CHAPTER 3

Plant Response to Stimuli

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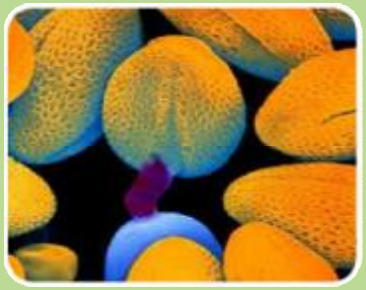
Plant Hormones

Tropism

Respond to Seasonal Changes

Plant Hormones

Tropism



Respond to Seasonal Changes

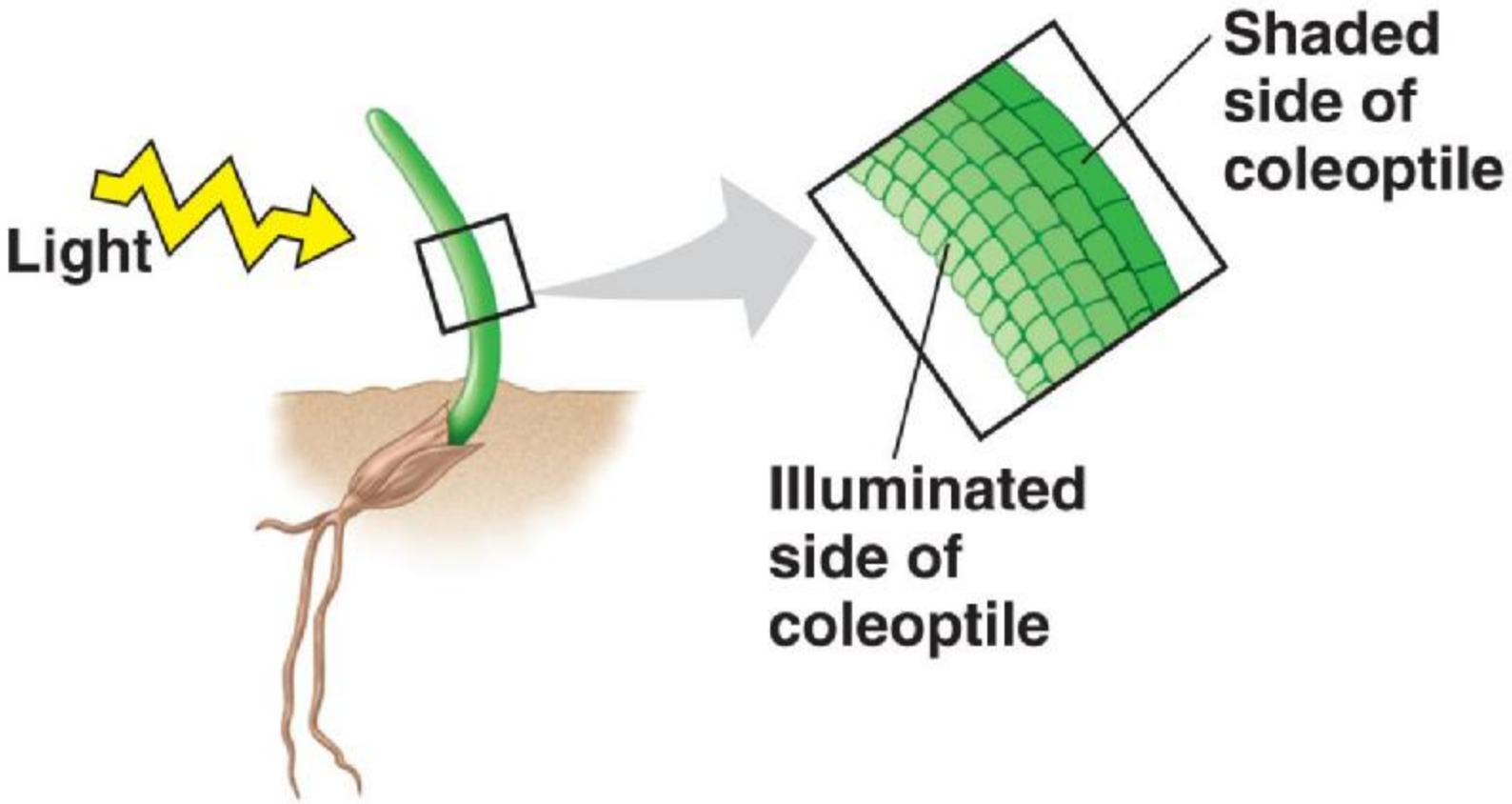
How Hormone Influence Plant Growth

- Plant responses are usually much more subtle (to us) than those of many animals—plants cannot run away from unfavorable conditions.
- Instead, plants adjust to the environment. Their responses are partly mediated by chemicals called **hormones**.
- Plants biologists have identified five major types of hormones: auxins, gibberellins, cytokinins, ethylene, and abscisic acid.

Auxin

- Auxins, from the Greek “to increase,” were the first plant hormones that scientists described.
- Charles Darwin and his son Francis learned that a plant-produced “influence” caused plants to grow toward light
- Auxins stimulate(kích thích) cells to elongate by altering the plasticity(tính dẻo) of cell walls, so the walls stretch.

