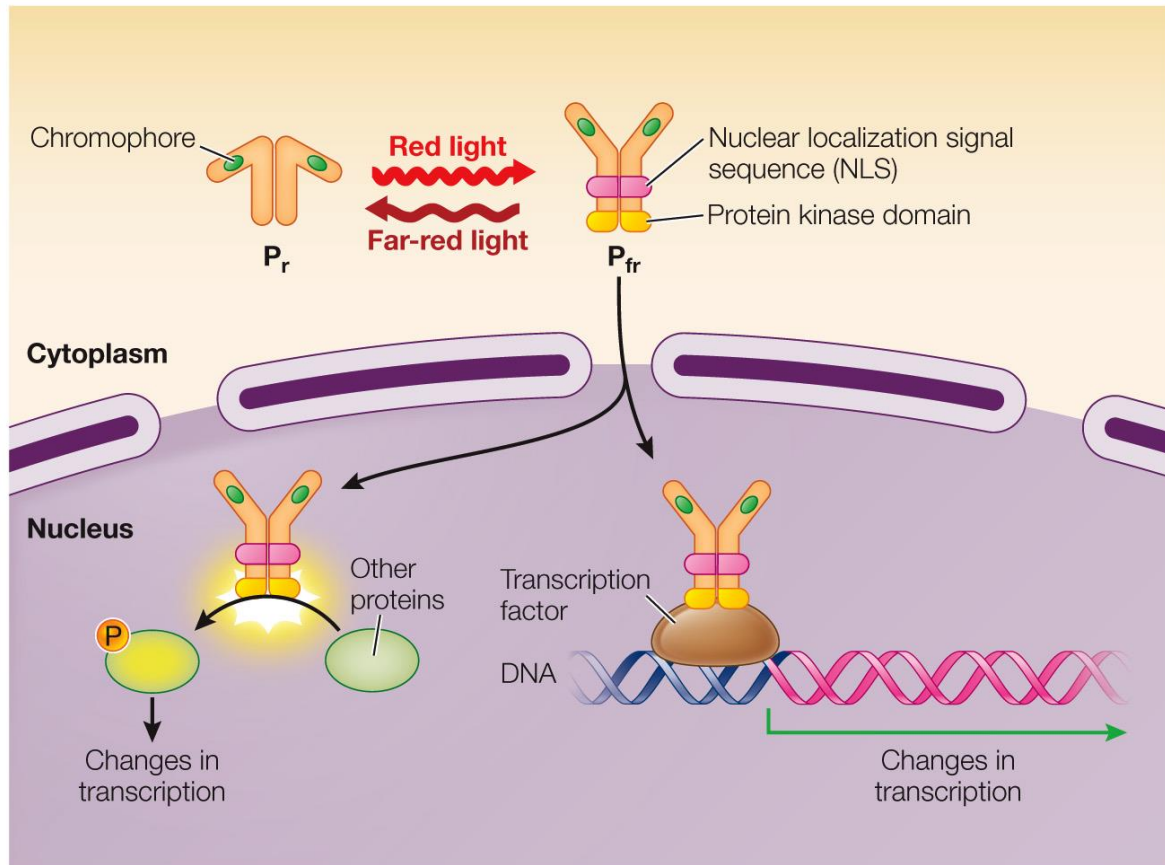


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(A) The *cis* and *trans* isomers of the chromophore pigment in phytochrome

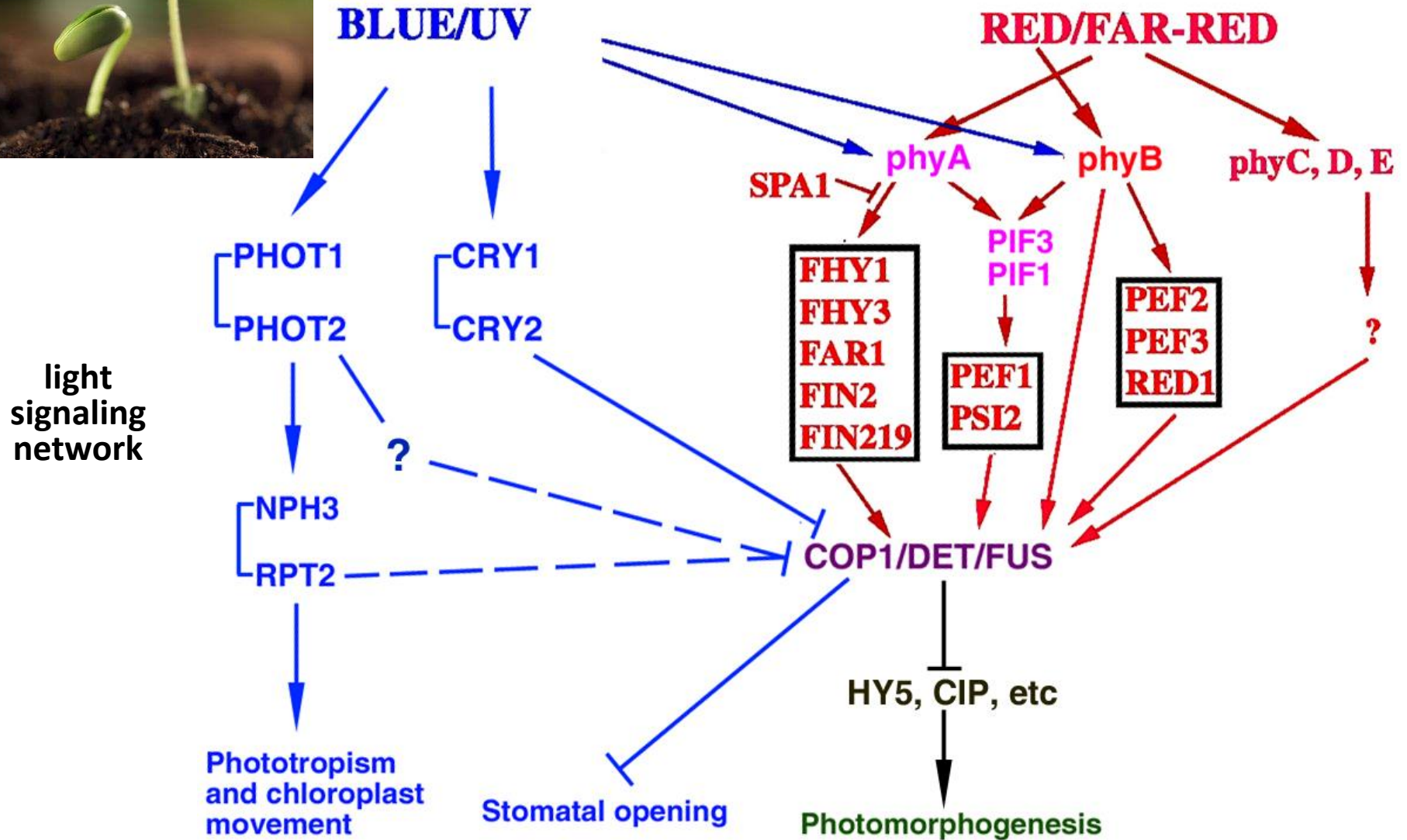


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Summary

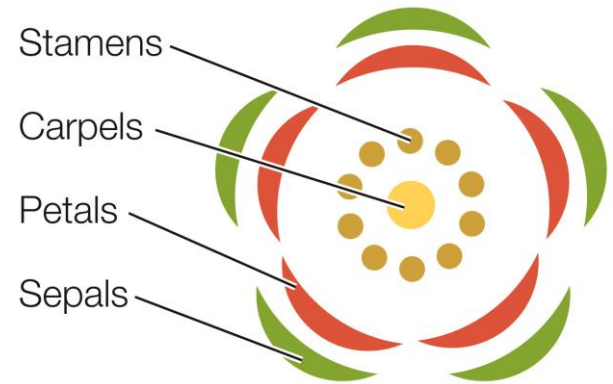
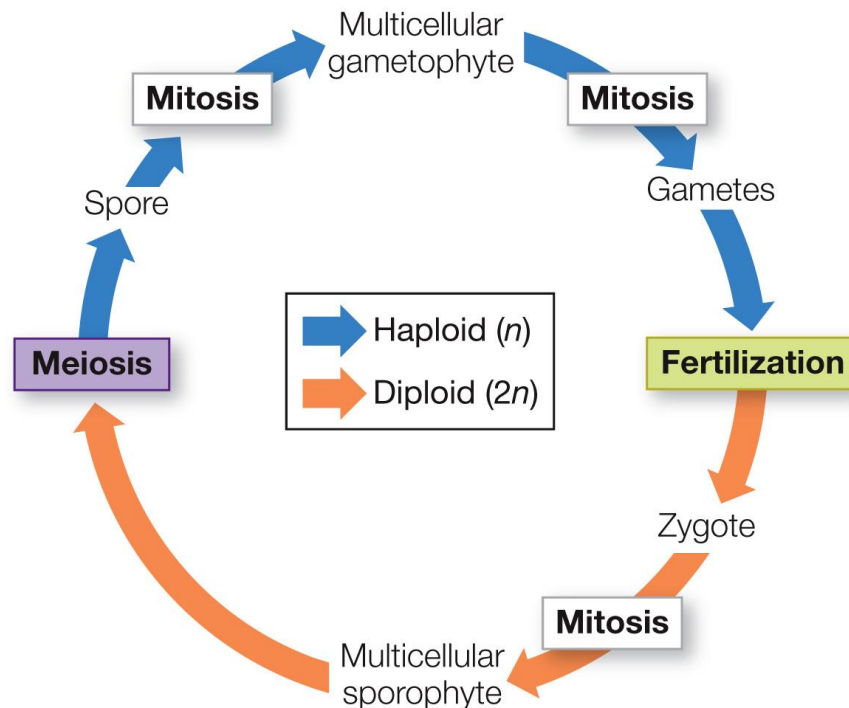


