I didn't make this up.
2.C.2.a Explain how organisms respond to changes in their environment through behavioral and physiological mechanisms.

*Use one example from below to help illustrate your explanation:*

- Photoperiodism and phototropism in plants

2.E.2.a. Describe how in plants, physiological events involve interactions between environmental stimuli and internal molecular signals. [See also 2.C.3]

2.E.2.a.1. Explain how plants undergo phototropism, or the response to the presence of light

2.E.2.a.2. Explain the effect of change in length of night or Photoperiodism.
• At the *organismal* level, plants and animals respond to environmental stimuli by very different means

  • Animals, being mobile, respond mainly by behavioral mechanisms, moving toward positive stimuli and away from negative stimuli.

  • Rooted in one location for life, a plant generally responds to environmental cues by adjusting its pattern of growth and development.

  • At the cellular level, however, plants and all other eukaryotes are surprisingly similar in their signaling mechanisms.
In order for an internal or external stimulus to elicit a physiological response, certain cells in the organism must possess an appropriate receptor, a molecule that is sensitive to and affected by the specific stimulus.

- Upon receiving a stimulus, a receptor initiates a specific series of biochemical steps, a signal transduction pathway, that eventually leads to a response.

- Plants are sensitive to a wide range of internal and external stimuli, and each of these initiates a specific signal transduction pathway.
For example, plant growth patterns vary dramatically in the presence versus the absence of light.

- A potato (a modified underground stem) can sprout shoots from its “eyes” (axillary buds).

- In the dark, these shoots are ghostly pale, have long, thin unexpanded leaves, and reduced roots.
• But once a shoot reaches the sunlight, it undergoes profound changes, collectively called **greening**.
  - The elongation rate of the stems slow.
  - The leaves expand and the roots start to elongate.
  - The entire shoot begins to produce chlorophyll.
The greening response is an example of how a plant receives a signal - in this case, light - and how this reception is transduced into a response (greening).

Fig. 39.2
• Stimuli are first detected by receptors, proteins that change shape in response to a specific stimulus.

• The receptor for greening in plants is called a **phytochrome**, which consists of a light-absorbing pigment attached to a specific protein.

  • Unlike many receptors, which are in the plasma membrane, this phytochrome is in the cytoplasm.

• These weak signals are then *amplified by second messengers*, meaning that each activated phytochrome may give rise to hundreds of molecules of a second messenger, each of which may lead to the activation of hundreds of molecules of a specific enzyme.
• The phytochrome, like many other receptors, activates a protein that may activate another, etc. but eventually produces a second messenger, usually molecules called cyclic AMP or cyclic GMP, both of which are nucleotides, right?

• Calcium can also act as a second messenger.
  • In some cases, cyclic nucleotides activate a specific protein kinase, enzymes that phosphorylate and activate other proteins.
• Phytochrome activation also induces changes in cytosolic Ca\(^{2+}\).
  
• A wide range of hormonal and environmental stimuli can cause brief increases in cytosolic Ca\(^{2+}\) like this.
  
• In many cases, Ca\(^{2+}\) binds directly to small proteins called calmodulins which bind to and activate several enzymes, including several types of protein kinases.
  
• Activity of kinases, through both the cyclic GMP and Ca\(^{2+}\)-calmodulin second messenger systems leads to the expression of genes for proteins that function in the greening response.
  
• Take a peek at this without getting a headache…
Fig. 39.3

*Doesn’t show amplification
• In most cases, these responses to stimulation involve the increased activity of certain enzymes.

• This occurs through two mechanisms: stimulating transcription of mRNA for the enzyme or by activating existing enzyme molecules (post-translational modification).

• In transcriptional regulation, transcription factors bind directly to specific regions of DNA and control the transcription of specific genes.
Section B1: Plant Responses to Hormones

1. Research on how plants grow toward light led to the discovery of plant hormones
2. Plant hormones help coordinate growth, development, and responses to environmental stimuli
The word hormone is derived from a Greek verb meaning “to excite.”

Found in all multicellular organisms, hormones are chemical signals that are produced in one part of the body, transported to other parts, bind to specific receptors, and trigger responses in target cells and tissues.

The new AP syllabus says you don’t have to know the names of any specific hormones, but to use them as examples, you must. We will focus on a couple.
2.C.2.a Explain how organisms respond to changes in their environment through behavioral and physiological mechanisms.