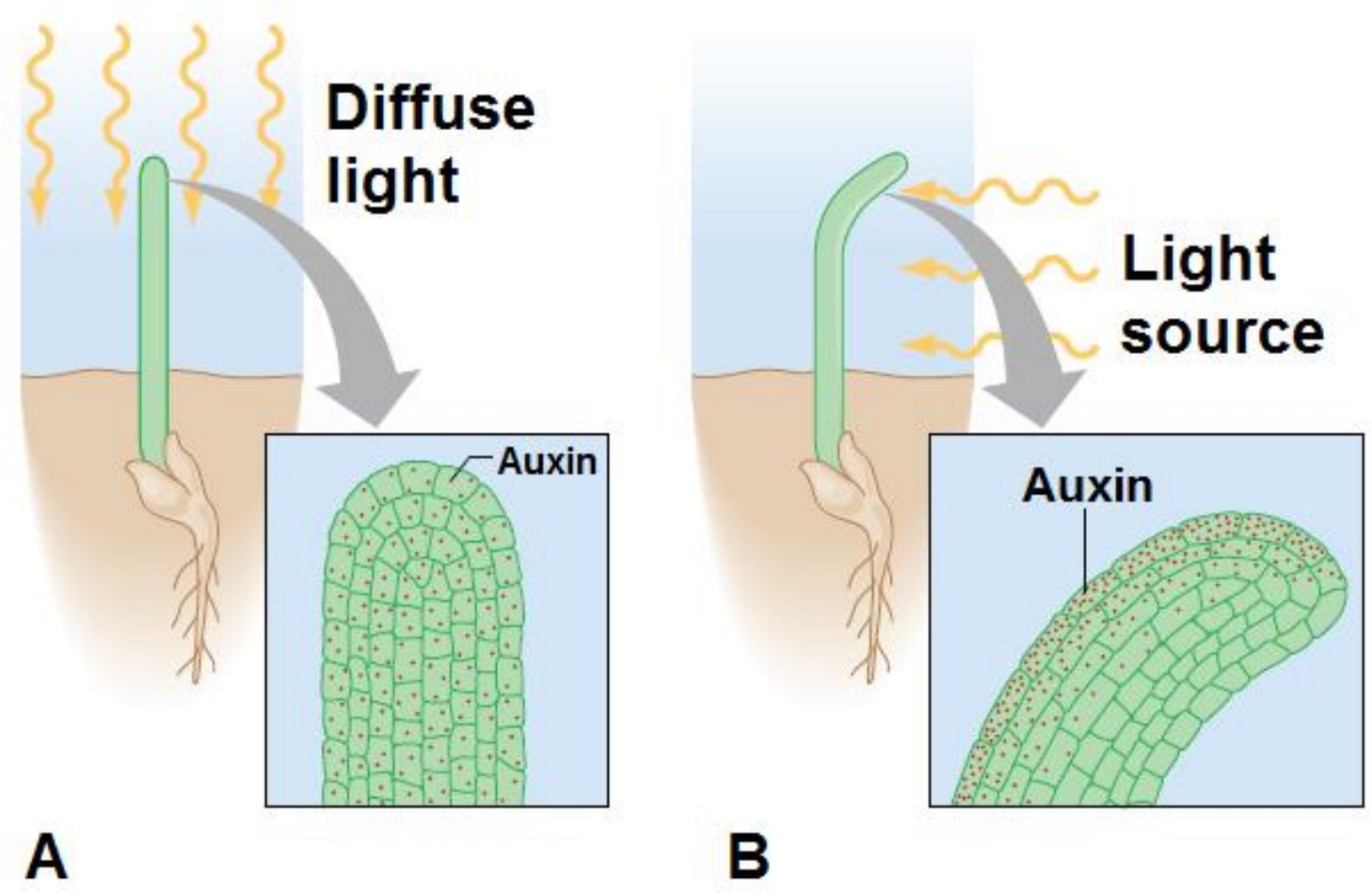
Plants Bend Toward Light



Auxin

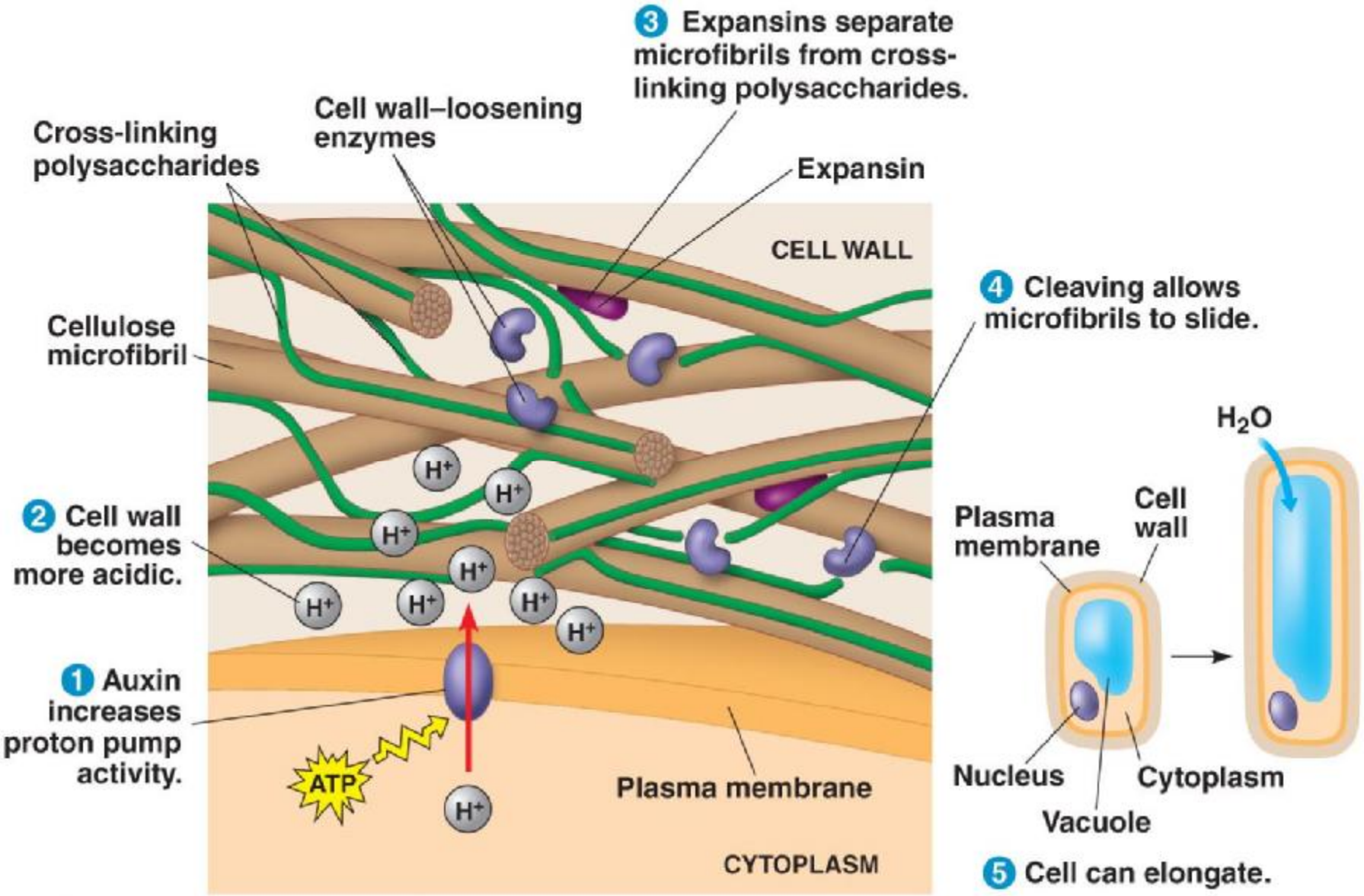
- Specifically, the hormone causes proteins in the cell membrane to pump protons (H^+) into the cell wall.
- Here, the protons activate enzymes that separate the cellulose microfibrils(sợi tới vi), enabling the wall to expand(mở rộng) and elongate against turgor (sức trương) pressure.
- More microfibrils form, stabilizing the new, longer cell shape.
- When this happens to several cells on one side of a stem, the plant bends(uốn cong).

Auxins Promote Cell Lengthening



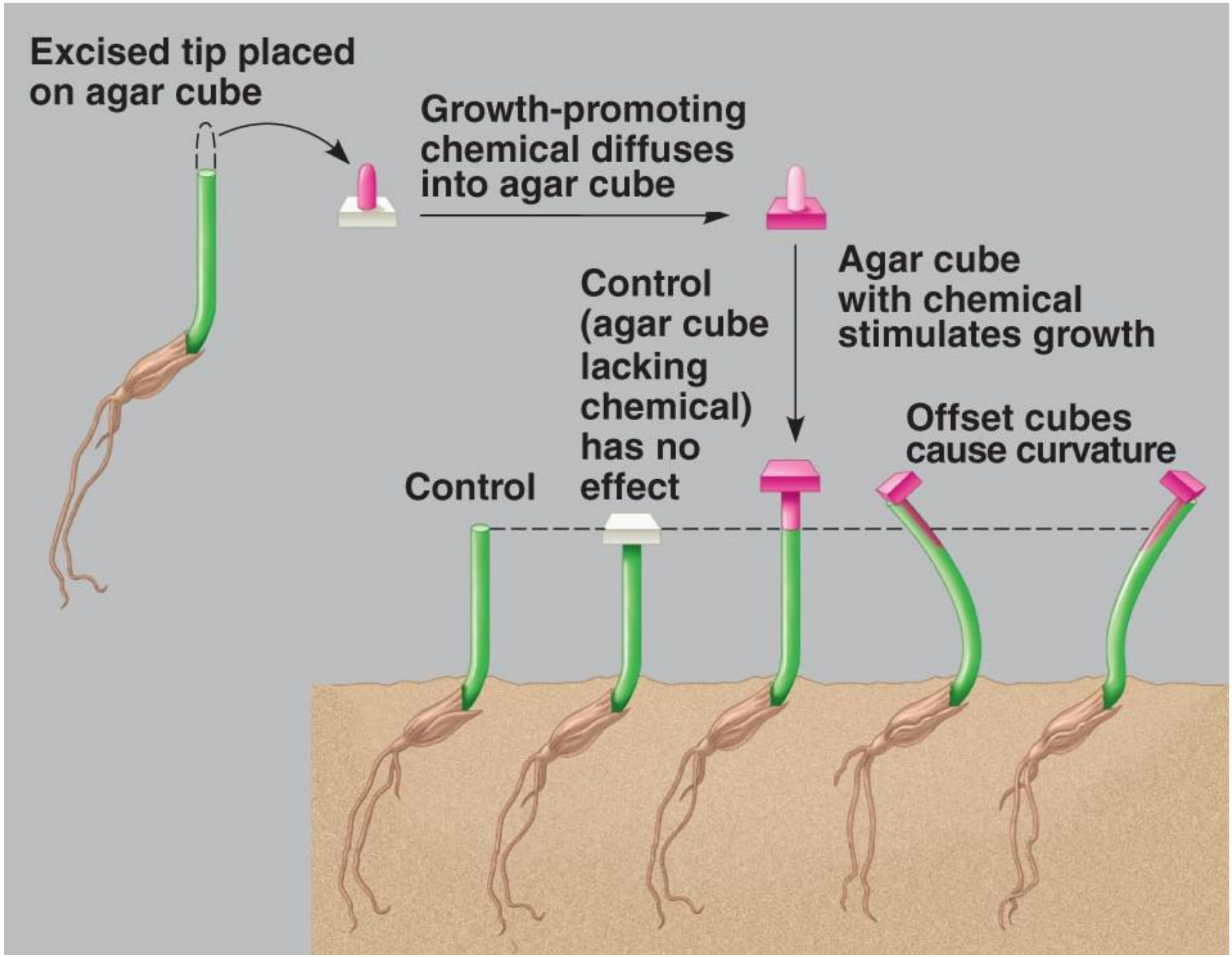
In diffuse light (A), seedlings grow straight upwards, but in directional light (B), the stem tips bend toward the light.

Auxins Promote Cell Lengthening

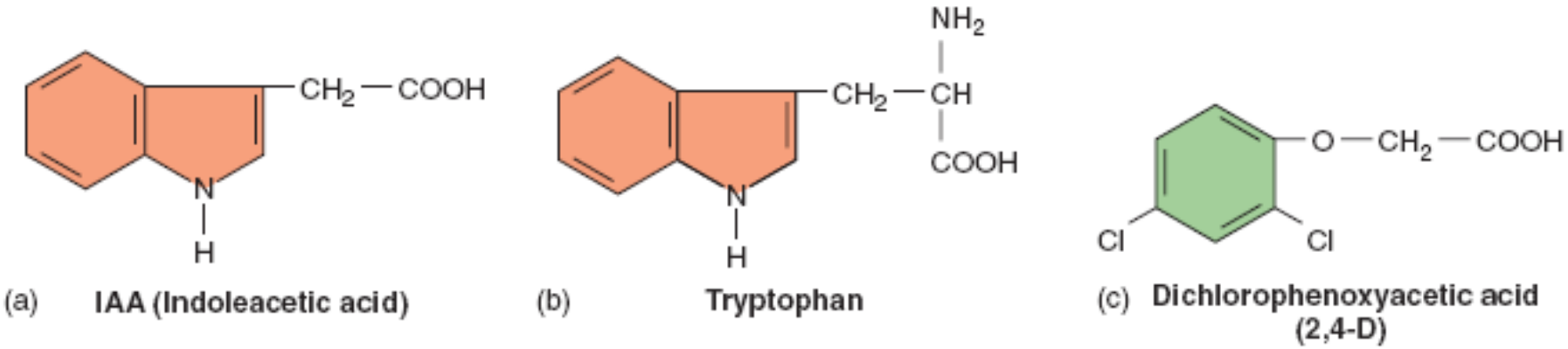


Went's experiment

- ***Experiment:***
  - Removed coleoptile tips and placed their cut surfaces on a block of gelatin.
  - Placed pieces of that gelatin on decapitated(bị cắt ngọn) coleoptiles(lá bao mầm)—positioned to cover only one side.
- ***Results:***
  - The coleoptiles curved toward the side away from the gelatin.
- ***Conclusion***: hormone had diffused into the gelatin block from the isolated coleoptile tips.


Excised tip placed on agar cube
Growth-promoting chemical diffuses into agar cube
Agar cube with chemical stimulates growth
Control (agar cube lacking chemical) has no effect
Control
Offset cubes cause curvature

- Went had at last isolated a hormone from a plant. Later chemical analysis showed that this hormone, named auxin, was indoleacetic acid.



(*a*) Indoleacetic acid (IAA), the principal naturally occurring auxin.
(*b*) Tryptophan, the amino acid from which plants probably synthesize IAA.
(*c*) Dichlorophenoxyacetic acid (2,4-D), a synthetic auxin, is a widely used herbicide

Synthetic Auxins

- NAA (naphthalene acetic acid), IBA (indolebutyric acid), and Dichlorophenoxyacetic acid (2,4-D) have many uses in agriculture.
  - to prevent fruit drop in apples before they are ripe.
  - to hold berries(quả mọng) on holly(cây nhựa rùi) that is being prepared for shipping.
  - to promote flowering and fruiting in pineapples(quả dứa)
  - to induce(tạo ra) the formation of roots in cuttings.
  - To control weeds(cỏ dại)

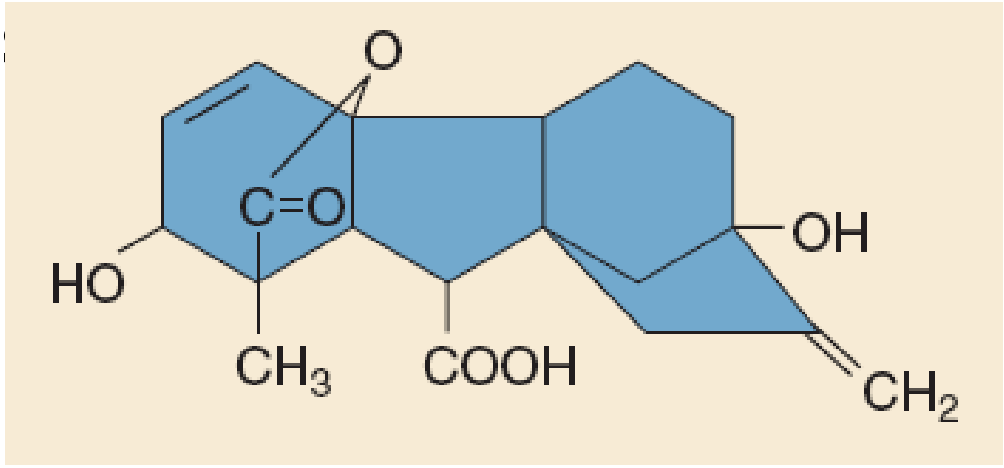
- **Red mangrove (*Rhizophora mangle)* seeds produce only low level of ABA, and their seed germinate while still on the tree.**
  In this case, early germination is a useful adaptation. When released, the radicle of the dark-like seedling deeply penetrates the soft mudflats in which the mangrove grow.