Reproduction in Flowering Plants

37.1 Most Angiosperms Reproduce Sexually

37.2 Hormones and Signaling Determine the Transition from the Vegetative to the Reproductive State

37.3 Angiosperms Can Reproduce Asexually



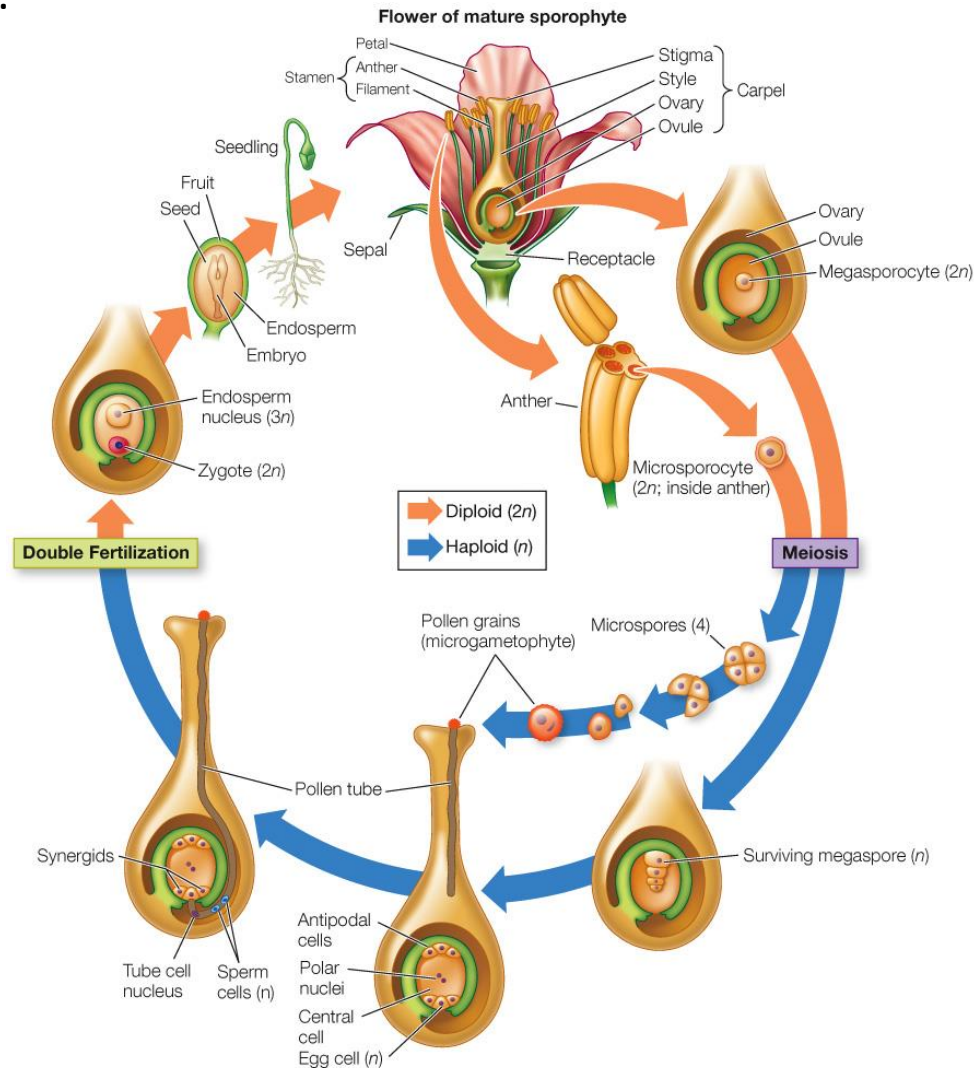
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The haploid gametophytes develop from haploid spores in the flower:

Megagametophytes (female) are called **embryo sacs**; develop in the ovules.

Microgametophytes (male) are called **pollen grains**; develop in anthers on the stamens.



A megasporocyte undergoes meiosis to produce 4 haploid megaspores; 3 undergo apoptosis.

The surviving megaspore undergoes 3 mitotic divisions with no cytokinesis to produce 8 haploid nuclei. Cell wall formation leads to a gametophyte (embryo sac) with 7 cells and 8 nuclei.

At one end of the gametophyte are 3 cells—the **egg** and 2 synergids.

Synergids attract the pollen tube.

Antipodal cells at the opposite end usually degenerate.

The central cell has 2 **polar nuclei**.

Microsporocytes undergo meiosis to produce 4 haploid microspores.

Each develops a cell wall and divides mitotically to form 2 haploid cells in each pollen grain:

After pollination, the generative cell divides by mitosis to form 2 sperm cells.

Tube cell forms the pollen tube that delivers sperm to the embryo sac.

Pollination: Transfer of pollen from anther to stigma.

Germination of the pollen grain involves uptake of water from the stigma and growth of the **pollen tube** through the style to reach the ovule.

Downward growth is guided by a chemical signal released by the synergids.

Double fertilization:

One synergid degenerates when the pollen tube arrives and the 2 sperm cells are released into its remains.

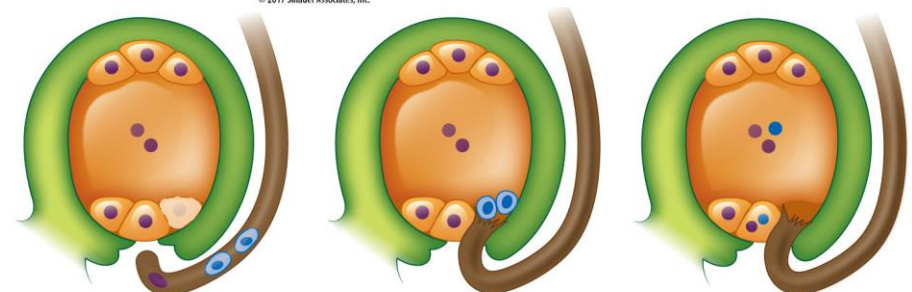
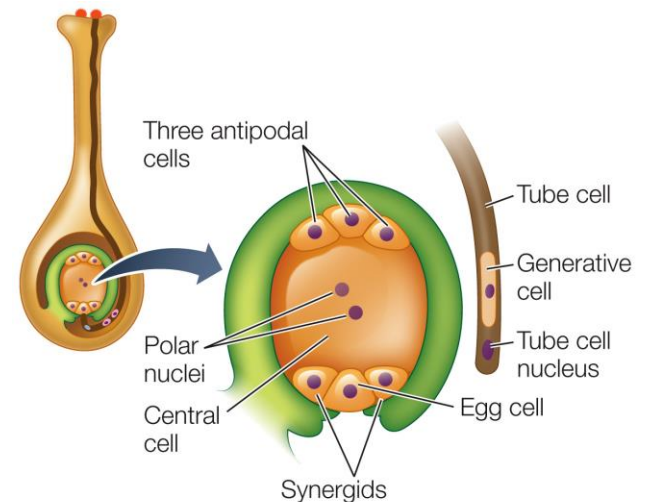
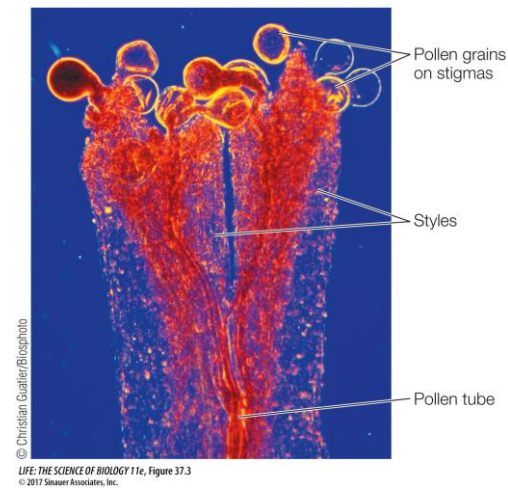
One sperm cell fuses with the egg cell, forming a diploid zygote.

The other sperm cell fuses with the two polar nuclei in the central cell, forming a **triploid (3n) cell**.

The zygote nucleus begins mitotic division to form the new sporophyte embryo. The triploid nucleus undergoes mitosis to form the endosperm. It will later be digested by the developing embryo for energy and building blocks.

In some plants, such as peas, **self-pollination** occurs before the flower opens, resulting in **self-fertilization**. This leads to homozygosity, which **reduces genetic diversity**.

Most plants have mechanisms to prevent self-fertilization.



1. Physical separation of male and female gametophytes:

In dioecious species, pollination occurs only when one plant pollinates another.

In monoecious species, separation of male and female flowers can reduce self-fertilization. In some species the two flower types bloom at different times.

2. Genetic self-incompatibility:

Some plants are **self-incompatible**; they reject pollen from their own flowers.

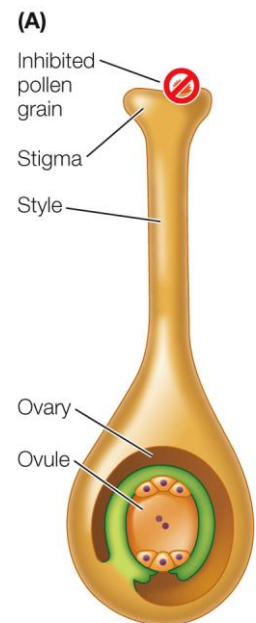
The plant must determine whether the pollen is genetically similar or not.

The *S* locus genes encode proteins in the pollen and style that interact during the recognition process.

The *S* locus has many alleles.

When pollen carries an allele that matches an allele of the recipient pistil, the pollen is rejected.

The rejected pollen either fails to germinate or is prevented from growing through the style.

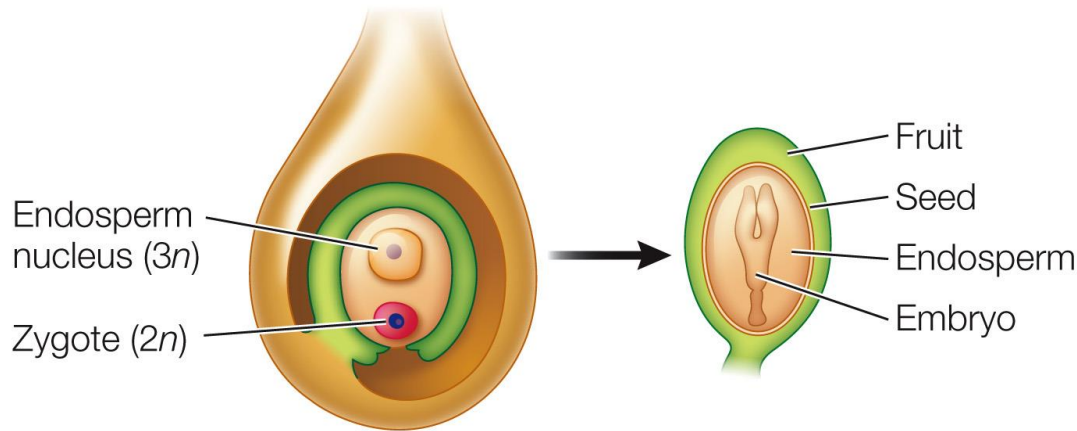


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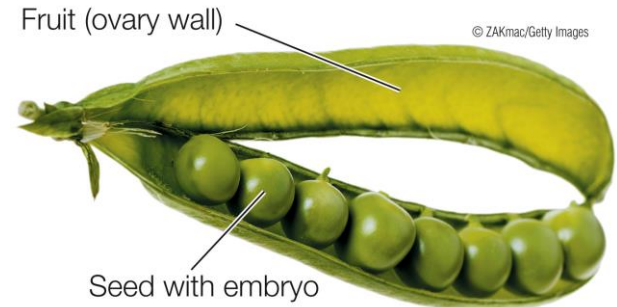
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(A) Seed and fruit



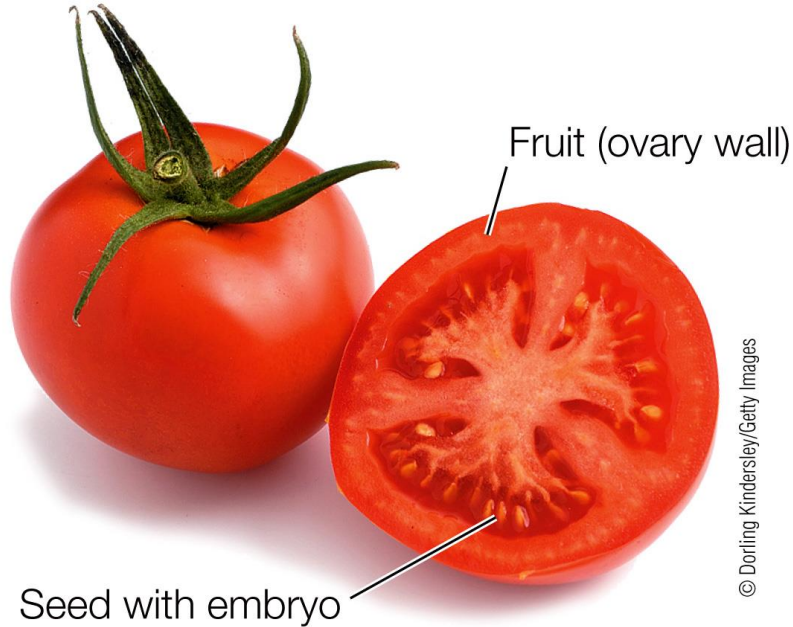
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(B) Garden pea



