Plant Hormones

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1 Introduction

Like animal hormones, plant hormones have a profound impact on a plant's growth, development, and environmental responses. However, unlike in animals, plants have a small number of hormones that each perform a multitude of functions. A strong knowledge of plant hormones is not only necessary for accurately answering a multitude of plant questions on the USABO, but also builds analytical skills that will help competitors in other sections of the tests.

2 A Brief Review of Signal Transduction

2.1 The Cellular Basis of Signal Transduction

The basic process of signaling is the same in plants and animals. A cell receives a signal (commonly a hormone) through a specialized receptor, transduces and amplifies that signal, and elicits a response to the initial signal. For more information, refer to the "Cell Bio" packets.

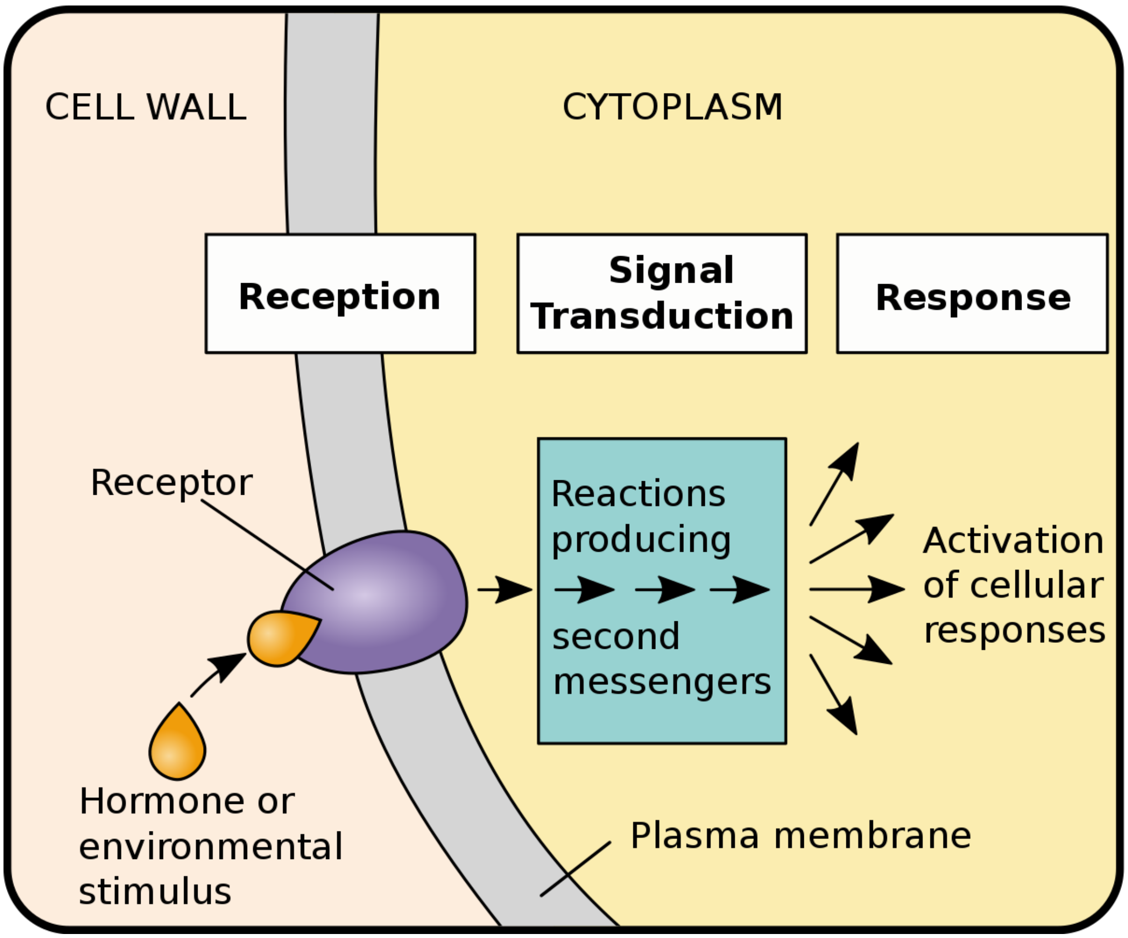

Figure 1: Simplified diagram of signal transduction. (Source: Pearson)

The process of signal transduction commonly uses **second messengers** like cAMP, cGMP, and Ca^2+ (calcium ions). These second messengers initiate a variety of signaling cascades that eventually lead to differential gene expression (a response) in the plant.