Gibberellins

- In 1926, Japanese botanists studying “foolish seedling disease” in rice discovered another plant hormone that causes shoot elongation
- Plants suffering from foolish seedling disease are infected by a fungus (*Gibberella fujikuroi*) that causes them to grow rapidly, becoming so spindly that they fall over and die.

Gibberellins

- The botanists(nhà thực vật học) discovered that a chemical extract of the fungus also produced the disease symptoms(tiệu chứng).
- In 1934, scientists isolated the active compound and named it **gibberellin**.
- We now know of at least 84 naturally occurring gibberellin



Gibberellins

- Gibberellins are present in all plant parts, in varying amounts.

Gibberellins

- They have several functions:
  - Stimulating shoot elongation in trees, shrubs(cây bụi), and a few other plants.
  - Promoting both cell division and elongation
  - Stimulating seed germination by inducing enzymes that mobilize(huy động) starch(tinh bột) reserves(dự trữ) in the seed.

Gibberellins

- In agriculture they are used to
  - Stimulate stem elongation
  - Increase the size of the fruit growth in seedless grapes(quả nho).

without gibberellin

with gibberellin

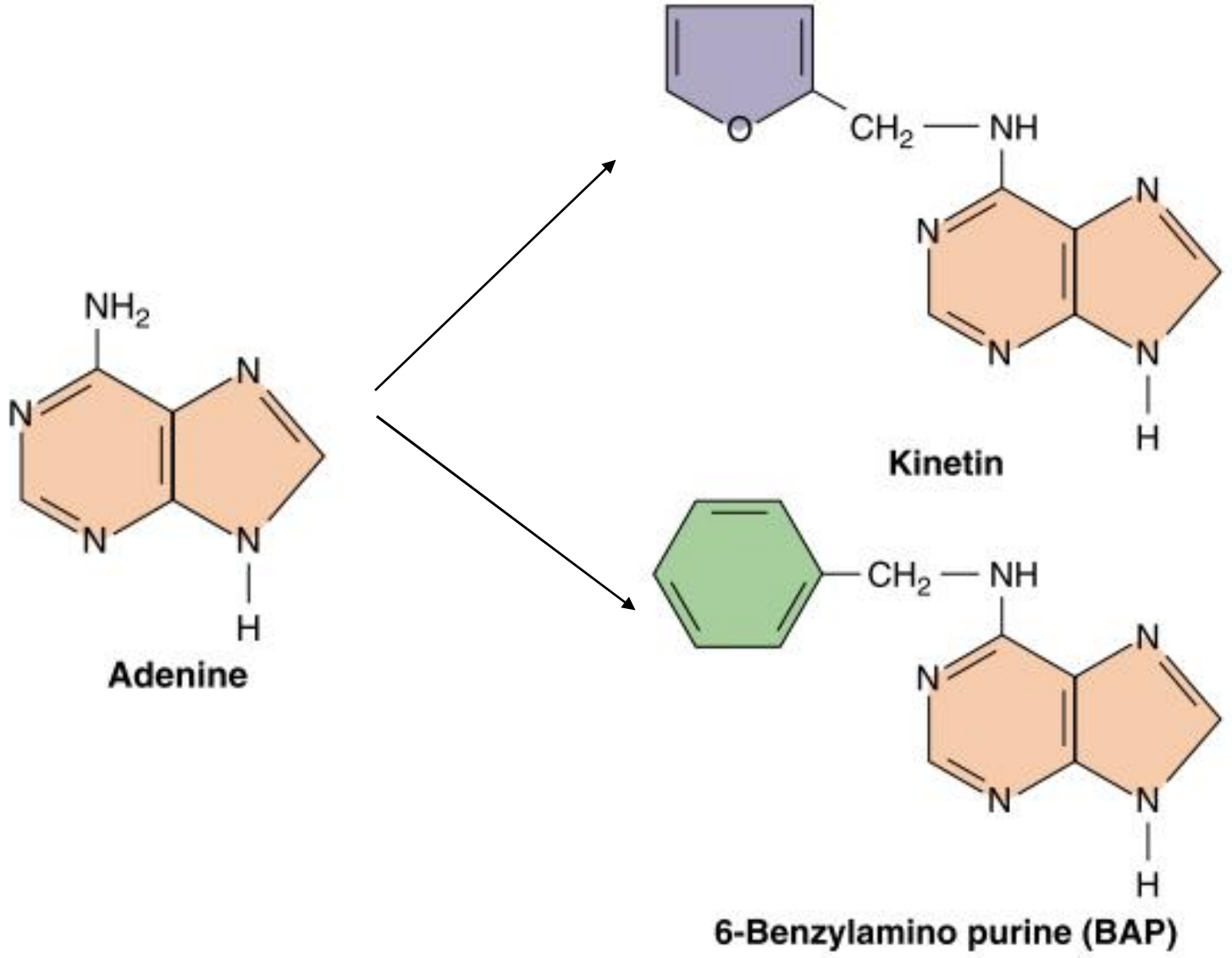
Cytokinin

- A cytokinin is a plant hormone that, in combination(kết hợp) with auxin, stimulates cell division and differentiation in plants.
- Most cytokinins are produced in the root apical meristems and transported throughout the plant.
- Developing fruits are also important sites of cytokinin synthesis.

Cytokinin

- All naturally occurring cytokinins are purines that appear to be derivatives(bắt nguồn) of adenine.

Two commonly used synthetic cytokinins



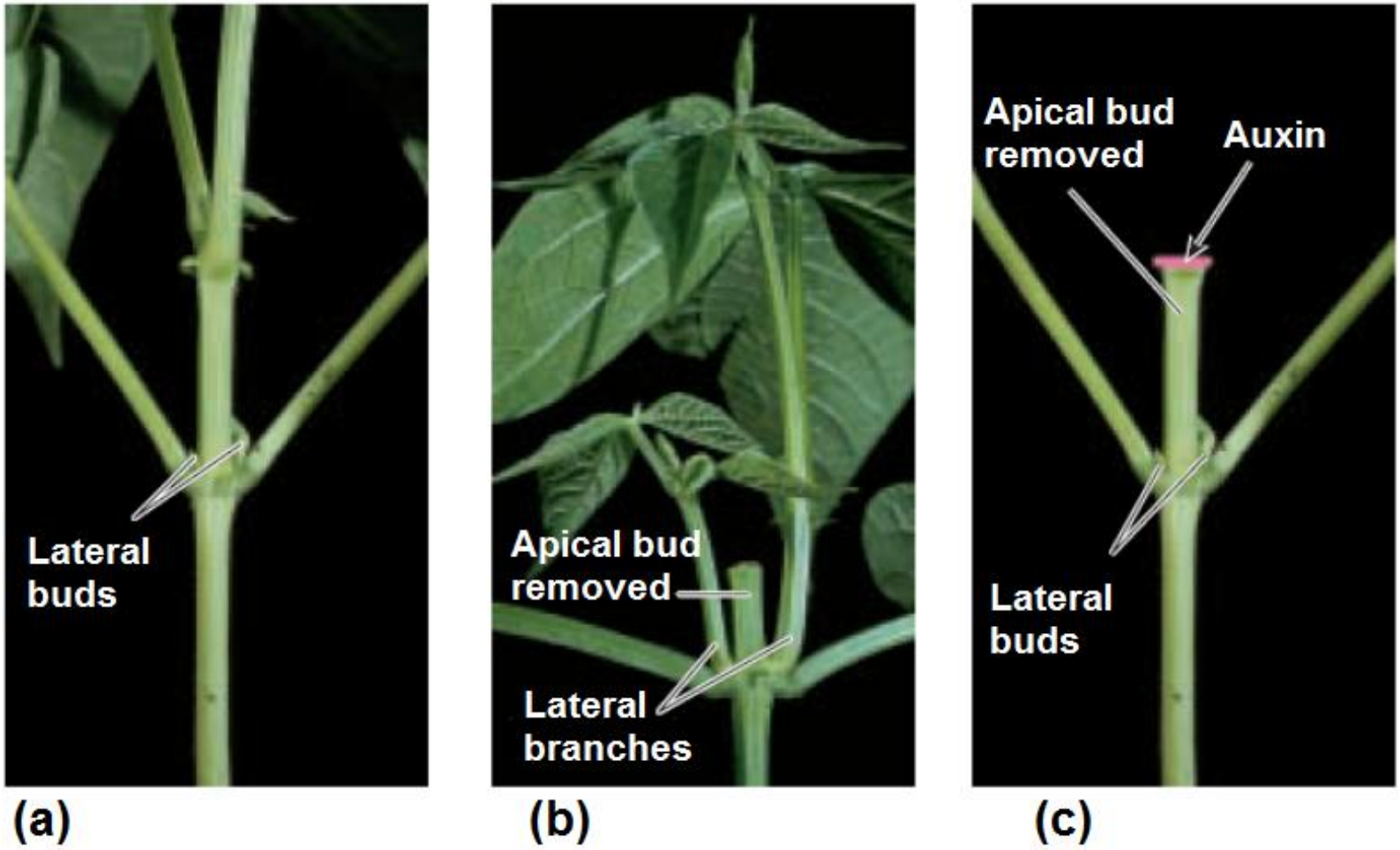
Cytokinin

- In mosses, cytokinins cause the formation of vegetative buds on the gametophyte(thể giao tử).
- In all plants, cytokinins, working with other hormones, seem to regulate growth patterns.

Cytokinin

- Cytokinins promote growth of lateral buds into branches
- However, along with auxin and ethylene, they play a role in apical dominance(ưu thế) (the suppression of lateral bud growth).