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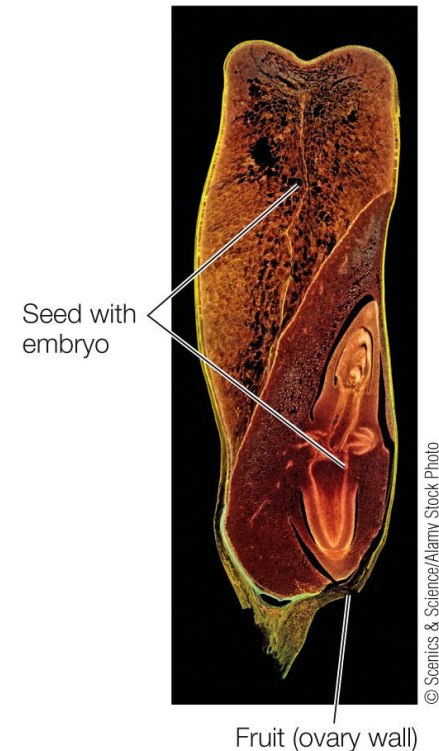
(C) Tomato



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(D) Corn



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Hormones and Signaling Determine the Transition from the Vegetative to the Reproductive State

Flowering is a major event in a plant's life.

When a plant is old enough, it can respond to internal or external signals (such as light or temperature) to start reproduction.

Or flowering occurs as part of a predetermined developmental program.

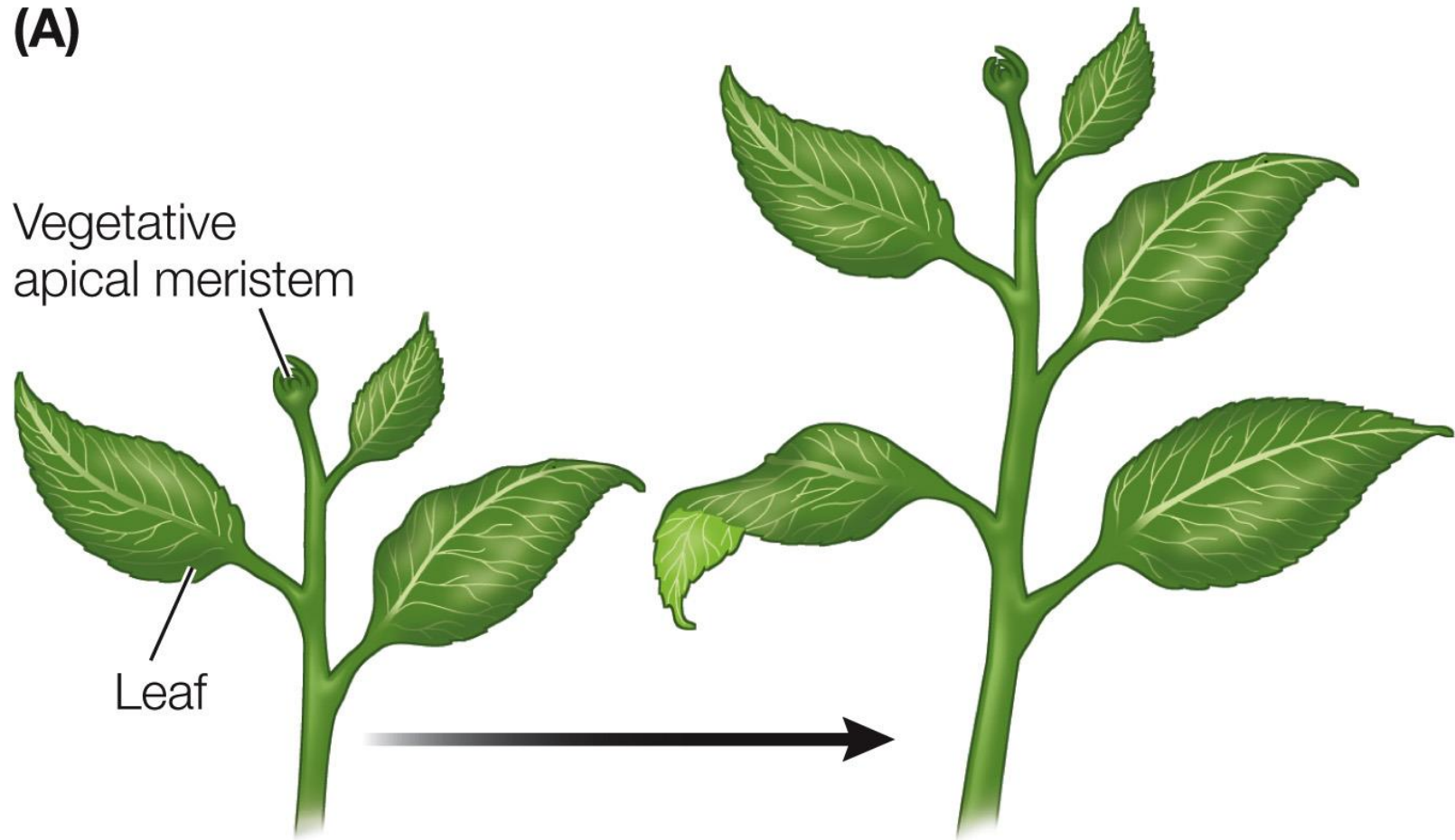
Plants fall into three categories in terms of maturation and flowering:

Annuals complete life cycle in one year; little or no secondary growth. After flowering, most of their energy is used to develop seeds and fruits and the plant dies.

Biennials take two years to complete the life cycle. They produce vegetative growth the first year and store carbohydrates in underground roots (carrots) or stems (celery). In the second year, stored carbohydrates are used to produce flowers and seeds.

Perennials live three or more years. They typically flower every year and keep growing for another season. In some species the reproductive cycle repeats each year. Others grow vegetatively for many years, flower once, and die.

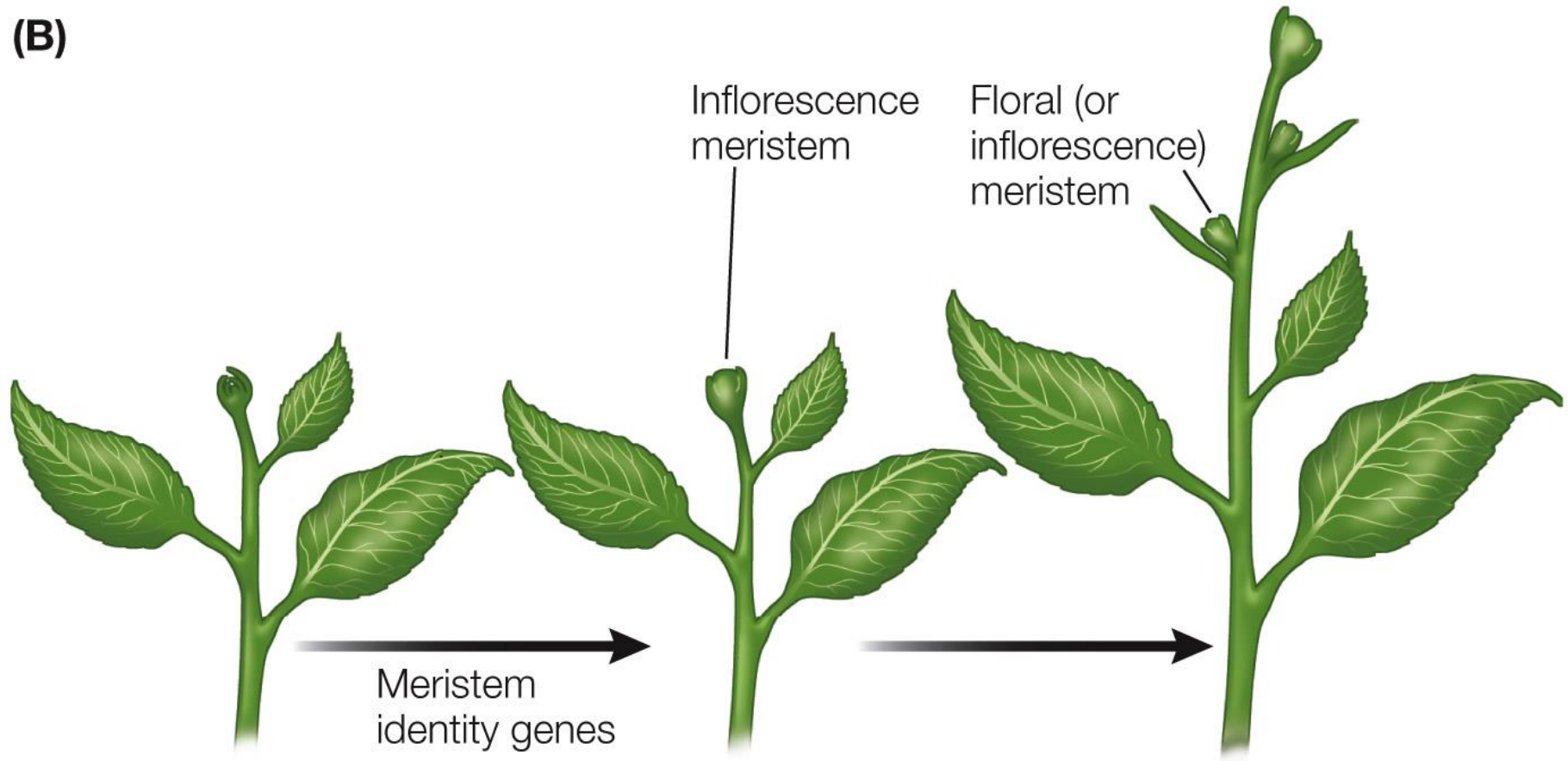
(A)



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During vegetative growth, apical meristems continuously produce leaves, stems, and axillary buds (indeterminate growth).

(B)



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If an apical meristem becomes an **inflorescence meristem** it produces bracts and new meristems in the angle between bract and stem.