*Use one example from below to help illustrate your explanation:*

- Photoperiodism and phototropism in plants

2.E.2.a. Describe how in plants, physiological events involve interactions between environmental stimuli and internal molecular signals. [See also 2.C.3]

- 2.E.2.a.1. Explain how plants undergo phototropism, or the response to the presence of light
- 2.E.2.a.2. Explain the effect of change in length of night or Photoperiodism.
Research on how plants grow toward light led to the discovery of plant hormones

- Plants grow toward light, and if you rotate a plant, it will re-orient its growth until its leaves again face the light.

- Any growth response that results in curvatures of whole plant organs toward or away from stimuli is called a tropism. NOT a “taxis”.

- The growth of a shoot toward light is called positive phototropism.
2.E.3.b. Explain why responses to information and communication of information are vital to natural selection. [See also 2.C.3]

2.E.3.b.1. How does phototropism in plants, result in differential growth and maximum exposure of leaves to light. Why is this important?
In the late 19th century, Charles Darwin and his son observed that a grass seedling bent toward light only if the tip of the coleoptile was present.

- This response stopped if the tip were removed or covered with an opaque cap (but not a transparent cap).
- While the tip was responsible for sensing light, the actual growth response occurred some distance below the tip, leading the Darwins to postulate that some signal was transmitted from the tip downward.
Later, Peter Boysen-Jensen demonstrated that the signal was a mobile chemical substance.

- He separated the tip from the remainder of the coleoptile by a block of gelatin, preventing cellular contact, but allowing chemicals to pass.

- These seedlings were phototropic.

- However, if the tip were segregated from the lower coleoptile by an impermeable barrier, no phototropic response occurred.
Fig. 39.4

Darwin and Darwin (1880)  
Boysen-Jensen (1913)
In 1926, F.W. Went extracted the chemical messenger for phototropism, naming it **auxin**.

Modifying the Boysen-Jensen experiment, he placed excised tips on agar blocks, collecting the hormone.

If an agar block with this substance were centered on a coleoptile without a tip, the plant grew straight upward.

If the block were placed on one side, the plant began to bend away from the agar block.
2. Plant hormones help coordinate growth, development, and responses to environmental stimuli

- In general, plant hormones control plant growth and development by affecting the division, elongation, and/or differentiation of cells.

- Each hormone has multiple effects, depending on its site of action, its concentration, and the developmental stage of the plant.
• Plant hormones are produced at very low concentrations.

• Signal transduction pathways amplify the hormonal signal many fold and connect it to a cell’s specific responses.

• These responses include altering the expression of genes, affecting the activity of existing enzymes, or changing the properties of membranes to make them let something in or stop letting it in.
• Response to a hormone usually depends not so much on its absolute concentration as on its relative concentration compared to other hormones.

• It is hormonal balance, rather than hormones acting in isolation, that may control growth and development of the plants.
• The term **auxin** is used for any chemical substance that promotes the elongation of coleoptiles, although auxins actually have multiple functions in both monocots and dicots.

• The natural auxin occurring in plants is indoleacetic acid, or IAA.

• Current evidence indicates that auxin is produced from the amino acid tryptophan at the shoot tips of plants.
Although auxin affects several aspects of plant development, one of its chief functions is to stimulate the elongation of cells in young shoots.

- The apical meristem of a shoot is a major site of auxin synthesis.

- As auxin moves from the apex down to the region of cell elongation, the hormone stimulates cell growth.

- Auxin stimulates cell growth only over a certain concentration range, at higher concentrations, auxins may inhibit cell elongation, probably by inducing production of ethylene, a hormone that generally acts as an inhibitor of elongation.
According to the acid growth hypothesis, in a shoot’s region of elongation, auxin stimulates plasma membrane proton pumps, increasing the voltage across the membrane and lowering the pH in the cell wall. Let’s watch

- Lowering the pH activates **expansin** enzymes that break the cross-links between cellulose microfibrils.
- Increasing the voltage enhances ion uptake into the cell, which causes the osmotic uptake of water.
- Uptake of water with looser walls elongates the cell.
Fig. 39.7
• Auxins are used commercially in the vegetative propagation of plants by cuttings.
  • Treating a detached leaf or stem with rooting powder containing auxin often causes adventitious roots to form near the cut surface.
  • Auxin is also involved in the branching of roots.
    • One *Arabidopsis* mutant that exhibits extreme proliferation of lateral roots has an auxin concentration 17-fold higher than normal.
• Synthetic auxins, such as 2,4-dinitrophenol (2,4-D), are widely used as selective herbicides.
  • Monocots, such as maize or turfgrass, can rapidly inactivate these synthetic auxins.
  • However, dicots cannot and die from a hormonal overdose. Most weeds are dicots.
    • Spraying cereal fields or lawn grass with 2,4-D eliminates dicot (broadleaf) weeds such as dandelions.
• Auxin also affects secondary growth by inducing cell division in the vascular cambium and by influencing the growth of secondary xylem.