Cytokinins stimulate lateral bud growth



(a) When the apical meristem of a plant is intact, auxin from the apical bud will inhibit the growth of lateral buds. (b) When the apical bud is removed, cytokinins are able to produce the growth of lateral buds into branches. (c) When the apical bud is removed and auxin is added to the cut surface, axillary bud outgrowth is suppressed.

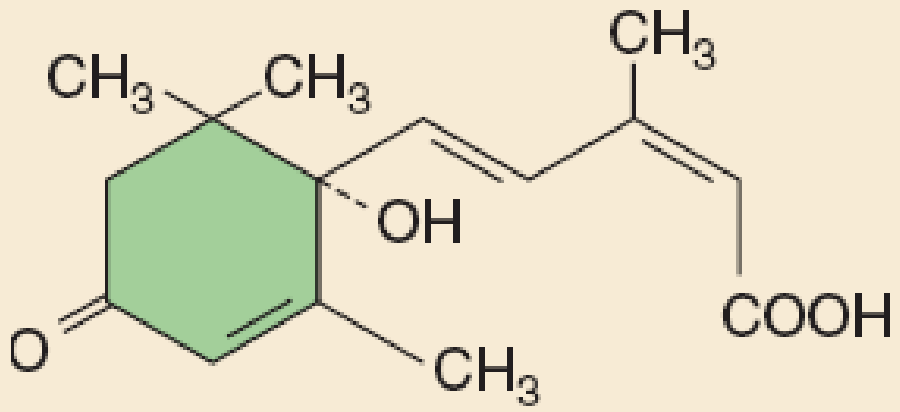
- Sometimes cytokinins can be used against the plant by a pathogen(mầm bệnh).
- In this case *Agrobacterium tumefaciens* (a bacteria) has incorporated(sát nhập) a piece of its DNA into the plant genome.
- This DNA contains genes coding for enzymes necessary for cytokinin and auxin biosynthesis.
- The increased levels of these hormones in the plant cause massive cell division and the formation of a tumor.(khối u)

Crown gall tumor

Abscisic acid

- Abscisic acid, or ABA, inhibits the growth-stimulating effects of many other hormones.

Abscisic acid



Abscisic acid

- ABA:
  - inhibits seed germination (countering the effects of gibberellins)
  - promotes leaf, flower, and fruit abscission(cắt bỏ) (shedding).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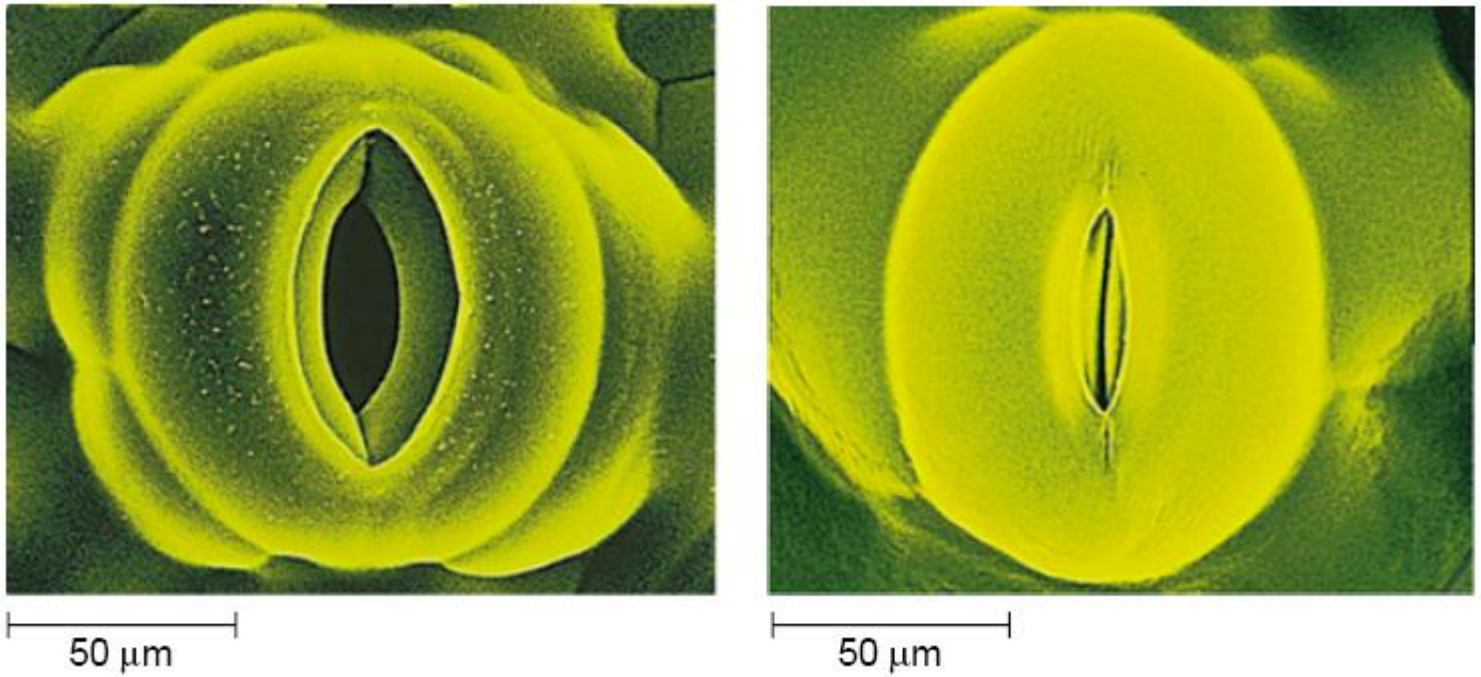
Abscisic acid

- ABA:
  - closes stomata by influencing the movement of potassium ions out of guard cells, which helps plants conserve water during drought.



Abscisic acid

- ABA:
  - is produced in higher amounts in response to stresses such as drought or frost, and it promotes protective responses.

Abscisic acid plays a role in the formation of these winter buds of an American basswood. These buds will remain dormant for the winter, and bud scales will protect the buds from desiccation. (sự làm khô)

Ethylen

- In 1910, scientists in Japan observed that bananas ripened(chính) prematurely(sớm) when stored with oranges.
- By 1934, scientists realized ethylene gas was hastening ripening.
- All parts of flowering plants synthesize ethylene, particularly the shoot apical meristem, nodes, flowers, and ripening fruits.

Ethylen

- In most species, ethylene gas causes flowers to fade(khô) and wither(héo).

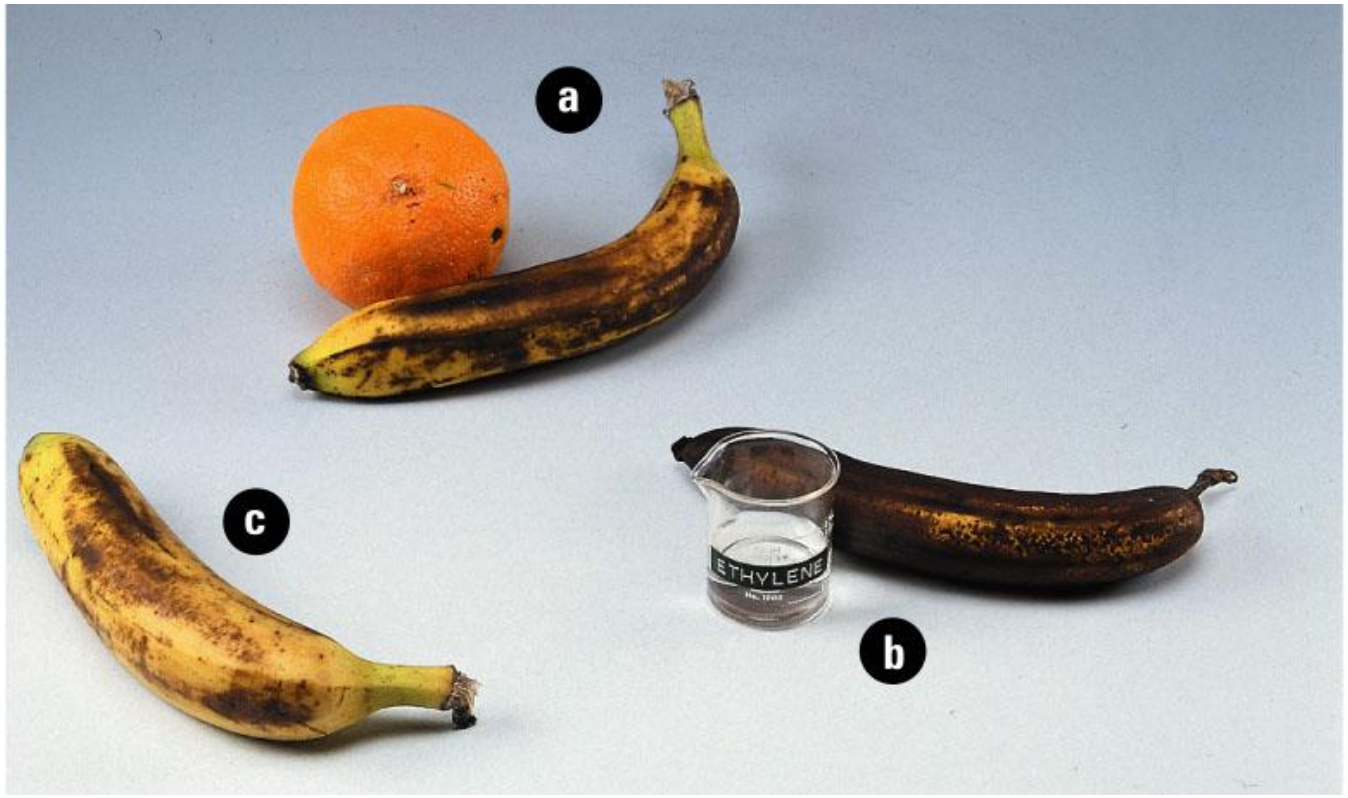
Ethylen

- Ethylene is a hormone that triggers a variety of aging responses in plants, including fruit ripening and dropping of leaves

Fruit ripening

- Fruit ripening is triggered by a burst of ethylene production in the fruit
- Ethylene is a gas causing the signal to ripen to spread(mǎm) from fruit to fruit

- Some fruits ripen faster if they are stored in a plastic bag so that ethylene accumulates(đồng chức)



Leaf drop

- The loss of leaves in autumn is affected by ethylene
- Leaf drop
  - Is triggered(gây ra) by environmental stimuli(sự kích thích), which cause a change in the balance of ethylene and auxin

Ethylen

- Ethylene also helps ensure(bảo đảm) that a plant will survive injury or infection(nhiễm độc).
  - When a damaged plant produces the hormone, it hastens(đẩy nhah) aging of the affected part so that it can be shed before the problem spreads(trải) to other regions of the plant.