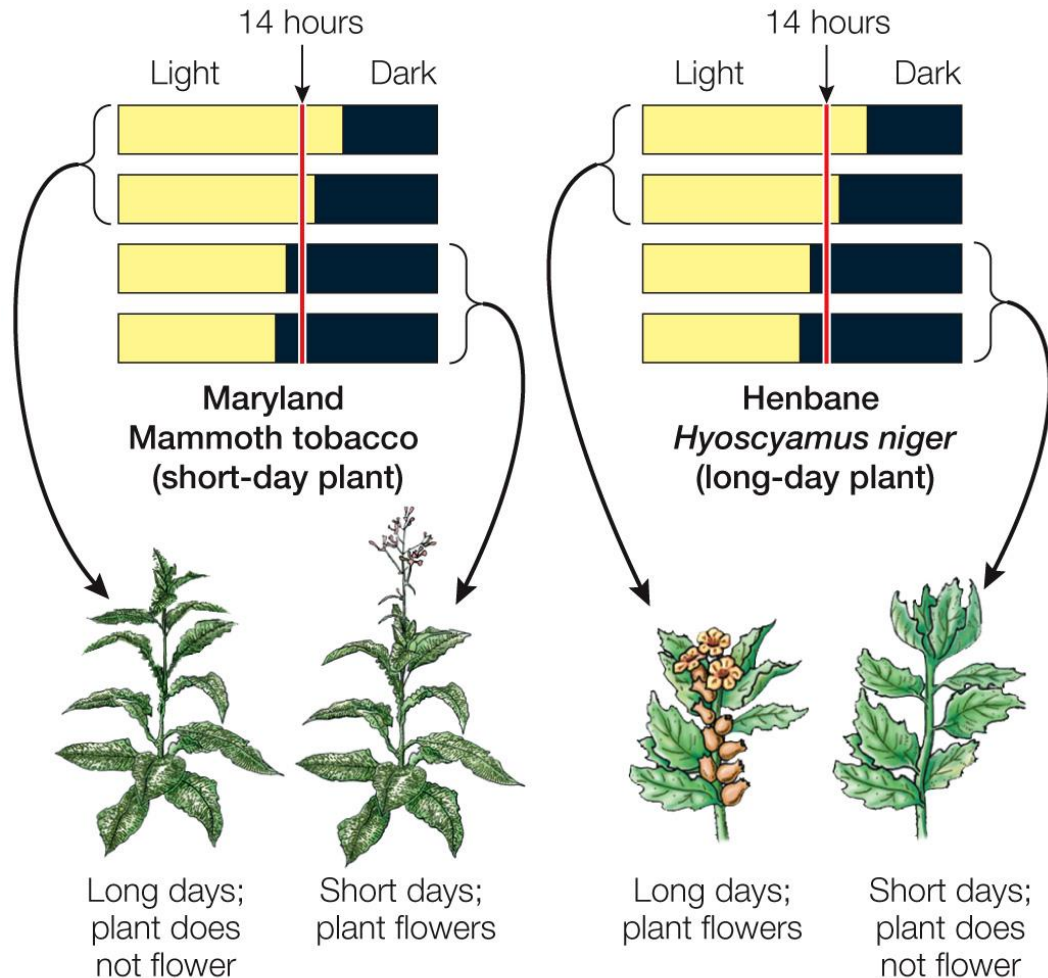
Floral organ identity genes are activated in response to **external cues (day length, temperature) or internal cues (hormones)**.

Photoperiod (day length)

Greenhouse experiments measured the day length required for different plant species to flower.

Maryland Mammoth tobacco flowered when day length became shorter than 14 hours, as it does in December.

Other plants (e.g., soybeans and henbane) flowered only when days were long.



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Photoperiodic plants actually measure length of night, not day.

Hypothesis: Red light participates in the photoperiodic timing mechanism.

Method:

Grow plants under short-day conditions, but interrupt the night with light of different wavelengths.

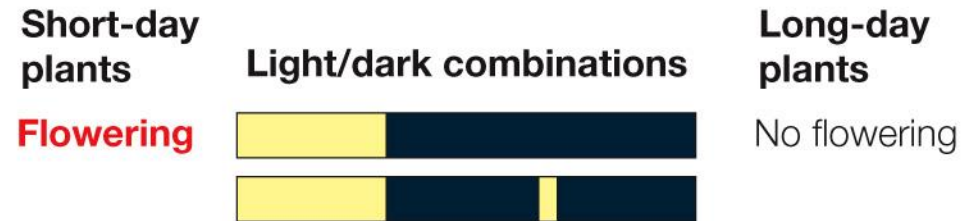
Conclusion:

When plants are exposed to red (R) and far-red (FR) light in alternation, the final treatment determines the effect. Phytochrome is the photoreceptor.

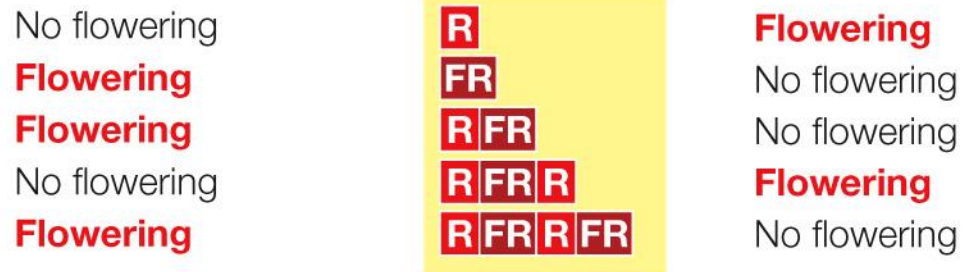
HYPOTHESIS ► Red light participates in the photoperiodic timing mechanism.

METHOD

Grow plants under short-day conditions, but interrupt the night with light of different wavelengths.



RESULTS

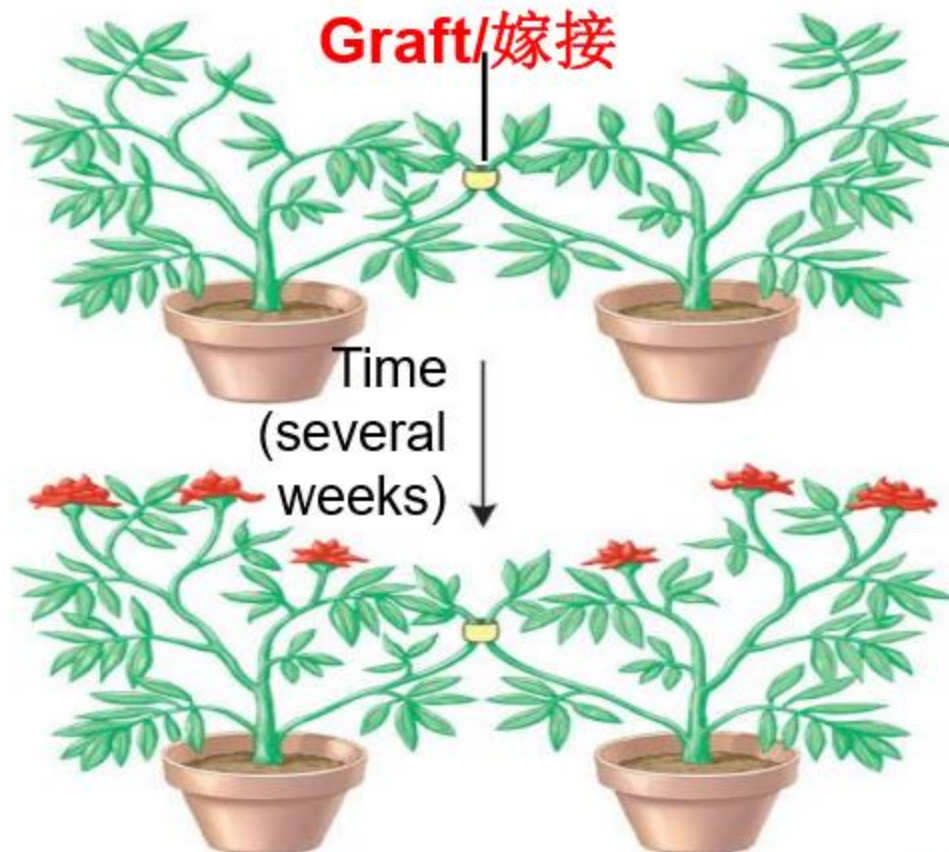


CONCLUSION ► When plants are exposed to red (R) and far-red (FR) light in alternation, the final treatment determines the effect. Phytochrome is the photoreceptor.

Signal conduction between Cells

Plant subjected to photoperiod that induces flowering

Plant subjected to photoperiod that does not induce flowering



- ◆ The Love Letter?
- ◆ Call?
- ◆ other?

- ◆ Both plants flowered, indicating the transmission of a **flower-inducing substance**.
- ◆ In some cases, the transmission worked even if one was a **short-day plant** and the other was a **long-day plant**.

1. ***FT (FLOWERING LOCUS T)*** codes for florigen, which is small and can travel through plasmodesmata.

2. **CO (CONSTANS)** codes for a transcription factor that activates synthesis of FT. *CO* is also expressed in phloem companion cells in the leaf.

Photoperiodic stimulus

CO

DNA

Transcription

Companion cell

FT

Sieve tube element

FT

CO: CONSTANS protein

FT: FLOWERING LOCUS T protein (florigen)

FD: FLOWERING LOCUS D protein

AP1: APETALA1 protein

Expression of the gene *CONSTANS* (*CO*) follows a circadian rhythm.

Experiments with *Arabidopsis*, an LDP, show that flowering is determined by interactions between photoreceptors and the *CO* protein.

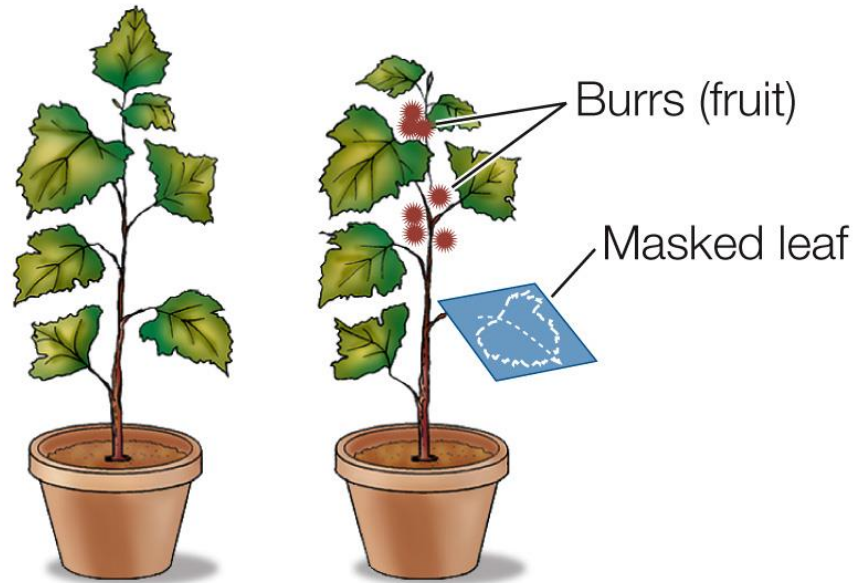
Peak *CO* expression is late in the day—in the afternoon on long days, but after dark on short days.

On long days, the active forms of phytochrome and blue-light receptors activate pathways that stabilize the *CO* protein, which promotes flowering.

This process does not occur on short days.

RESULTS

If even one leaf is masked for part of the day—thus shifting that leaf to short days and long nights—the plant will flower.



CONCLUSION ▶ The leaves measure the photoperiod. Therefore some signal must move from the induced leaf to the flowering parts of the plant.

In strains of *Arabidopsis* that require vernalization, *FLC* (*FLOWERING LOCUS C*) encodes a transcription factor that inhibits expression of FT and FD in the florigen pathway.

Cold temperature inhibits synthesis of FLC protein, allowing FT and FD to be expressed.