2.2 Kinases and Phosphatases

The concept of **phosphorylation** is an integral part of biology. In many cases, signals will initiate a "phosphorylation cascade" in the cell, meaning that the addition of a phosphate group to a specific protein catalyzes the addition of a phosphate group onto the subsequent protein in the pathway, and so on and so forth until the end of the pathway (final response).

- The enzymes that *add* phosphate groups to specific proteins are called **kinases**.
- The enzymes that *remove* phosphate groups from proteins are called **phosphatases**.

Working together, these two classes of enzymes can regulate a cell's protein activity.

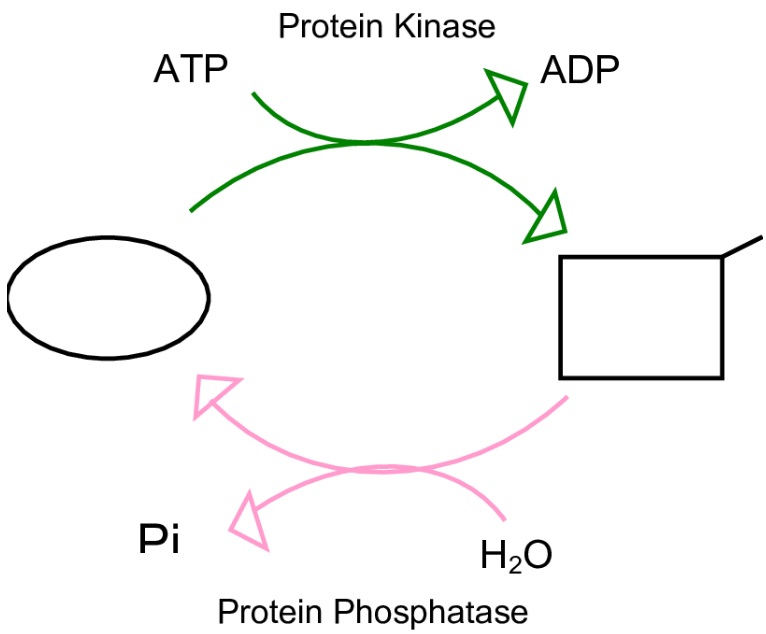

Figure 2: Simple diagram of the reversibility of kinases and phosphatases.
(Source: Mukhopadhyay 2006)

2.3 Etiolation and De-etiolation: Reactions to Environmental Cues

When a flowering plant is grown in the dark, it undergoes morphological adaptations collectively known as **etiolation**. These adaptations include long, thin stems, small leaves, and a general lack of chlorophyll (leading to chlorosis, or yellowing, of the leaves).

You can think of etiolation as a plant's "desperate attempt" to reach a light source. By focusing energy on stem elongation and expansion, the plant increases its chances of finding a suitable light source by chance.

When a plant reaches a light source, it begins to adapt in a process called **de-etiolation**. Stem elongation slows, leaves expand, roots grow, and chlorophyll production increases (leading to the term "greening"). A group of receptors known as **phytochromes** respond to red and far-red light imbalances (explained later in this handout), leading to significant changes in gene expression throughout the plant.

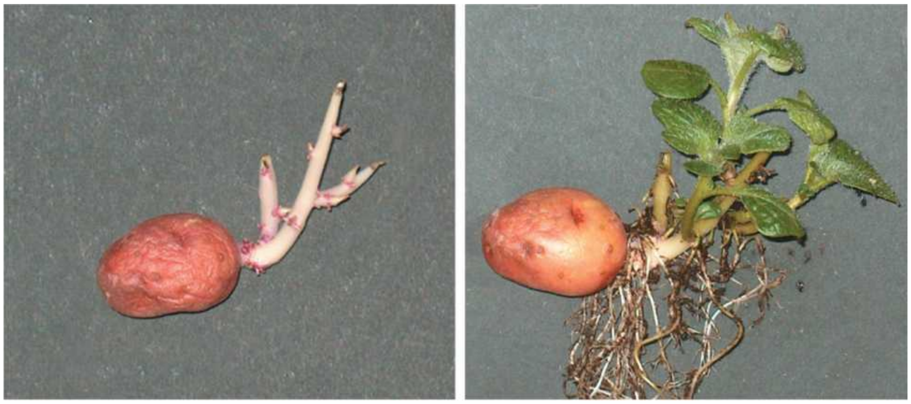

Figure 3: Diagram of etiolation and de-etiolation in a potato. (Source: Pearson)

3 The Major Plant Hormones

3.1 Auxin

Charles Darwin and his *Origin of Species* had a profound impact on our understanding of evolution and natural selection, but he was also instrumental in the discovery of phototropism and the major plant hormone **Auxin**. Auxin is the most well-known plant hormone, and it's involved in phototropism, apical dominance, and shoot elongation.