Major classes of Plant Hormones

Auxins	
Selected Actions	Elongate cells in seedlings, shoot tips, leaves, embryos(phôi) Adventitious root growth of cuttings Inhibit leaf and fruit abscission Stimulate synthesis of ethylene Inhibit growth of lateral buds
Synthesis Site	Developing leaves and seeds, shoot tips
Route of Transport	Cell to cell, usually downward

Major classes of Plant Hormones

Gibberellin	
Selected Actions	Elongate and divide cells in seeds, roots, shoots, young leaves Seed germination Stimulate flowering
Synthesis Site	Young shoot, developing seeds
Route of Transport	Xylem and phloem.

Major classes of Plant Hormones

Cytokinins	
Selected Actions	Stimulate cell division in seeds, roots, young leaves, fruits Delay leaf senescence(sự già) Allow lateral buds to grow
Synthesis Site	Root tips
Route of Transport	Xylem (roots to shoots)

Major classes of Plant Hormones

Ethylene	
Selected Actions	Hastens fruit ripening Leaf and flower senescence Leaf and fruit abscission
Synthesis Site	All parts, especially under stress, aging, or ripening.
Route of Transport	Diffusion

Major classes of Plant Hormones

Abscisic acid	
Selected Actions	Inhibits shoot growth Closes stomata Induces and maintains seed dormancy Stores proteins in seeds
Synthesis Site	Mature leaves, plants under stress
Route of Transport	Xylem and phloem

Plant Hormones

Tropism

Respond to Seasonal Changes

Tropisms(tính hướng kích thích)

- Growth patterns in plants are often guided by environmental signals.
- Tropisms (from trope, the Greek word for “turn”) are positive or negative growth responses(sự phản ứng) of plants to external stimuli that usually come from one direction.

Tropisms

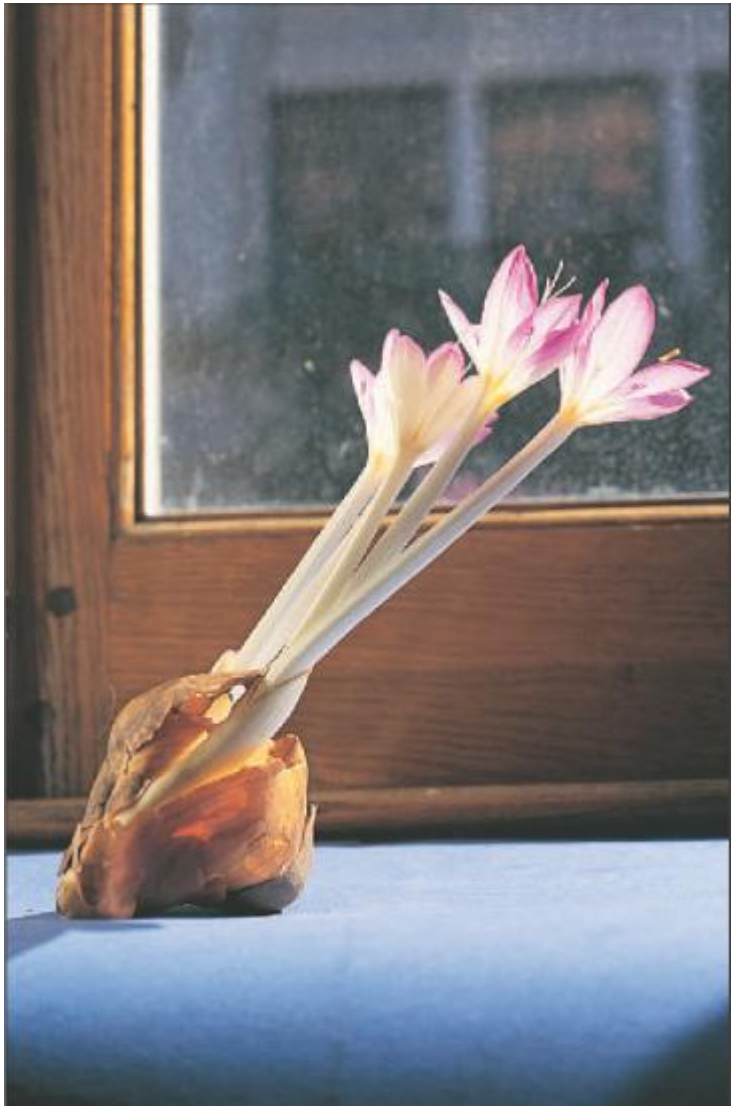
- There are many types of plant tropisms:
  - phototropism (response to uinidirection light)
  - gravitropism (response to gravity)
  - thigmotropism (response to touch)
  - electrotropism (responses to electricity)
  - chemotropism (response to chemicals)
  - thermotropism (response to temperature)
  - aerotropism (response to oxygen)
  - hydrotropism (response to water)
  - geomagnetotropism (response to magnetic fields).

Tropisms

- Here we only consider three best known tropisms: phototropism, gravitropism, and thigmotropism.

Phototropism

- Phototropic responses involve the bending of growing stems and other plant parts toward sources of light.



Phototropism

- In general, stems are positively phototropic, growing toward a light source, while most roots do not respond to light or, in exceptional cases, exhibit only a weak negative phototropic response.

Phototropism

- The phototropic reactions of stems are clearly of adaptive value, giving plants greater exposure(hướng) to available light.
- Individual leaves may display phototropic responses. The position of leaves is important to the photosynthetic efficiency of the plant.

The Darwins' Phototropism Experiment

- The experiment was done in the 1880s by C.Darwin and his son Francis. They asked, What part of the plant senses the light?
- To answer this question, the Darwins worked with canary grass (*Phalaris canariensis*) seedlings grown in the dark. A young grass seedling has a coleoptile(lá bao mầm)

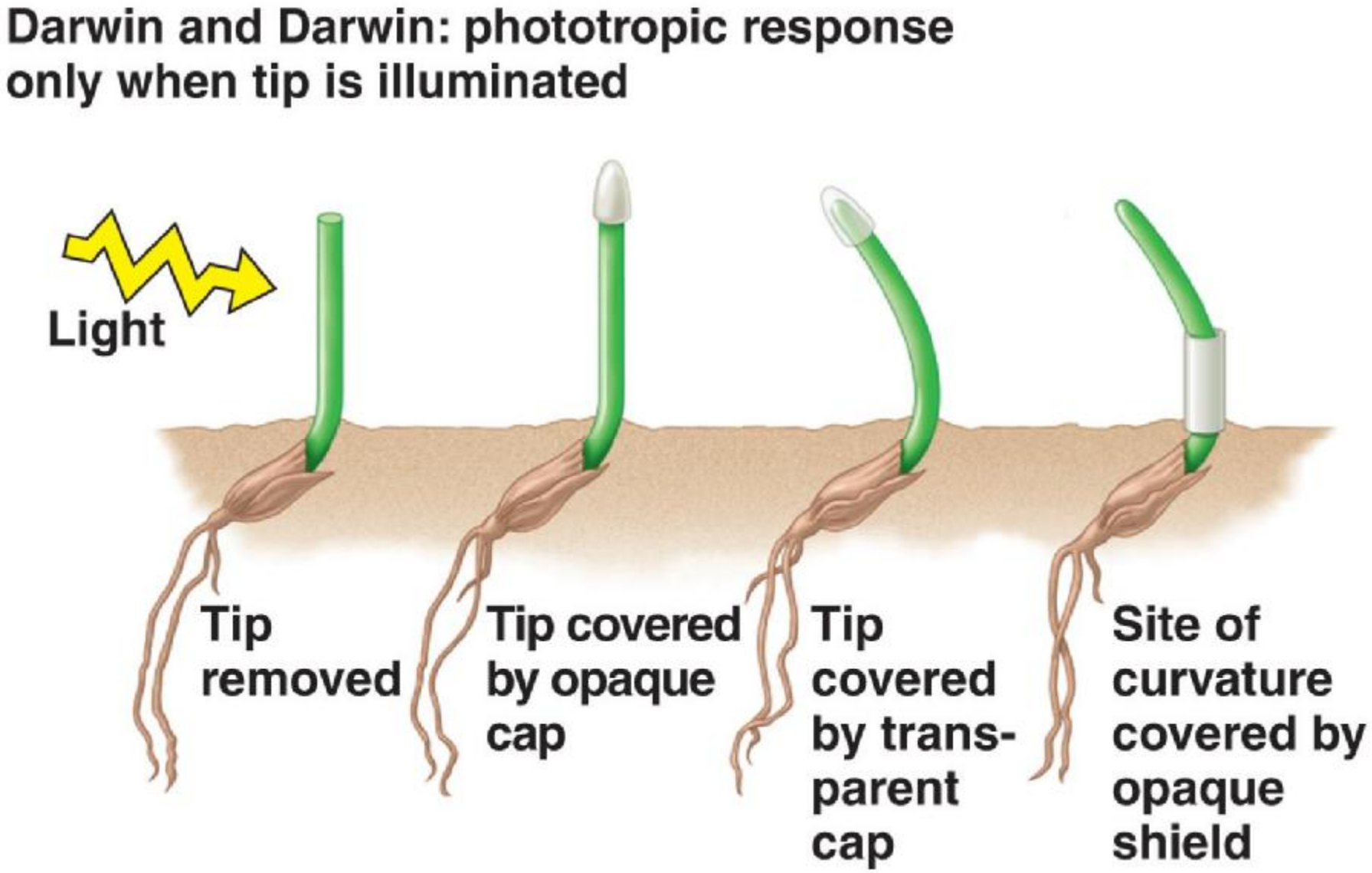
The Darwins' Phototropism Experiment

- To find the light-receptive region of the coleoptile, the Darwins tried "blindfolding" the coleoptiles of dark-grown canary grass seedlings in various places, then illuminating them from one side. The coleoptile grew toward the light whenever its tip was exposed.
- If the top millimeter or more of the coleoptile was covered, however, there was no phototropic response.

The Darwins' Phototropism Experiment

- Thus, the Darwins were able to conclude that the tip contains the photoreceptor that responds to light.
- The actual bending toward the light, however, takes place in a growing region a few millimeters below the tip.
- Therefore, the Darwins reasoned, some type of signal must travel from the tip of the coleoptile to the growing region.