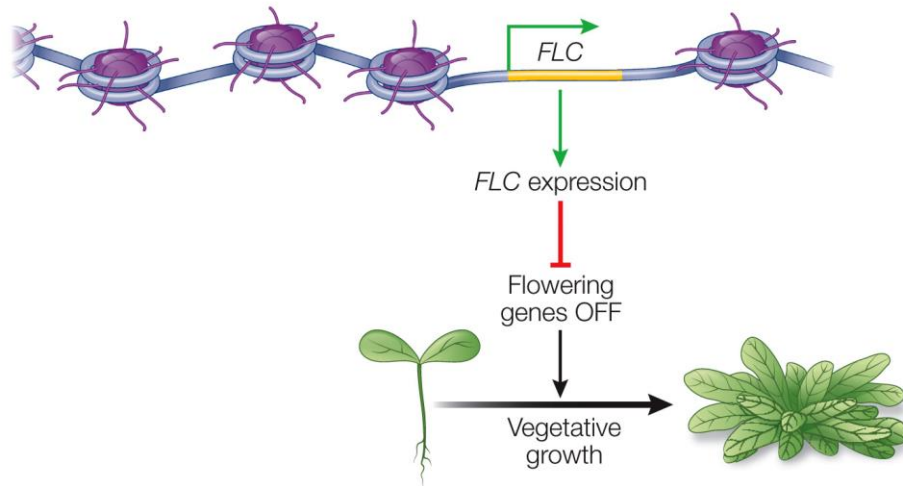
Epigenetics plays a role in vernalization:

Before vernalization, chromatin at the promoter of the *FLC* gene is relaxed; and DNA can be transcribed.

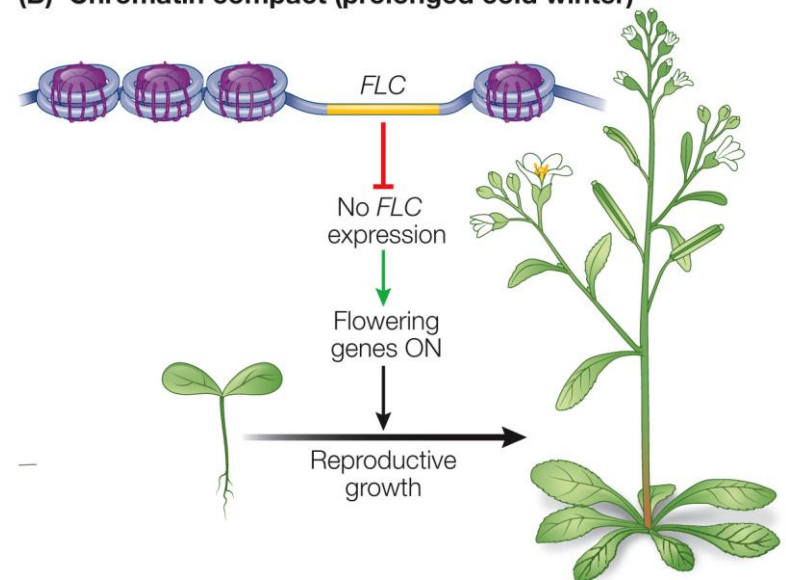
During vernalization, chromatin remodeling results in more compact chromatin and reduced expression of *FLC*.



(A) Chromatin relaxed



(B) Chromatin compact (prolonged cold winter)



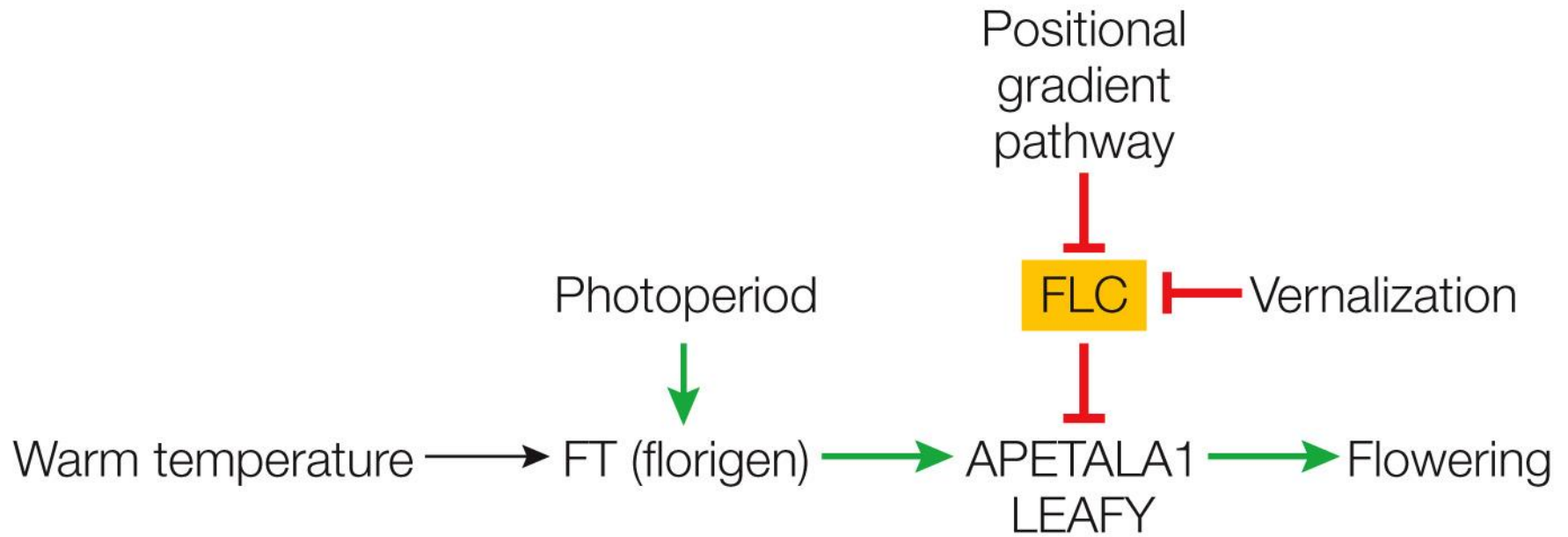
Gibberellins are also involved in flowering.

Application of gibberellins to *Arabidopsis* buds results in activation of the meristem identity gene *LEAFY*, which in turn promotes the transition to flowering.

Some plant species flower on cue from an “internal clock.”

In some tobacco strains, flowering is initiated in the terminal bud when the stem has grown four phytomers in length.

The position of the bud determines transition to flowering.



Angiosperms Can Reproduce Asexually

Stems, leaves, and roots are the *vegetative organs* of a plant.

Asexual reproduction often occurs by modification of vegetative organs; also called **vegetative reproduction**.

(A) Rhizomes



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(B) Bulbs



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(C) Plantlets



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Grafting is the process of attaching a bud or piece of stem from one plant onto the root or stem of another plant.

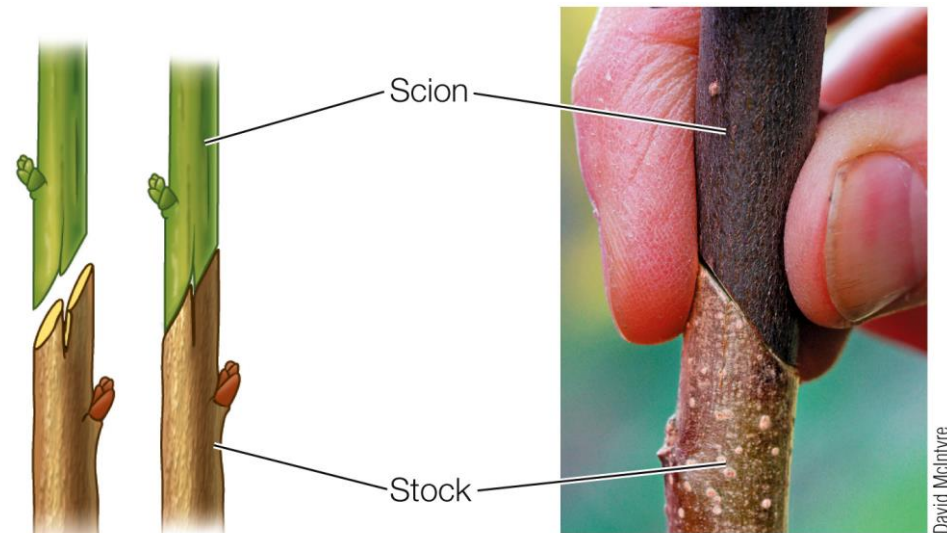
The root-bearing plant is the **stock**; the part grafted onto it is the **scion**.

The vascular cambia of each must grow together so that water and minerals can be transported to the scion. Usually closely related species are used.

Apomixis (单性生殖): Asexual production of seeds.

The megasporocyte fails to undergo meiosis, resulting in a diploid egg cell, which then forms an embryo and seed.

Or, diploid cells from the integument around the embryo sac form a diploid embryo sac, and the sac forms an embryo and seed.



Plant Responses to Environmental Challenges

38.1 Plants Respond to Pathogens with Constitutive and Induced Responses

38.2 Plants Have Mechanical and Chemical Defenses against Herbivores

38.3 Plants Can Adapt to Environmental Stresses



Plant pathogens include bacteria, fungi, protists, nematodes, and viruses.

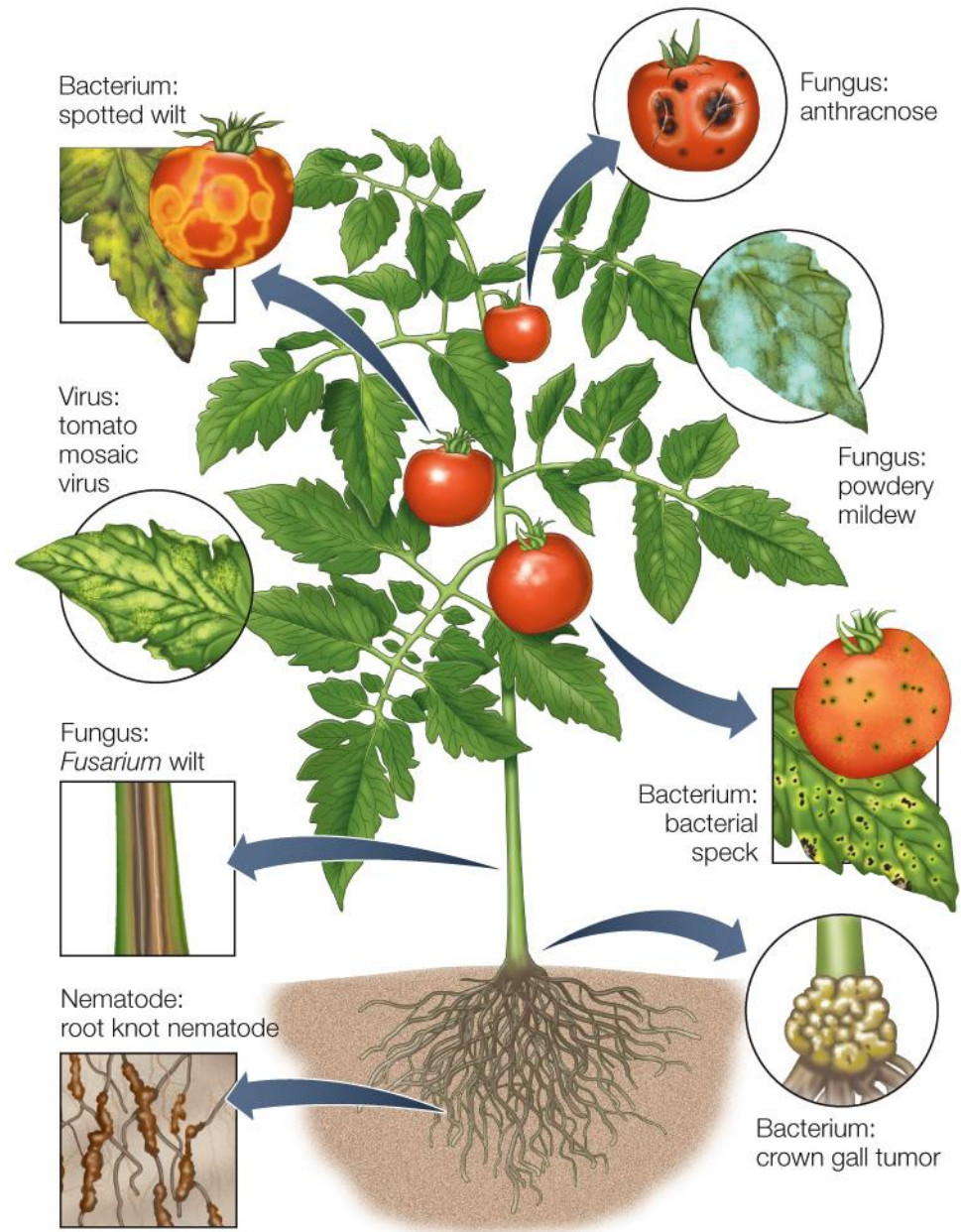
Plants and pathogens have been evolving together in a continuing “arms race.”