- The main form of auxin is called **indoleacetic acid**, or IAA, which is a small polar molecule with two rings.
- Auxins are produced in the **shoot tip** and transported down towards the base through a complex process called **polar transport**. Efflux trasnporters called *PIN proteins* drive constant auxin transport away from the shoot tip.

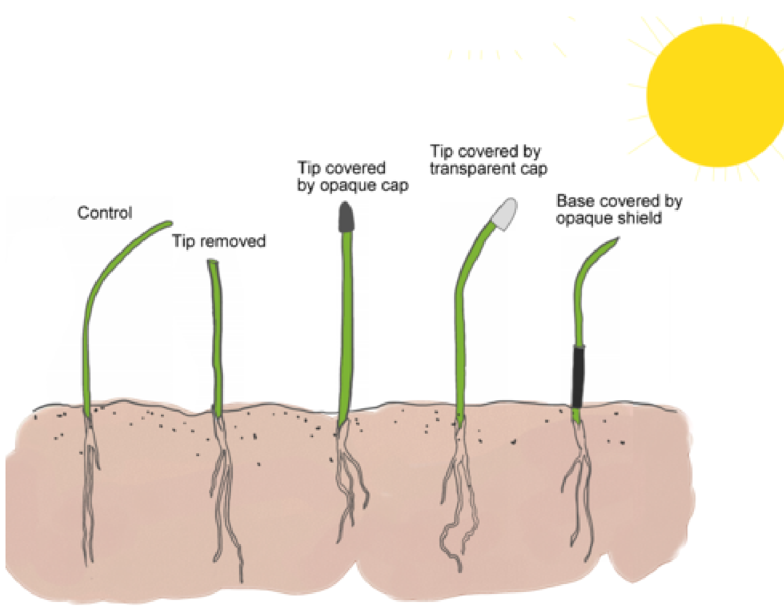

Figure 4: Darwin's experiments exploring the phototropic response in plants. Notice how phototropism occurs only when light touches the shoot tip. (Source: Learning Pathwayz)

At this point, you may be wondering how auxin actually leads to phototropism. When a light source hits the stem from a specific side, auxins are produced at the tip and *associate at the shaded side* through polar transport. Afterwards, H+ is pumped across the membrane, decreasing the pH of the cell wall.

The increased acidity of the cell wall allows the cells to grow by a process known as the **acid growth hypothesis**. As cell wall pH decreases, proteins called **expansins** are activated, breaking hydrogen bonds and loosening the cell wall. The subsequent increased permeability of the cell wall leads to ion and water uptake, finally resulting in cell elongation. The elongated cells on the shaded side "push" the stem towards the light, leading to the phototropic response.

Auxins also play the general roles of activating growth-related proteins in the plant, controlling branch formation, and determining phyllotaxy (leaf arrangement).

Example 3.1 (USABO 2015 Open Exam) You are given an Arabidopsis mutant PIN3, in which an auxin efflux protein is disabled. Which of the following phenotypes would you expect?

A. Accelerated seed germination.
B. Delayed seed germination.
C. Diminished phototropic response.
D. Increased rate of fruit ripening.
E. Reduced stomatal response to soil drying.

Solution: The only option that has a direct relationship to auxin function is C. Auxin is instrumental in phototropism, and disabled PIN proteins would greatly diminish phototropism. The other options have indirect or no association with auxin.

3.2 Cytokinins

The second major class of plant hormones are **cytokinins**. Derived from *adenine*, cytokinins are named due to their role in promoting cytokinesis. The most common naturally occurring cytokinin is called **zeatin**, named because it was first found in *Zea mays*, or corn.

Cytokinins are produced in growing tissues like roots, fruits, and embryos. They are generally transported from the roots to the shoots through the xylem sap, where they regulate cell division, growth, and apical dominance.

The **auxin to cytokinin ratio** is an incredibly important concept in plant growth and cell division. When only cytokinins are present, cultured plant cells cannot divide. However, when both auxin and cytokinins are present in balanced amounts, cell division occurs, and a *callus* (undifferentiated parenchyma tissue) is formed. When there is a higher ratio of cytokinins, the cells form shoot tissue, and when the ratio of auxins is higher, the cells form roots.