The Darwins' Phototropism Experiment



Gravitropism

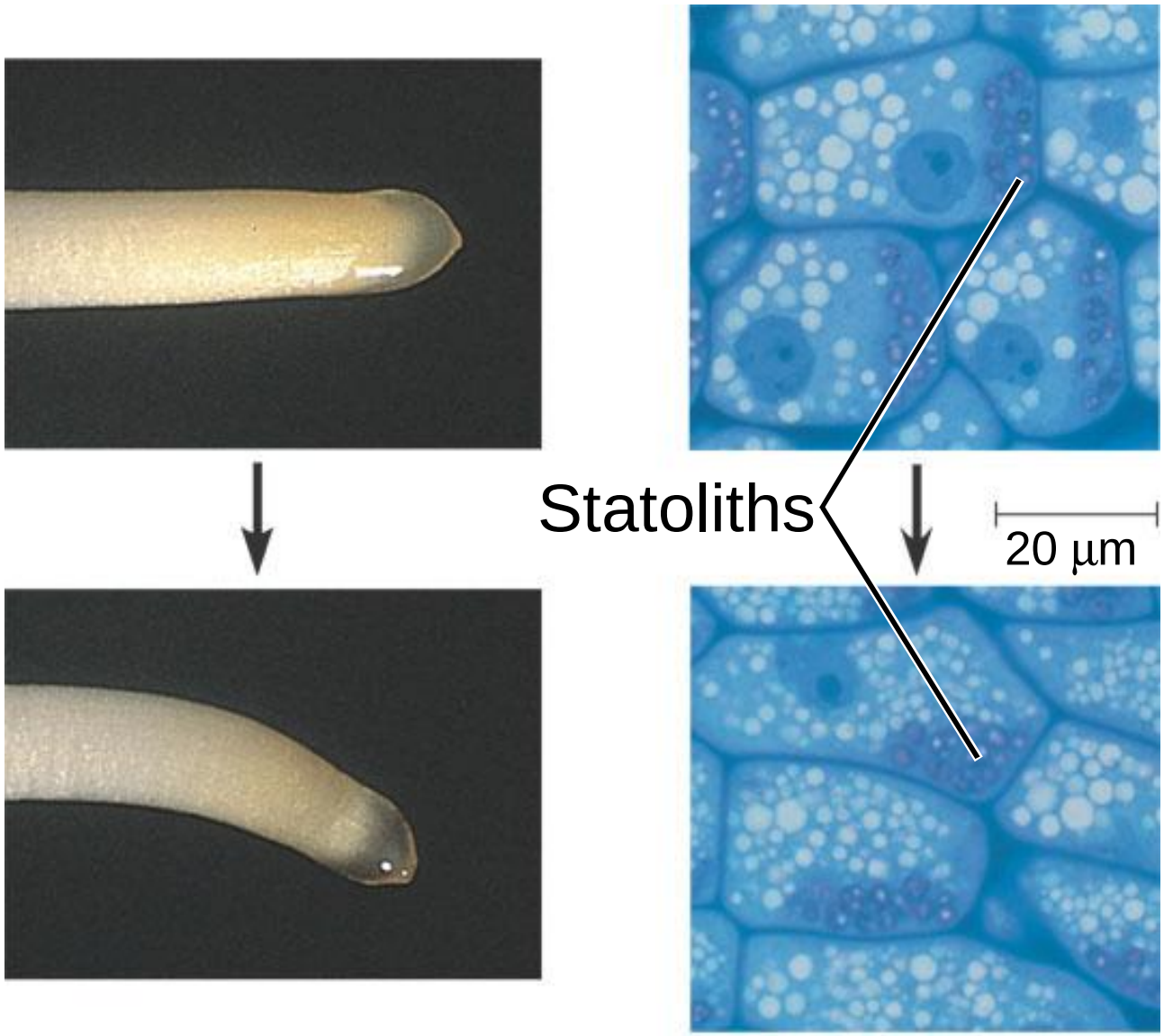
- Even as a seed germinates, its shoot grows upward, toward light, while its root heads downward into the soil.
- The seedling's response to gravity is called gravitropism.

Gravitropism

- In the late 1800s, it was already known that roots would not respond to gravity if their root caps were cut off, suggesting that something in the root cap is necessary for gravitropism.
- Despite more than a century of subsequent research, the role of the root cap in sensing gravity is still not completely understood.

Gravitropism

- One hypothesis for how a plant senses gravity centers on cells in the root that have modified(bị biến đổi) amyloplasts(bột lạp), which are starch-containing plastids that function as statoliths(sỏi thăng bằng), or gravity detectors(máy dò).
- These granules normally sink to the bottoms of the cells, somehow telling the cells which direction is down.


Statoliths
20 μm

Thigmotropism

- A thigmotropism is a response of a plant or plant part to contact with the touch of an object, animal, plant, or even the wind.
- When a tendril makes contact with an object, specialized epidermal cells, whose action is not clearly understood, perceive(thấy) the contact and promote uneven growth, causing the tendril to curl around the object.

Nastic movement

- Plant movements that are not oriented with respect to a stimulus are called **nastic movements**.
- A nastic movement resulting from physical contact or mechanical disturbance is **thigmonasty**.
- When the leaves of Mimosa are touched, the leaflets immediately fold, and the petiole droops.

Nastic movement

- **Nyctinasty**, the nastic response to daily rhythms of light and dark, is also known as “sleep movement”

Noon

Midnight

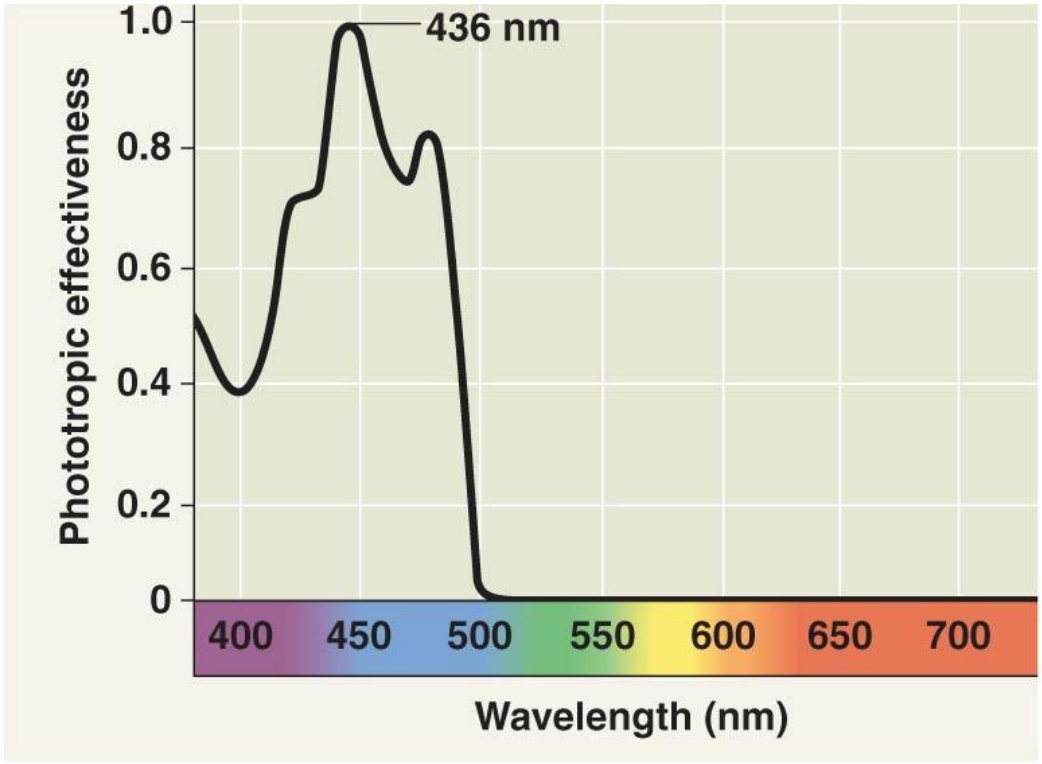
Plant Hormones

Tropism

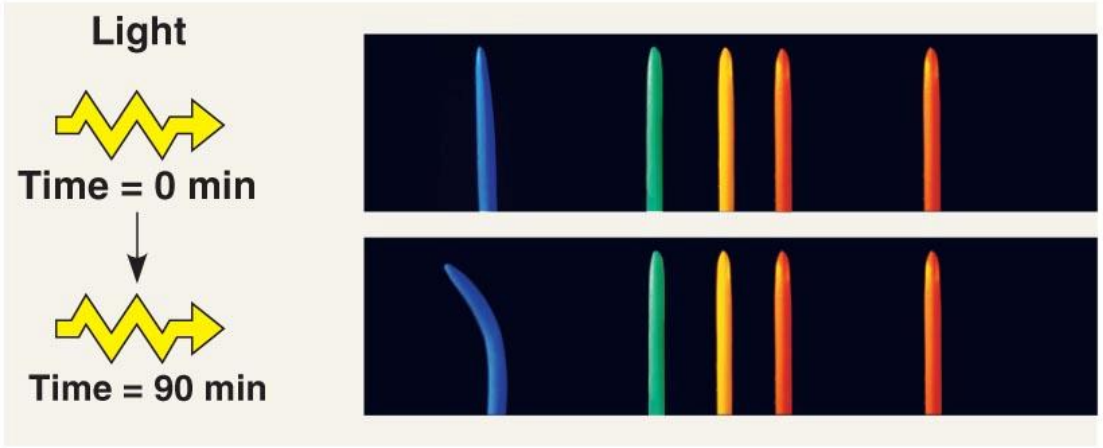
Respond to Seasonal Changes

- Responses to light are critical(tới hạn) for plant success
- Light cues many key events in plant growth and development
- Effects of light on plant morphology
  - Are what plant biologists call photomorphogenesis

- Plants not only detect the presence of light
  - But also its direction, intensity, and wavelength (color)
- A graph called an action spectrum
  - Depicts the relative response of a process to different wavelengths of light



(a) Action spectrum for blue-light phototropism



(b) Coleoptile response to light colors

- Research on action spectra and absorption spectra of pigments
  - Led to the identification of two major classes of light receptors: blue-light photoreceptors and phytochromes

Blue-Light Photoreceptors

- Various blue-light photoreceptors
  - Control hypocotyl elongation, stomatal opening, and phototropism

Phytochromes as Photoreceptors

- Phytochromes
  - Regulate many of a plant's responses to light throughout its life

Phytochromes and Seed Germination

- Studies of seed germination
  - Led to the discovery of phytochromes

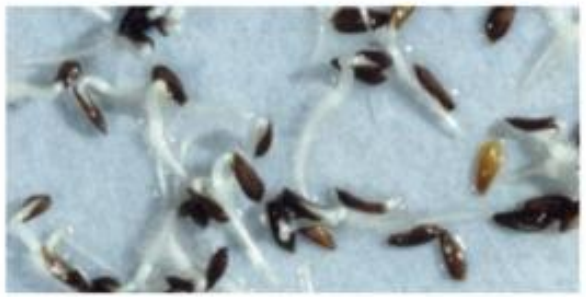
- In the 1930s, scientists at the U.S. Department of Agriculture
  - Determined the action spectrum for light-induced germination of lettuce seeds

- Experiment:
  - After the light exposure, the seeds were placed in the dark, and the results were compared with control seeds that were not exposed to light.
- Results:
  - The germination rate increased greatly in groups of seeds that were last exposed to red light (left). Germination was inhibited in groups of seeds that were last exposed to far-red light (right).