• Developing seeds synthesize auxin, which promotes the growth of fruit.

  • Synthetic auxins sprayed on tomato vines induce development of seedless tomatoes because the synthetic auxins substitute for the auxin normally synthesized by the developing seeds.
A century ago, farmers in Asia noticed that some rice seedlings grew so tall and spindly that they toppled over before they could mature and flower.

In 1926, E. Kurosawa discovered that a fungus in the genus *Gibberella* causes this “foolish seedling disease.”

The fungus induced hyperelongation of rice stems by secreting a chemical, called *gibberellin*.
In the 1950s, researchers discovered that plants also make gibberellins and have identified more than 100 different natural gibberellins.

- Typically each plant produces a much smaller number.
- Foolish rice seedlings, it seems, suffer from an overdose of growth regulators normally found in lower concentrations.
• Roots and leaves are major sites of gibberellin production.
  • Gibberellins stimulate growth in both leaves and stems but have little effect on root growth.
  • In stems, gibberellins stimulate cell elongation and cell division.
  • One hypothesis proposes that gibberellins stimulate cell wall loosening enzymes that facilitate the penetration of expansin proteins into the cell wall.
  • Thus, in a growing stem, auxin, by acidifying the cell wall and activating expansins, and gibberellins, by facilitating the penetration of expansins, act in concert to promote elongation.
The effects of gibberellins in enhancing stem elongation are evident when certain dwarf varieties of plants are treated with gibberellins.

- After treatment with gibberellins, dwarf pea plant grow to normal height.
- However, if applied to normal plants, there is often no response, perhaps because these plants are already producing the optimal dose of the hormone.

Fig. 39.10
The most dramatic example of gibberellin-induced stem elongation is bolting, the rapid formation of the floral stalk.

In their vegetative state, some plants develop in a rosette form with a body low to the ground with short internodes.

As the plant switches to reproductive growth, a surge of gibberellins induces internodes to elongate rapidly, which elevates the floral buds that develop at the tips of the stems, such as happens in a dandelion.
• The embryo of seeds is a rich source of gibberellins.

• After hydration of the seed, the release of gibberellins from the embryo signals the seed to break dormancy and germinate.

• Gibberellins support the growth of cereal seedlings by stimulating the synthesis of amylase to break down amylose into maltose.
• In 1901, Dimitry Neljubow demonstrated that the gas ethylene was the active factor which caused leaves to drop from trees that were near leaking gas mains.

• Plants produce ethylene in response to stresses such as drought, flooding, mechanical pressure, injury, and infection.

• Ethylene production also occurs during fruit ripening and during programmed cell death.

• Ethylene is also produced in response to high concentrations of externally applied auxins.
• The cells, organs, and plants that are genetically programmed to die on a particular schedule do not simply shut down their cellular machinery and await death. Note that lysosomes are NOT used for this.

• Rather, during programmed cell death, called **apoptosis**, there is active expression of new genes, which produce enzymes that break down many chemical components, including chlorophyll, DNA, RNA, proteins, and membrane lipids.

• A burst of ethylene productions is associated with apoptosis whether it occurs during the shedding of leaves in autumn, the death of an annual plant after flowering, or as the final step in the differentiation of a xylem vessel element.
• The loss of leaves each autumn is an adaptation that keeps deciduous trees from desiccating during winter when roots cannot absorb water from the frozen ground.

• Classic example of response to environmental stimuli; this gets plants ready to endure the winter.
• When an autumn leaf falls, the breaking point is an abscission layer near the base of the petiole.

• The parenchyma cells here have very thin walls, and there are no fiber cells around the vascular tissue.

• The abscission layer is further weakened when enzymes hydrolyze polysaccharides in the cell walls.

• The weight of the leaf, with the help of the wind, causes a separation within the abscission layer.

Fig. 39.16
• A change in the balance of ethylene and auxin controls abscission.

• An aged leaf produces less and less auxin and this makes the cells of the abscission layer more sensitive to ethylene.