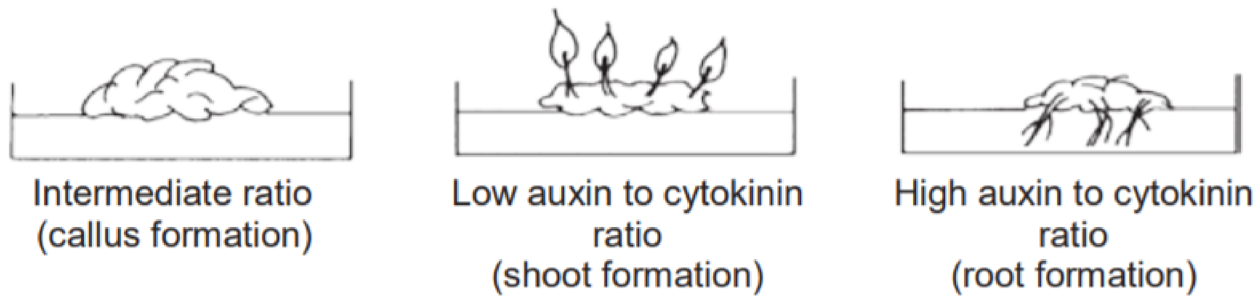

Figure 5: auxin to cytokinin ratio and its effect on plant cell differentiation. (Source: Aladdin)

Another important role of cytokinins (along with auxin and strigolactones) is the regulation of **apical dominance**. Auxin and strigolactones, produced in the apical shoot, repress the formation of *axillary* (secondary) shoots and promote apical dominance. Meanwhile, cytokinins play the opposite role, suppressing apical dominance and promoting axillary bud growth. Since auxins travel *downwards* from shoot tips and cytokinins travel *upwards* from the roots, the plant can detect the auxin to cytokinin ratio at specific locations and respond accordingly (with apical or axillary bud growth).

Finally, cytokinins play a role in slowing **plant aging**. For example, if a singular leaf is placed in a cytokinin solution, the leaf will stay green for longer than if there were no cytokinins in the solution.

3.3 Gibberellins

In the early 20th century, farmers found that some rice plants were growing incredibly fast and dying before reaching maturity. It was later found that a fungus called *Gibberella* caused this "foolish seedling disease," secreting chemicals that scientists termed **gibberellins**. In the following century, gibberellins were found to primarily control stem elongation, fruit growth, and seed germination.

As shown in foolish seedling disease, gibberellins promote elongation in young plant tissues. Interestingly, experiments have shown that dwarf mutants treated with gibberellins can induce growth to a normal phenotype, but wild-type plants cannot grow taller with gibberellin treatment alone (because they typically have sufficient gibberellin concentration). Gibberellins can also induce **bolting**, or rapid growth of the floral stalk during a plant's reproductive stage.

Figure 6: Gibberellins inducing bolting (stem elongation and flowering) during the reproductive stage of *Arabidopsis*. (Source: NASA)

Gibberellins also contribute to fruit growth (along with auxin). For example, if grapes are sprayed with gibberellins, they will grow larger. For this reason, farmers will often spray their grapes with gibberellins to increase yield during harvests. Additionally, the internodes (spaces) between grape bunches will grow larger, leading to higher air circulation and a lesser likelihood of pathogen infection.

Another interesting function of gibberellins is that they are used in determining the sex of cucurbits (plants like cucumbers and squash). In cucurbits, high levels of gibberellins result in male flowers while high levels of ethylene (discussed later) result in female flowers.

Along with abscisic acid, the hormone described in the next section, gibberellins majorly regulate seed germination. While abscisic acid inhibits germination, increased gibberellin content in the seed leads to germination, commonly instigated by a seed's water uptake.

3.4 Abscisic Acid

Though the previous hormones generally promote growth, abscisic acid (ABA) slows down growth. ABA was originally thought to promote leaf abscission (the reason for its name), but researchers have found that ABA is actually not involved in leaf abscission. However, ABA's name has not changed since its initial discovery.

A primary function of ABA is **seed dormancy**. High ABA levels are known to inhibit germination, opposing the action of gibberellins in the dormant seed. Consequently, the gibberellin to ABA ratio in the seed is incredibly important for determining if germination occurs. If ABA levels are too low, the seed will undergo **precocious/premature germination**, making the fledgling plant susceptible to subpar environmental conditions.