Dark (control)

Red | Dark

Red | Far-red | Dark



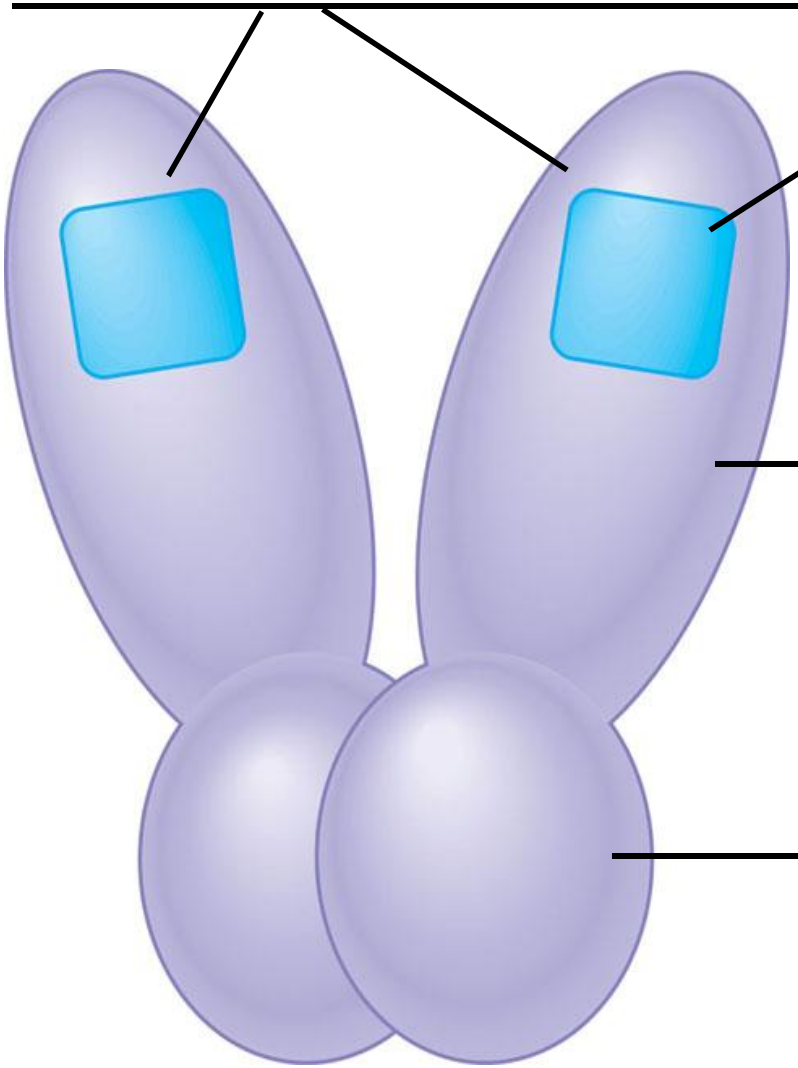
Red | Far-red | Red | Dark

Red | Far-red | Red | Far-red

- Conclution:
  - Red light stimulated germination, and far-red light inhibited germination

- A phytochrome
  - Is the photoreceptor responsible for the opposing effects of red and far-red light

A phytochrome consists of two identical proteins joined to form one functional molecule. Each of these proteins has two domains.

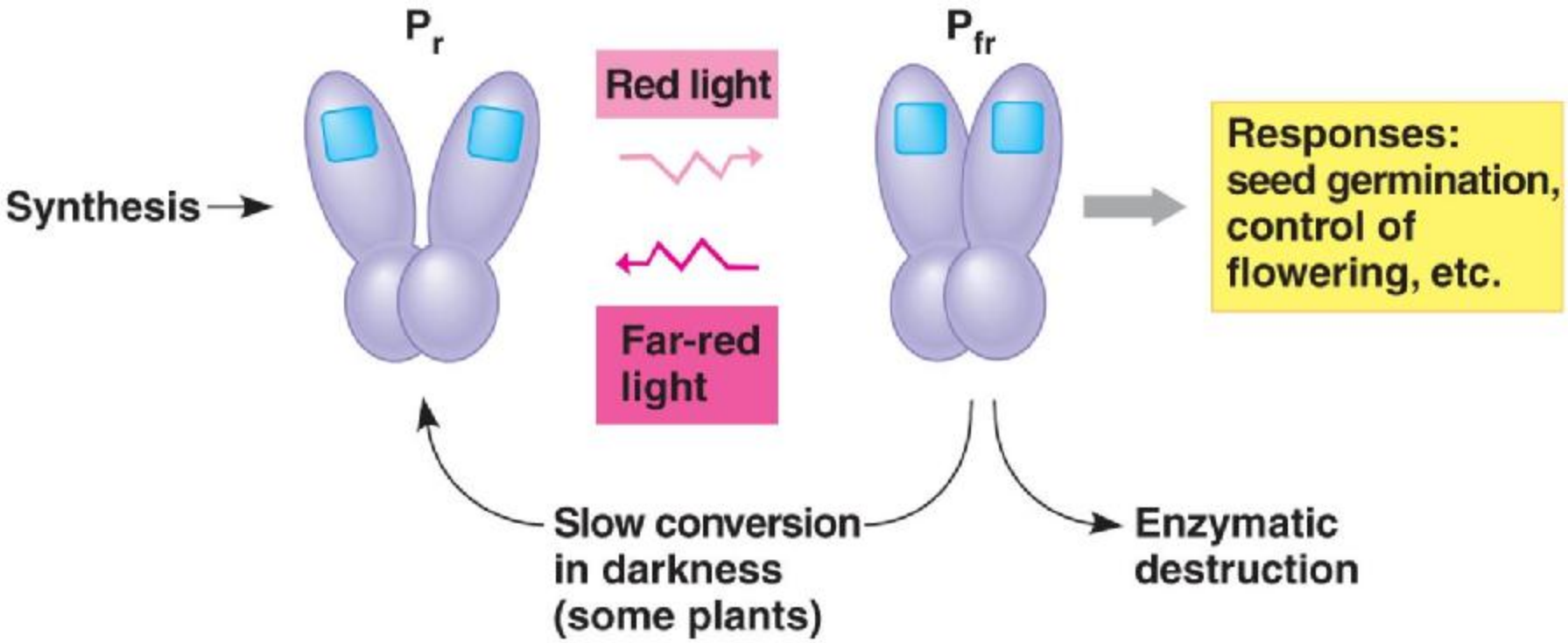


Chromophore

Photoreceptor activity. One domain, which functions as the photoreceptor, is covalently bonded to a nonprotein pigment, or chromophore.

Kinase activity. The other domain has protein kinase activity. The photoreceptor domains interact with the kinase domains to link light reception to cellular responses triggered by the kinase.

- Phytochromes exist in two photoreversible states
  - With conversion of P_r to P_{fr} triggering many developmental responses



Phytochromes and Shade Avoidance

- The phytochrome system
  - Also provides the plant with information about the quality of light
- In the “shade avoidance” response of a tree
  - The phytochrome ratio shifts in favor of P_r when a tree is shaded

Biological Clocks and Circadian Rhythms

- Many plant processes
  - Oscillate(dao động) during the day

- Many legumes
  - Lower their leaves in the evening and raise them in the morning

Noon

Midnight

- Cyclical responses to environmental stimuli are called circadian rhythms
  - And are approximately 24 hours long
  - Can be entrained to exactly 24 hours by the day/night cycle

The Effect of Light on the Biological Clock

- Phytochrome conversion marks sunrise and sunset
  - Providing the biological clock with environmental cues

Photoperiodism and Responses to Seasons

- Photoperiod, the relative lengths of night and day
  - Is the environmental stimulus plants use most often to detect the time of year
- Photoperiodism
  - Is a physiological response to photoperiod

Photoperiodism and Control of Flowering

- Some developmental processes, including flowering in many species
  - Requires a certain photoperiod

Critical Night Length

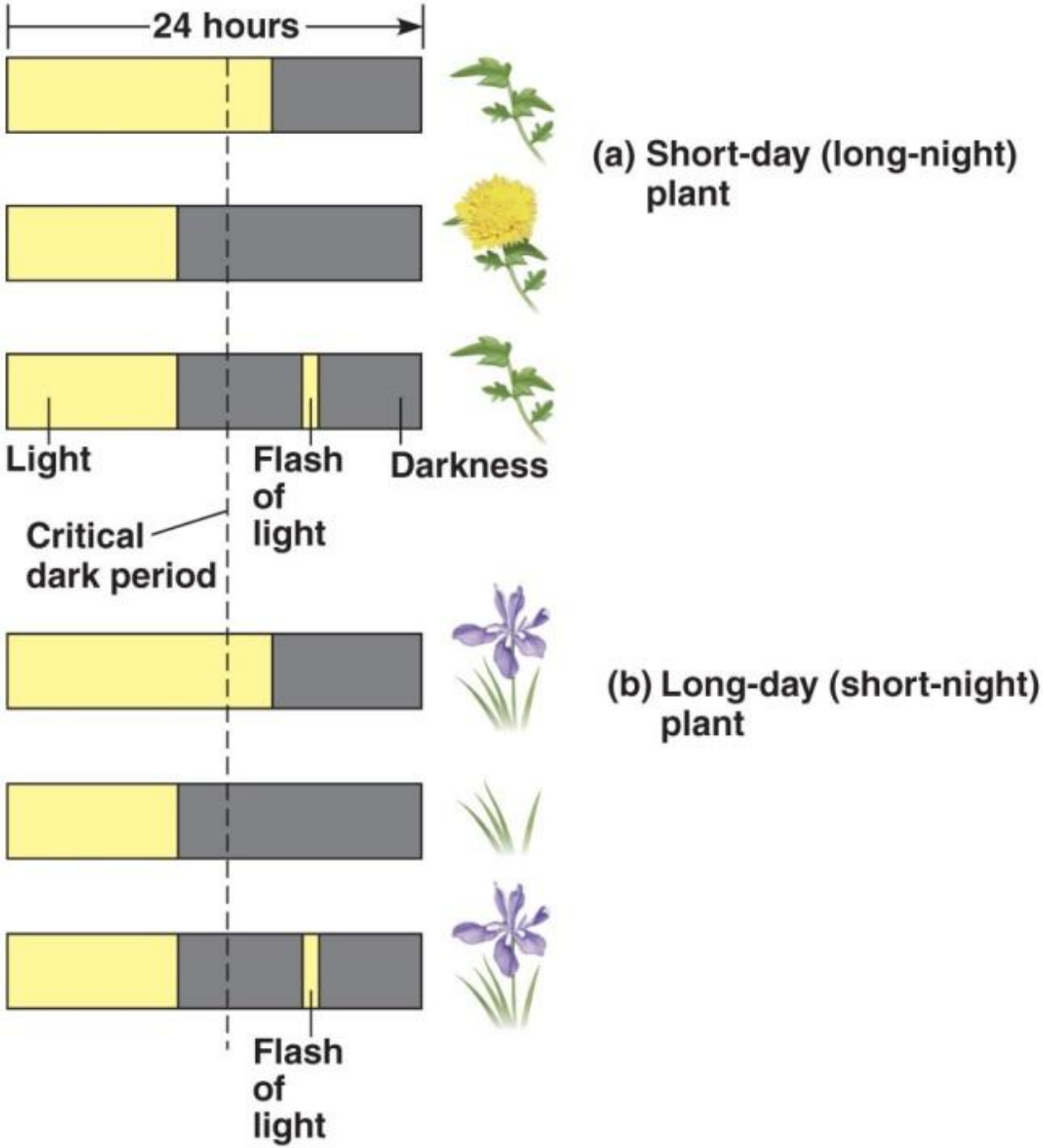
- In the 1940s, researchers discovered that flowering and other responses to photoperiod
  - Are actually controlled by night length, not day length