• As the influence of ethylene prevails, the cells in the abscission layer produce enzymes that digest the cellulose and other components of cell walls.
• The consumption of ripe fruits by animals helps disperse the seeds of flowering plants.

  • Immature fruits are tart, hard, and green but become edible at the time of seed maturation, triggered by a burst of ethylene production.

  • Enzymatic breakdown of cell wall components softens the fruit, and conversion of starches and acids to sugars makes the fruit sweet.

  • The production of new scents and colors helps advertise fruits’ ripeness to animals, who eat the fruits and disperse the seeds.

  • How about a clip from Branching Out (9:25).
• A chain reaction occurs during ripening: ethylene triggers ripening and ripening, in turn, triggers even more ethylene production - a rare example of **positive feedback** on physiology. AP says know one example of this!

• Because ethylene is a gas, the signal to ripen even spreads from fruit to fruit.

• Fruits can be ripened quickly by storing them in a plastic bag, accumulating ethylene gas or by enhancing ethylene levels in commercial production.

• Alternatively, to prevent premature ripening, apples are stored in bins flushed with carbon dioxide, which prevents ethylene from accumulating and inhibits the synthesis of new ethylene.
Genetic engineering of ethylene signal transduction pathways have potentially important commercial applications after harvest.

- For example, molecular biologists have blocked the transcription of one of the genes required for ethylene synthesis in tomato plants.
- These tomato fruits are picked while green and are induced to ripen on demand when ethylene gas is added.
Section C: Plant Responses to Light

1. Blue-light photoreceptors are a heterogeneous group of pigments
2. Phytochromes function as photoreceptors in many plant responses to light
3. Biological clocks control circadian rhythms in plants and other eukaryotes
4. Light entrains the biological clock
5. Photoperiodism synchronizes many plant responses to changes of season
• The photoreceptor responsible for opposing effects of red and far-red light is a phytochrome.

• It consists of a protein (a kinase) covalently bonded to a nonprotein part that functions as a chromophore, the light absorbing part of the molecule.

• The chromophore reverts back and forth between two isomeric forms with one (P\(_{\text{r}}\)) absorbing red light and becoming (P\(_{\text{fr}}\)), and the other (P\(_{\text{fr}}\)) absorbing far-red light and becoming (P\(_{\text{r}}\)).
• This interconversion between isomers acts as a switching mechanism that controls various light-induced events in the life of the plant.

• The $P_{fr}$ form triggers many of the plant’s developmental responses to light, including flowering.

• Exposure to far-red light inhibits the seed germination response. [Watch here](#)
• Plants synthesize phytochrome as $P_r$ and if seeds are kept in the dark or leaves above block out red light (but not far red light) the pigment remains almost entirely in the $P_r$ form.

• If the seeds are illuminated with sunlight, the phytochrome is exposed to red light and much of the $P_r$ is converted to ($P_{fr}$), triggering germination.

Fig. 39.20

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3. Biological clocks control circadian rhythms in plants and other eukaryotes

- Many plant processes, such as transpiration and synthesis of certain enzymes, oscillate during the day.
- This is on the new AP syllabus for plants and animals.
For example, many legumes lower their leaves in the evening and raise them in the morning.

These movements will be continued even if plants are kept in constant light or constant darkness.

Such physiological cycles with a frequency of about 24 hours and that are not directly paced by any known environmental variable are called circadian rhythms.

These rhythms are ubiquitous features of eukaryotic life.

Fig. 39.21
The appropriate appearance of seasonal events are of critical importance in the life cycles of most plants. These seasonal events include seed germination, flowering, and the onset and breaking of bud dormancy.

The environmental stimulus that plants use most often to detect the time of year is the photoperiod, the relative lengths of night and day.

A physiological response to photoperiod, such as flowering, is called photoperiodism.
2.C.2.a Explain how organisms respond to changes in their environment through behavioral and physiological mechanisms.

*Use one example from below to help illustrate your explanation:

  - Photoperiodism and phototropism in plants

2.E.2.a. Describe how in plants, physiological events involve interactions between environmental stimuli and internal molecular signals. [See also 2.C.3]

  2.E.2.a.1. Explain how plants undergo phototropism, or the response to the presence of light

  2.E.2.a.2. Explain the effect of change in length of night or Photoperiodism.
One of the earliest clues to how plants detect the progress of the seasons came from a mutant variety of tobacco studied by W.W. Garner and H.A. Allard in 1920.