Figure 7: Desert plants have high levels of abscisic acid to prevent precocious germination. When a desert receives significant rainfall, the water will wash the ABA out of the seeds, allowing for germination in a moist environment conducive to growth. (Credit: planthormones.info)

Another function of abscisic acid is **drought tolerance**. When there are prolonged droughts, ABA will close plant stomata to reduce transpiration. This protects the plant from losing too much water and wilting.

3.5 Ethylene

Unlike the other hormones mentioned before, **ethylene** is a gas hormone. One of its functions is in fruit ripening, which is why you're able to ripen bunches of fruit by putting them in a paper bag.

In terms of plant growth, one of the most important functions of ethylene is the **triple response**. Whenever a plant encounters a physical barrier, it slows its stem elongation, thickens its stem, and curves horizontally. These three responses orient the plant away from the obstacle, allowing the plant to grow around it without breaking its stem.

A sudden increase in ethylene is generally associated with apoptosis and **senescence**. For example, when a leaf is preparing to fall, the cells at the petiole will undergo apoptosis. This forms an *abscission layer* at the petiole, eventually leading to leaf abscission. However, the plant makes sure to store the majority of the essential nutrients that the leaf was carrying before, waiting until spring to reuse those precious resources.

So, ironically, ethylene, not abscisic acid, controls leaf abscission in deciduous plants. Specifically, as the auxin level in the leaf falls, ethylene becomes more effective and induces cellular senescence, leading to an abscission layer, and finally leading to leaf abscission.

Furthermore, ethylene is involved in **fruit ripening**. The fruit softens (cell walls broken), molecules are converted into sugars, and the fruit produces attractive scents and colors. A burst of ethylene initiates ripening, but a sustained positive feedback loop sustains the process. This is why putting fruits in a paper bag (mentioned before) can help ripen the whole bunch – as a gas hormone, ethylene can spread among the fruits and sustain positive-feedback ripening loops. Interestingly, carbon dioxide inhibits ethylene (just a thing to keep in mind).

> **Example 3.2** (USABO 2019 Semifinal Exam) You notice that a houseplant is growing abnormally and decide to sequence its genome. Once the results are in, you find that it is a mutant which is resistant to ethylene. Which of the following functions would not be affected?
>
> A. Pollen production.
> B. Fruit ripening.
> C. Leaf abscission.
> D. Triple response.
> E. Senescence.

Solution: Fruit ripening, leaf abscission, triple response, and senescence are all canonical functions of ethylene. However, pollen production is not directly associated with ethylene, so this is the **correct answer (A)**.

3.5.1 Ethylene Mutants

Many ethylene mutants have been generated, leading to significant differences in height and ability to perform the triple response.

- *ein* (ethylene-insensitive) mutants cannot respond to ethylene and often grow higher than usual (no triple response).
- *eto* (ethylene-overproducing) mutants produce too much ethylene and often grow shorter than usual (too much triple response).
- *ctr* (constitutive triple response) mutants undergo the triple response even in the absence of ethylene (constitutive means always active), meaning that these mutant plants will be very short.

Example 3.3 (USABO 2018 Open Exam) Observe the seedlings growing below which have a loss of function mutation in the ethylene receptor.

Source: University of Queensland, Australia

Which of the following statement(s) is (are) TRUE regarding this mutant's growth response NOT being related to a triple response? Select one response A, B, C, D, or E.

I. This mutant will not respond to the exposure of ethylene under any circumstances.

II. This mutant has a constitutive activity where it leads to the activation of kinase, which is important for the triple response.

III. This mutant has a constitutive activity where it leads to the inactivation of kinase, which is important for the triple response.

IV. If this mutant is treated with aminoethoxyvinylglycine (ethylene synthesis inhibitor), this mutant will be able to undergo triple response.

V. If this mutant is treated with aminoethoxyvinylglycine (ethylene synthesis inhibitor), this mutant will not respond to the treatment and not undergo triple response.

A. I.
B. II, IV.

C. III, V.
D. I, II, IV.
E. I, III, V.

Solution: Since our mutant has a mutation in the ethylene receptor, that means it will be unable to recognize and respond to ethylene, making it an *ein* mutant. Therefore, I is true. Since it does not respond to ethylene, it will not undergo the triple response, meaning that III is true and II is false. Finally, the ethylene synthesis inhibitor treatment would be better suited for an *eto* mutant and will have no effect on our mutant, meaning that V is true and IV is false. Therefore, our **answer is E**.