Pathogens evolve mechanisms to attack plants; plants evolve defenses against pathogens.

Plant defenses can be both mechanical and chemical.

Constitutive defenses—always present in the plant.

Induced defenses—produced in reaction to damage or stress.



Physical barriers (constitutive defenses):

Plant organs are covered with cutin, suberin, and waxes that prevent water loss and can prevent bacteria or fungal spores from entering.

Some fungi secrete chemicals that break down these substances.

Induced defenses:

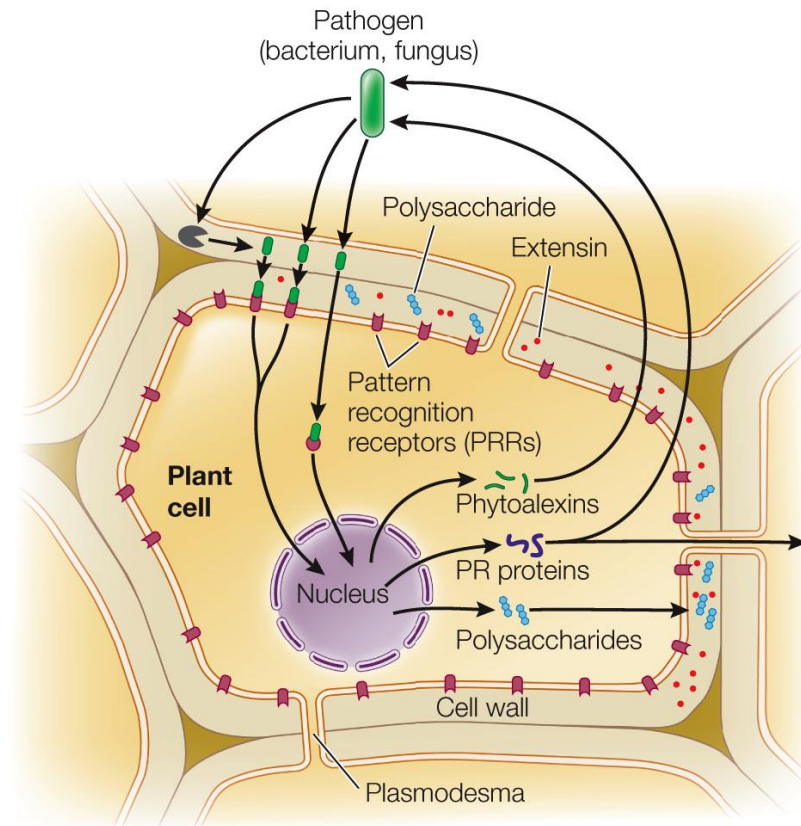
Plants generally do not repair tissue damaged by pathogens, but instead seal it off to prevent the rest of the plant from being infected.

Plants can replace damaged parts by growing new ones.

Induced responses are controlled by receptors.

Elicitors are chemicals that trigger plant defenses.

Elicitors can be peptides made by bacteria, cell wall fragments from fungi, even fragments of plant cell walls that have been broken down by pathogens.



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The Plant Immune System:

1. *General immunity* is triggered by pathogen associated molecular patterns (PAMPs).

PAMPs are molecules produced by classes of pathogens (e.g., flagellin by bacteria or chitin by fungi).

PAMPs are recognized by transmembrane receptors called **pattern recognition receptors (PRRs)**.

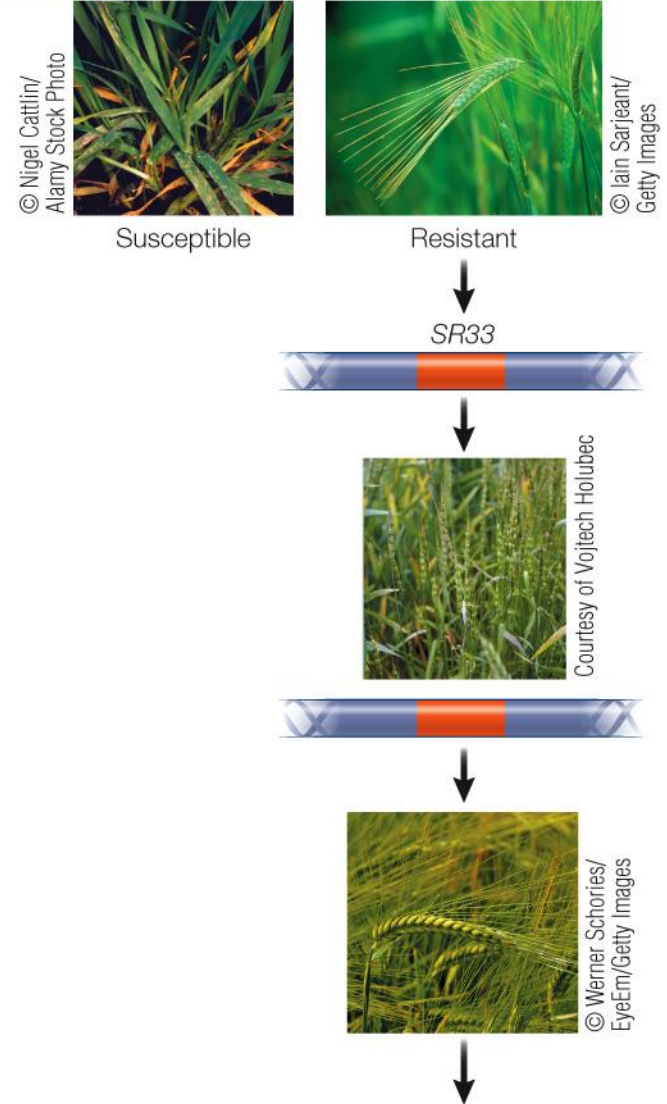
They activate signaling pathways that lead to general immunity.

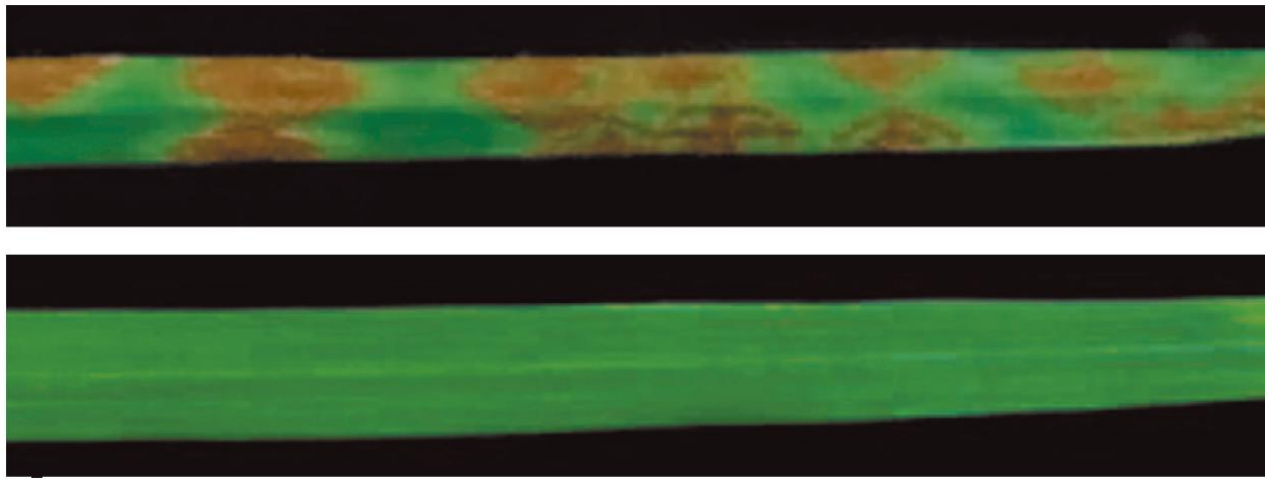
2. *Specific immunity* is triggered by specific pathogen-produced molecules called **effectors**.

Once inside the cell, effectors bind to R proteins that trigger the specific immunity response.

HYPOTHESIS ▶ A wild relative of wheat carries a gene for resistance to the wheat rust pathogen.

METHOD





From P. Sambasivam et al.
2013. *Science* 341: 786

General and specific immune responses:

Formation of reactive oxygen and NO: Toxic to some pathogens, and are components of signal transduction pathways.

Callose deposition (胼胝质沉积): On the inside of the cell wall—strengthens wall and seals off cell.

Hormone signaling: Production of plant hormones, including salicylic acid and jasmonic acid.

Changes in gene expression: up-regulated genes include pathogenesis-related (PR) genes and genes for production of antimicrobial phytoalexins (植物抗生素).

Phytoalexins are antibiotics that are toxic to many fungi and bacteria.

Produced by infected cells and their immediate neighbors within hours of infection.

Activity is non-specific and also kills the plant cells, sealing off the infection.

They are induced defenses.

Camalexin is made by *Arabidopsis*.

A protein kinase pathway results in up-regulation of genes for enzymes to convert tryptophan to camalexin.

In response, plants have evolved receptors (R proteins) that recognize specific effectors and activate specific immune responses.

Resistance genes (*R*) encode R proteins.

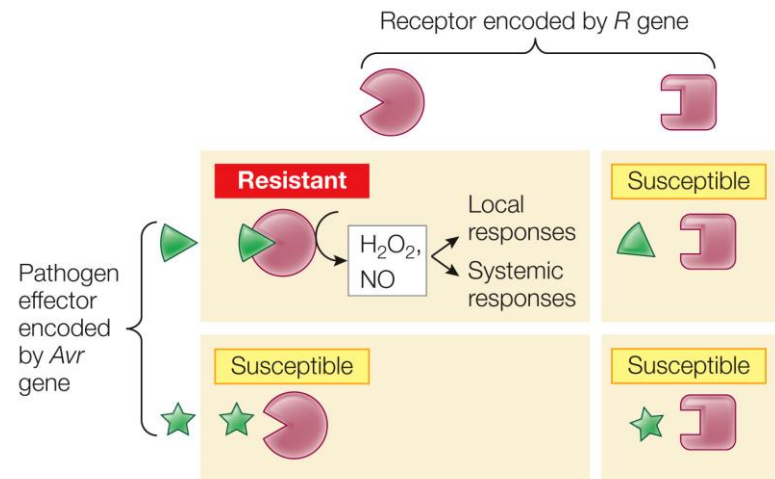
Pathogen genes that code for effectors are called **avirulence genes (*Avr*)**.