This variety, Maryland Mammoth, does not flower in summer like normal tobacco plants, but in winter.

In light-regulated chambers, they discovered that this variety would only flower if the day length was 14 hours or shorter, which explained why it would not flower during the longer days of the summer.
Garner and Allard termed the Maryland Mammoth a **short-day plant**, because it required a light period *shorter* than a critical length to flower.

- Other examples include chrysanthemums, poinsettias, and some soybean varieties.

**Long-day plants** will only flower when the light period is *longer* than a critical number of hours.

- Examples include spinach, iris, and many cereals.

**Day-neutral plants** will flower when they reach a certain stage of maturity, regardless of day length.

- Examples include tomatoes, rice, and dandelions.
• In the 1940s, researchers discovered that it is actually **night length**, not day length, that controls flowering and other responses to photoperiod.

• Research demonstrated that the cocklebur, a short-day plant, would flower if the daytime period was broken by brief exposures to darkness, but not if the nighttime period was broken by a few minutes of dim light.
• Short-day plants are actually long-night plants, requiring a minimum length of uninterrupted darkness.

• Cocklebur is actually unresponsive to day length, but it requires at least 8 hours of continuous darkness to flower.

![Diagram showing photoperiodic responses of short-day and long-day plants](image)
• Similarly, long-day plans are actually short-night plants.

• A long-day plant grown on photoperiods of long nights that would not normally induce flowering will flower if the period of continuous darkness are interrupted by a few minutes of light.

• While the critical factor is night length, the terms “long-day” and “short-day” are embedded firmly in the jargon of plant physiology.

• In 2007, the long sought hormone that actually is released to cause flowering was isolated. It is called florigen.
DNA-binding protein (OsFD1)

DNA

Florigen (Hd3a)

Florigen receptors (14-3-3)
Pfr730 is the physiologically active form of phytochrome and inhibits flowering in short-day plants and promotes flowering in long-day plants. There is a critical Pfr730 level below which flowering is no longer inhibited in short-day plants and flowering is no longer promoted in long-day plants. With respect to phytochrome conversion, sunlight functions as red light, therefore, Pfr730 predominates at the beginning of the dark period. So the Pfr730 form is rapidly produced in the light and the Pr form is slowly produced in darkness. Under the long days of summer, the nights are not sufficiently long enough to allow enough Pfr730 to revert to Pr660 so the level Pfr730 does not drop below the critical level. Therefore, short-day plants do not flower and long-day plants flower. During the short days of winter, the nights are long enough for sufficient quantities of Pfr730 to revert to Pr660 so that the level pf Pfr730 does drop below the critical level. Therefore, short-day plants flower and long-day plants grow vegetatively.
• Red light is the most effective color in interrupting the nighttime portion of the photoperiod.

• Action spectra and photoreversibility experiments show that phytochrome is the active pigment.

• If a 5 min. flash of red light during the dark period is followed immediately by a flash of far-red light, then the plant detects no interruption of night length, demonstrating red/far-red photoreversibility.
• Plants measure night length very accurately.
  • Some short-day plants will not flower if night is even one minute shorter than the critical length.
  • Some plants species always flower on the same day each year.

• Humans can exploit the photoperiodic control of flowering to produce flowers “out of season”.
  • By punctuating each long night with a flash of light, the floriculture industry can induce chrysanthemums, normally a short-day plant that blooms in fall, to delay their blooming until Mother’s Day in May.
    • The plants interpret this as not one long night, but two short nights.
1. Plants respond to other environmental stimuli through a combination of mechanisms

- Both the roots and shoots of plants respond to gravity, or gravitropism, although in diametrically different ways.
  - Roots demonstrate positive gravitropism and shoots exhibit negative gravitropism.
  - Gravitropism ensures that the root grows in the soil and that the shoot reaches sunlight regardless of how a seed happens to be oriented when it lands.
  - Auxin plays a major role in gravitropic responses.
• Plants may tell up from down by the settling of **statoliths**, specialized plastids containing dense starch grains, to the lower portions of cells.

• In one hypothesis, the aggregation of statoliths at low points in cells of the root cap triggers the redistribution of calcium, which in turn causes lateral transport of auxin within the root.

• The high concentrations of auxin on the lower side of the zone of elongation inhibits cell elongation, slowing growth on that side and curving the root downward.
Please try to contain your tears....

• Our plant units are now completed.

• How about a Plant Challenge worksheet??