Critical Night Length

- **Experiment**
  - During the 1940s, researchers conducted experiments in which periods of darkness were interrupted with brief exposure to light to test how the light and dark portions of a photoperiod affected flowering in “short-day” and “long-day” plants.

Critical Night Length

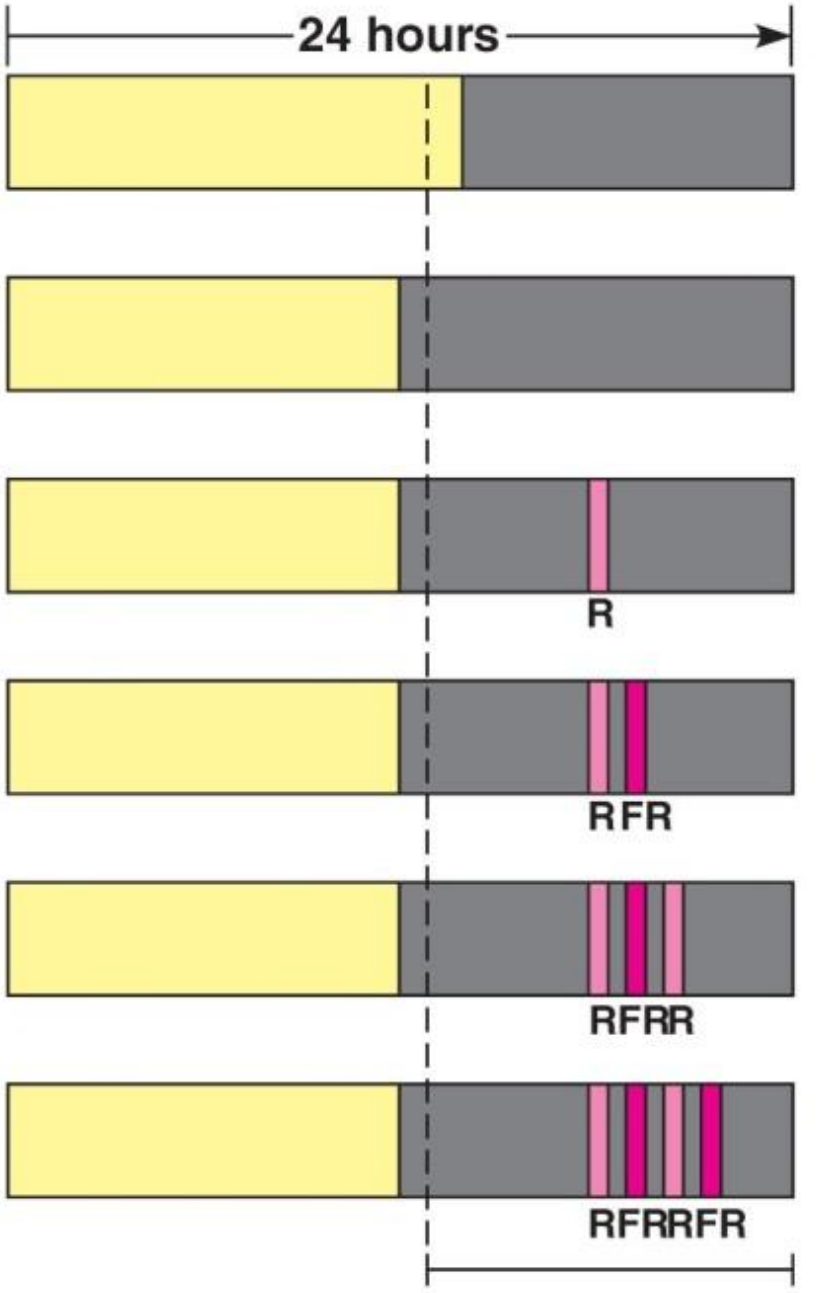
- **Results**
  - **“Short-day” plants** flowered only if a period of continuous darkness was *longer* than a critical dark period for that particular species (13 hours in this example). A period of darkness can be ended by a brief exposure to light.
  - **“Long-day” plants** flowered only if a period of continuous darkness was *shorter* than a critical dark period for that particular species.


24 hours
(a) Short-day (long-night) plant
Light
Flash of light
Darkness
Critical dark period
(b) Long-day (short-night) plant
Flash of light

Critical Night Length

- **Conclusion:**
  - The experiments indicated that flowering of each species was determined by a critical period of *darkness* ("critical night length") for that species, *not* by a specific period of light. Therefore, "short-day" plants are more properly called "long-night" plants, and "long-day" plants are really "short-night" plants.

- Action spectra and photoreversibility experiments
  - Show that phytochrome is the pigment that receives red light, which can interrupt the nighttime portion of the photoperiod


24 hours
R
RFR
RFRR
RFRRFR
Critical dark period

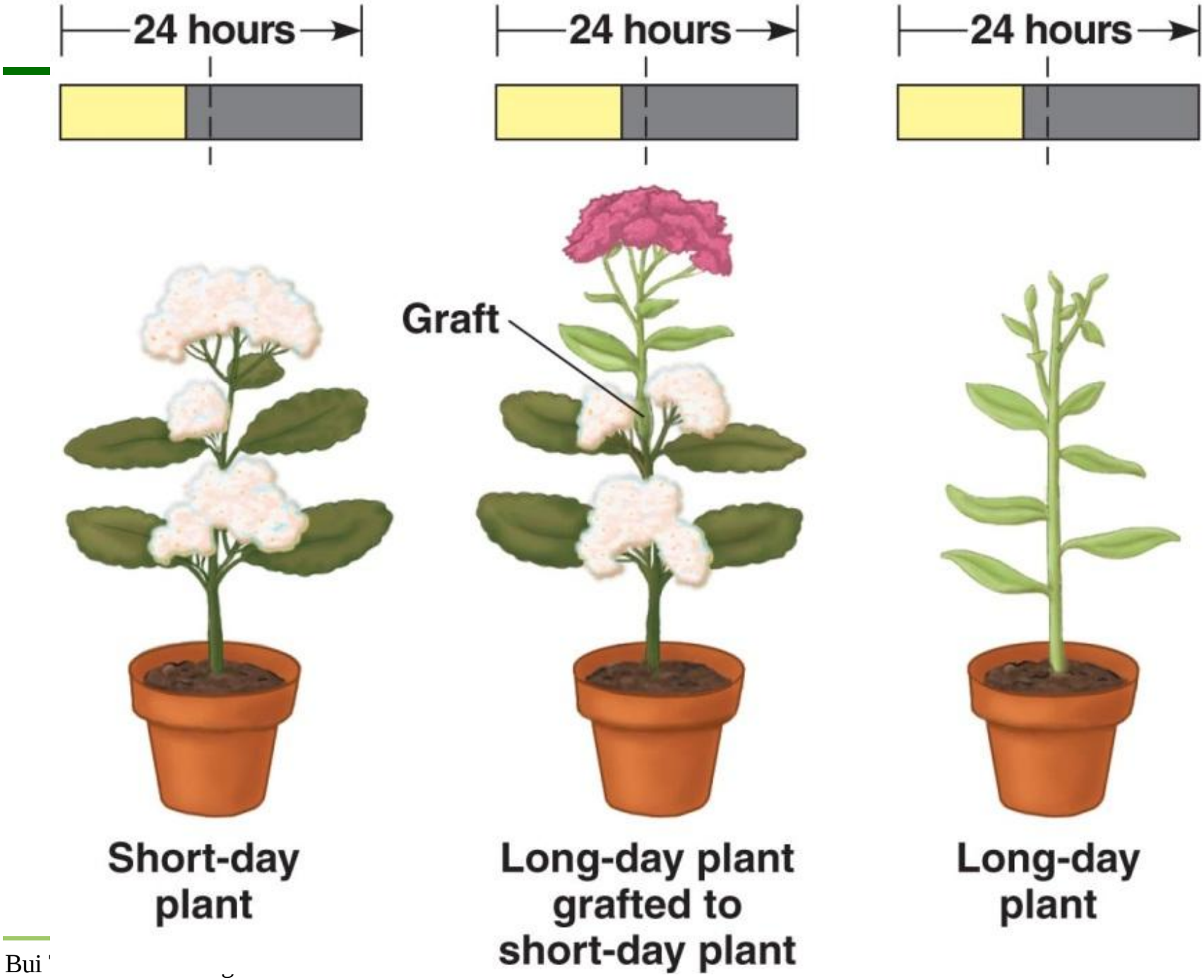

Short-day (long-night) plant
Long-day (short-night) plant

A Flowering Hormone?

- The flowering signal, not yet chemically identified
  - Is called florigen, and it may be a hormone or a change in relative concentrations of multiple hormones

Meristem Transition and Flowering

- Whatever combination of environmental cues and internal signals is necessary for flowering to occur
  - The outcome is the transition of a bud's meristem from a vegetative to a flowering state


24 hours
24 hours
24 hours
Graft
Short-day plant
Long-day plant grafted to short-day plant
Long-day plant