If a plant has an R protein receptor for an effector, a signal transduction pathway starts a specific response. If there is no receptor, the plant cannot respond.

Gene-for-gene concept: If *R* and *Avr* genes match, there is resistance.

Hundreds of *R* and *Avr* genes have been identified.

Plant breeders try to breed new *R* genes into crops to make them more resistant to pathogens.

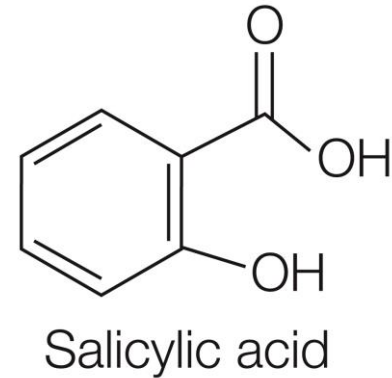


Specific immunity usually leads to a form of programmed cell death called the **hypersensitive response**.

Plant cells around the infection site die, forming a necrotic lesion (坏死斑), which deprives the pathogen of nutrients and prevents it from spreading.



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Systemic acquired resistance: General increase in resistance of the whole plant to a wide range of pathogens; can be long-lasting. Initiated by salicylic acid:

- Triggers production of reactive oxygen species

- Induces genes that encode PR proteins

- A derivative of salicylic acid forms a gas that can travel through air to signal other parts of the plant and nearby plants.

- Plant-to-plant signaling is also done through mycorrhizae (菌根) associated with roots. The siRNAs spread quickly throughout the entire plant via plasmodesmata, providing systemic resistance.

Herbivores cause physical damage to plants and can spread pathogens. Most herbivores are insects, but many vertebrates (脊椎动物) are also herbivores. Plants cannot evade consumers by running away but have many other ways to protect themselves.



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Associates, Inc.

(B) *Manduca sexta*



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Courtesy of Thomas Eisner, Cornell U

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Mechanical defenses against herbivory

Many features, such as trichomes, thorns, spines, or hairs, are specialized for defense (constitutive)

Production of latex (induced)— *Euphorbia* species produce a thick, white latex that traps insects.

Constitutive chemical defenses

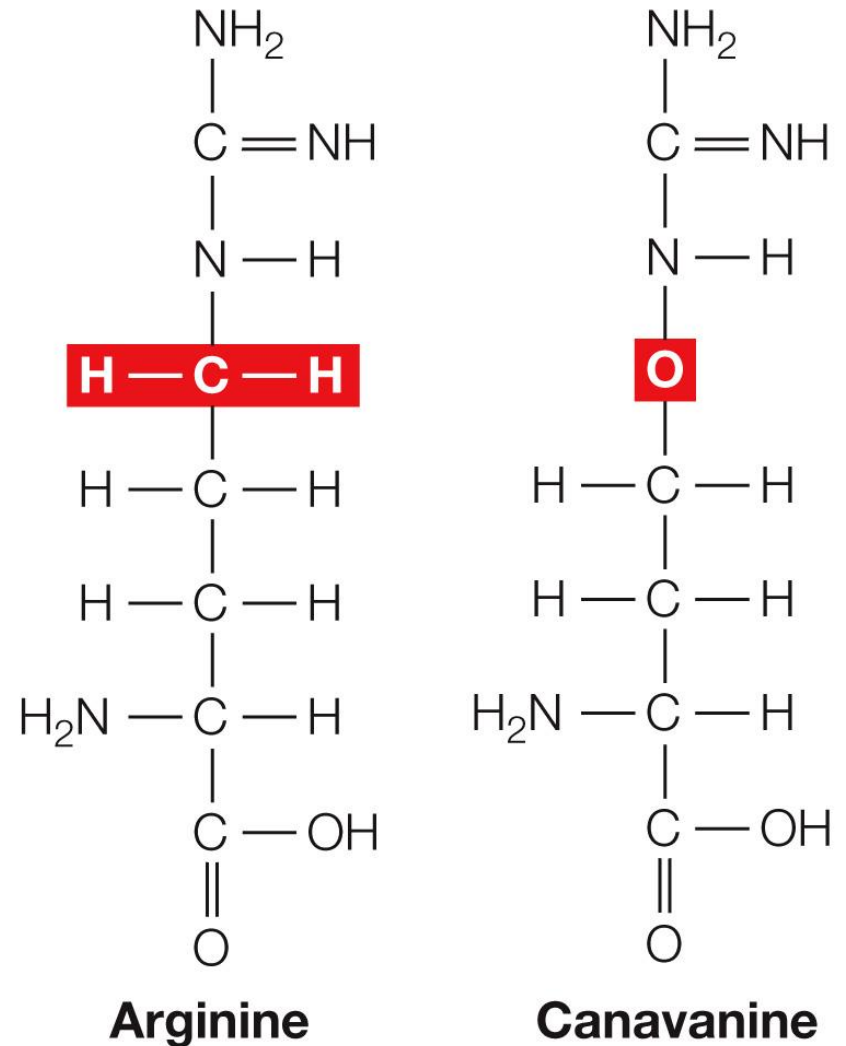
Secondary metabolites: Compounds not used for basic cellular processes.

Over 10,000 secondary metabolites are known, with diverse effects such as affecting herbivore nervous systems or mimicking insect hormones.

Some have non-defense roles as well.

When insects eat plants with canavanine, it is incorporated into their proteins where arginine should be.

Results in defective proteins, developmental abnormalities, and death.



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Induced defenses against herbivory

The elicitors are derived from the herbivore or are the products of digested plant tissue.

When herbivorous insects lay eggs on plants, some compounds are secreted that act as elicitors.

Some elicitors are produced as plant tissue passes through the insect digestive tract.

Volicitin is produced by insects feeding on corn plants—it induces production of volatile (挥发性的) signals that can travel to other plant parts and to neighboring plants and stimulate defense responses.

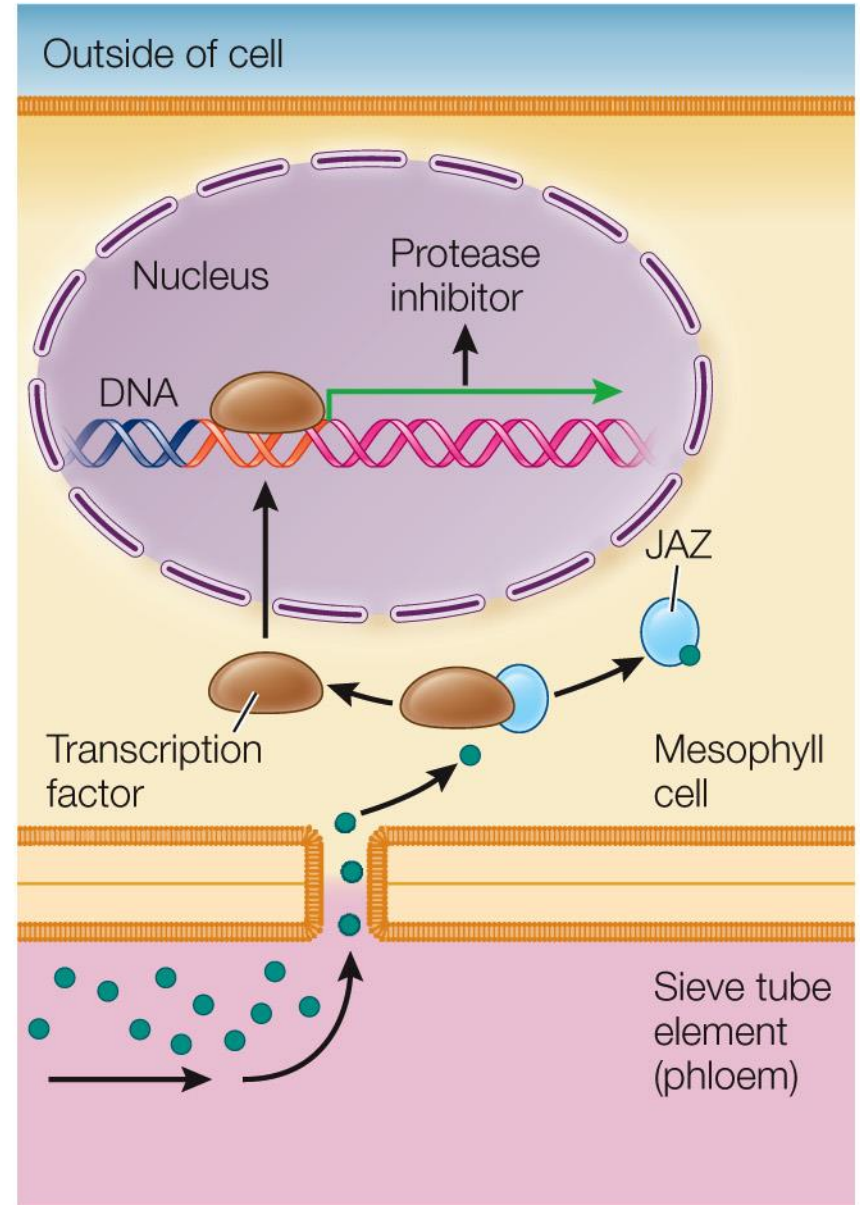
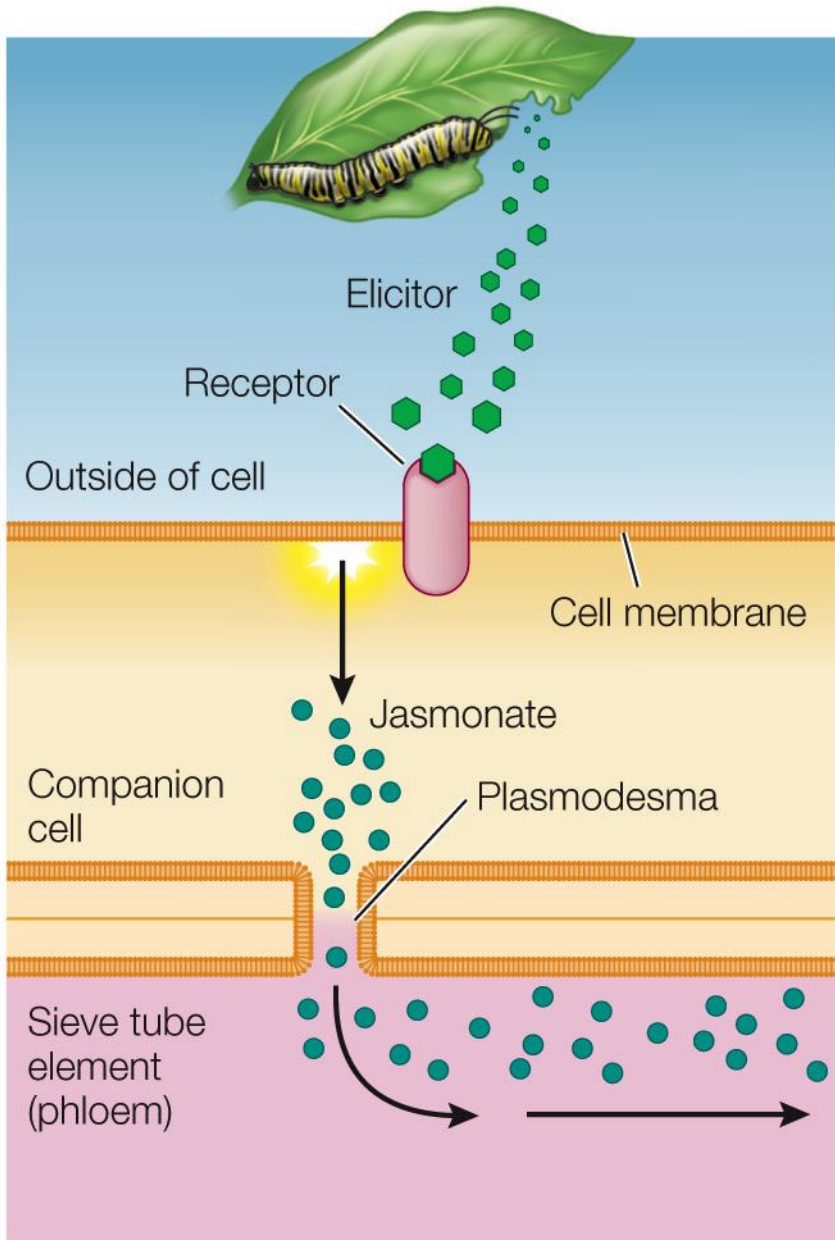
Signal transduction pathways activated by herbivory are similar to those activated by pathogens.

Membrane signaling—when an herbivore strikes, changes in electric potential of the cell membrane occur in the damaged area. Continuity of the symplast ensures that the signal travels over much of the plant within 10 minutes.

Reactive oxygen species: Wounding and herbivory induce the production of oxygen species that lead to changes in gene expression.

Hormone signaling: Herbivory induces the production of hormones that stimulate plant responses.

A Signal Transduction Pathway for Induced



Jasmonic acid (jasmonate), a hormone that triggers systemic defenses.



When the plant senses an herbivore-produced elicitor, it makes jasmonate, which triggers a variety of defenses:

- Production of secondary metabolites and defensive proteins.

- Changes in gene expression by binding a transcription inhibitor called a JAZ protein; binding by jasmonate targets JAZ for degradation.

- Synthesis of a protease inhibitor that interferes with protein digestion in the insect and stunts the insect's growth.

- Jasmonates also “call for help” by triggering formation of volatile compounds that attract insects to prey on the herbivores.

Plants are not harmed by the toxic defense chemicals they make.

- Many defense chemicals target organs not found in plants.

- Toxins can be sequestered in a vacuole or stored as harmless precursors until needed.

Herbivores can circumvent plant defenses.

Milkweeds store toxic chemicals in latex, in tubes called **laticifers**. When damaged by an herbivore, latex is released, keeping some insects from eating the leaves.

But one beetle first cuts some leaf veins and causes latex flow, then moves to an “upstream” part of the leaf to feed.

Environmental Stresses on Plants

table 38.2 Environmental Stresses on Plants

Condition	Effect on plants
Drought	Reduced water potential, dehydration
Flooding	Reduced O ₂ and respiration
High temperature	Changes in membrane fluidity and in proteins
Low temperature	Changes in membrane fluidity, damage by ice crystals
Salinity	Reduced water potential, dehydration
Metal element toxicity	Disruption of metabolism

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Drought avoiders

Some desert annuals have no special adaptations for dry conditions, but complete their whole life cycle during brief periods of rainfall.

Deciduous plants, particularly in Africa and South America, shed their leaves during drought to conserve water.

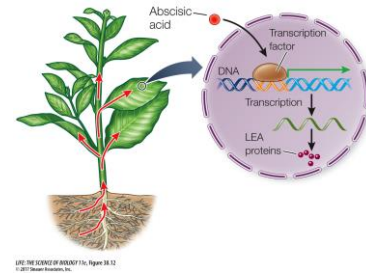
Xerophytes (旱生植物) are adapted to dry environments. The leaves have many adaptations.

Specialized anatomy to reduce water loss

Thick cuticles and hairs on the epidermis retard water loss

Trichomes reflect sunlight, decreasing risk of damage by excess light

- The stomata may be in sunken pits called **stomatal crypts** to shelter them from air currents.
- Cacti have spines rather than typical leaves; photosynthesis occurs in the fleshy stems. Spines may reflect sunlight or dissipate heat, and repel herbivores.
- **Succulence (多肉植物)**: Thick, water-storing stems or leaves. Succulent plants can take up a lot of water when it is available. They have fewer stomata and use CAM photosynthesis, which both reduce water loss.



Roots may also have adaptations.

Cacti have shallow, fibrous root systems that intercept water near the surface, even after light rains.

Mesquite trees have long taproots, reaching water far underground. They also use water from condensation on their leaves.

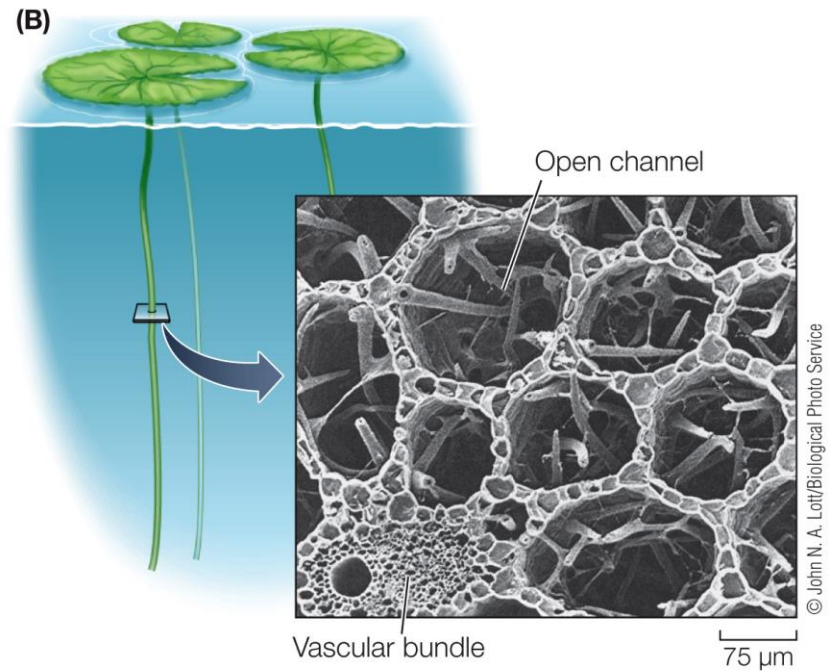
Some xerophytes accumulate proline or secondary metabolites in central vacuoles.

This lowers water potential in the plant cells below the water potential in the soil, resulting in water uptake by osmosis. Plants in salty environments also do this.



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(A)



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Some plants live in environments with too much water in the soil, which limits diffusion of oxygen to roots.

Many aquatic plants have **aerenchyma** tissue with large air spaces.

Temperature extremes can also stress plants.

High temperatures can denature proteins and destabilize membranes.

Low temperatures cause membranes to lose fluidity and alter permeability.

Freezing can cause ice crystals to form, damaging membranes.

Plants have both constitutive adaptations and inducible responses to cope with temperature extremes. Plants can respond to high temperatures by producing **heat shock proteins**. Some are chaperonins, which help prevent other proteins from denaturing. Similar proteins are also produced to protect against chilling injury.

Low temperatures (above freezing) can cause chilling injury. Many plants can be acclimated or **cold-hardened** by repeated exposure to cool temperatures. The proportion of unsaturated fatty acids in cell membranes increases, allowing cell membranes to retain fluidity and function normally.

Ice crystals inside cells can puncture organelles and membranes. Ice crystal growth outside the cells draws water from the cells and can dehydrate them. Freeze-tolerant plants have many adaptations to cope, including production of antifreeze proteins that slow formation of ice crystals.



Saline (salty) habitats support few plant species. These habitats include deserts, coastal marshes, estuaries, and oceans.

Salinization of agricultural land is an increasing global problem.

In irrigated fields, sodium ions from the water accumulate in the soil as the water evaporates.

Saline environments pose osmotic problems for plants because of the negative water potential of the environment.

Plants must have an even more negative water potential to obtain water from that environment.

Sodium can also be toxic.

Halophytes (盐生植物) are plants adapted to saline conditions.

Most accumulate sodium and chloride ions in leaf cell vacuoles. The increased salt concentration makes the water potential of cells more negative.

Some halophytes have **salt glands** in the leaves that excrete salt (some desert plants and mangroves).

One desert shrub secretes salt into small bladders on the leaves. This increases the water potential gradient, helping leaves get more water from roots. It also reduces transpirational loss of water.



High concentrations of heavy metal ions, such as chromium, mercury, lead, and cadmium, are toxic to most plants.

Heavy metals may occur naturally, or result from acid rain that releases Al ions or mining of metal ores.

Some plants can survive in mine tailings.

Tolerant plants take up the heavy metals in concentrations that would kill other plants.

Over 200 plant species have been identified as **hyperaccumulators**—plants that store large quantities of metals such as arsenic, cadmium, nickel, aluminum, and zinc.

Hyperaccumulators have several mechanisms:

- Increased ion transport into the roots
- Increased rates of translocation of ions to the leaves
- Accumulation of ions in vacuoles in the shoot
- Resistance to the ions' toxicity



Phytoremediation (植物治理法) is a form of bioremediation that uses plants to clean up environmental pollution.

Both natural and transgenic hyperaccumulators are used. They are grown in contaminated soils, then harvested and disposed of.

Phytoremediation was used after the Chernobyl, Ukraine nuclear power plant accident in 1986.

Sunflower plants were used to remove uranium from the soil.

Phytoremediation is now being used in Japan after the Fukushima Daiichi reactor accident in 2011.

Summary of plant section

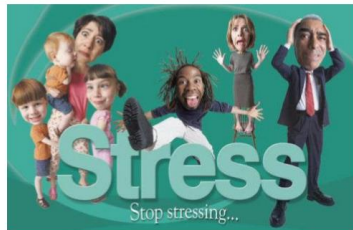
What is plant?

What are differences between plant and animal?

How important is plant?

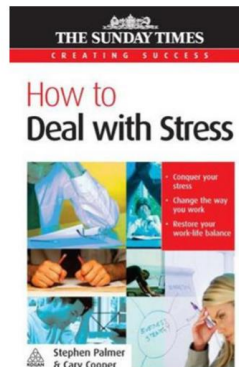
- The Plant Body Is Organized in a Distinctive Way. Meristems Build a Continuously Growing Plant.
- Water and Minerals Are Transported in the Xylem. Solutes Are Transported in the Phloem
- Plants Acquire Nutrients from the Soil. Soil Structure Affects Plant Nutrition
- Plants Develop in Response to the Environment.
- Hormones and other Signaling Determine the Transition from the Vegetative to the Reproductive State
- Plants Can Adapt to Environmental Stresses, Including Abiotic and Biotic Stress.

How to Deal with Stress



- ◆ Crying
- ◆ Running/Boxing
- ◆ Tourism(旅游)
- ◆ Shopping
- ◆ Engorge(暴食)
- ◆?

New stress??



Plant Stress