Example 3.4 (USABO 2018 Open Exam) Three groups of *Arabidopsis* seedlings are subjected to a short burst of ethylene. Group A is comprised of ethylene-insensitive (*ein*) mutants. Group B consists of constitutive triple-response (*ctr*) mutants. Group C is also subjected to high levels of abscisic acid. Group D serves as a control (wild type) and receives the ethylene treatment. Which group is likely to be the tallest after a few days of the treatment?

A. Group A.
B. Group B.
C. Group C.
D. Group D.
E. They will be equally as tall.

Solution: As discussed previously, ABA slows plant growth and ethylene would induce the triple response, which slows stem elongation. Therefore, the only group that does not respond to ethylene nor is exposed to abcisic acid is **Group A** (*ein*).

4 Other Plant Hormones

Here we'll cover the more minor plant hormones. Less is known about the functions of these hormones, but they still play crucial roles in the plant.

4.1 Brassinosteroids

Brassinosteroids are steroids molecularly similar to cholesterol in animals and functionally similar to auxin. They can stimulate cell **elongation** and **division** in "super young" plant components like seedlings and new stems. Brassinosteroids also help slow leaf abscission and promote xylem differentiation, which is similar to some of auxin's roles.

4.2 Jasmonates

Jasmonates are fatty acid-based (linolenic acid) hormones that mainly function in **plant defense** (though they also minorly function in nectar production, fruit ripening, pollen production, flowering, germination, root growth, tuber formation, mycorrhizal symbioses, and tendril formation). They communicate with gibberellins, auxins, and ethylene to perform these various functions.

4.2.1 Plant Defenses Against External Threats

Plants generally have to defend against pathogens and herbivores. Plants have physical barriers against pathogens (bark, epithelium, etc.), but these barriers are easily bypassed due to the many holes (e.g., stomata) on the plant surface. Plants can recognize **PAMPS** (pathogen-associated molecular patterns), special molecules that indicate the presence of pathogens. **Phytoalexins** are activated to kill pathogens, and **effector-triggered immunity** is activated. The plant has special **R genes** (resistance genes) that activate specific immune responses like the **hypersensitive** (local, specific) response and **systemic acquired resistance** (SAR) (general defense). For example, *systemin* initiates SAR by synthesizing jasmonic acid, and *salycylic acid* is a component of SAR that spreads through the entire plant, prepping the immune system for defense.

Against herbivores, plants can use specialized **idioblasts** with **raphides** (calcium oxalate crystals that cut the herbivore's tongue) to deter herbivory. However, humans can eat most plants because cooking destroys raphides.

4.3 Strigolactones

Strigolactones stimulate **germination**, control **apical dominance** (along with auxin), and regulate **mycorrhizal associations** between the plant and external fungi. They were discovered from the study of *Striga* plants, which are parasites of food-producing grains. Since their seeds can stay dormant in the soil for many years, they are near-impossible to eradicate.

5 Plant Responses to Environmental Factors

5.1 Light and Phototropism

5.1.1 Photoreceptors

Plant photoreceptors are specialized proteins that detect and respond to specific wavelengths of light, playing a crucial role in various aspects of growth and development. They allow plants to regulate various physiological processes and optimize environmental interactions.

The first class of photoreceptors we'll discuss are called **blue-light photoreceptors**. Since the sun emits mostly blue light, these receptors are able to put the plant in tune with the sun's activity. **Cryptochromes**, one class of blue-light photoreceptors, inhibits stem elongation in response to blue light (e.g., when a seedling breaks out of the soil). Another receptor, known as **phototropin**, controls stomatal opening and phototropism.

Phytochromes are red (660 nm)/far-red (730 nm) photoreceptors. Phytochromes come in 2 forms, P_r and P_{fr}. When P_r receives red light, it changes to the P_{fr} state, which can receive far-red light to convert back to P_r. Basically, P_r can receive red light and P_{fr} can receive far-red light, but receiving its respective wavelength converts the phytochrome to its other form.

In the plant, P_{fr} promotes **germination** while P_r inhibits germination. So when the plant receives red light, P_r will be converted to P_{fr}, and the plant will germinate (as well as vice versa). Additionally, P_r induces **vertical growth** in plants, while P_{fr} induces horizontal growth. You can think of a plant under the canopy receiving an excess of far-red light (direct sunlight is blocked). This plant would want to reach the canopy, so it would grow as high as possible. On the other hand, a plant that's already in the canopy would want to expand to absorb as much light as possible (growing horizontally).

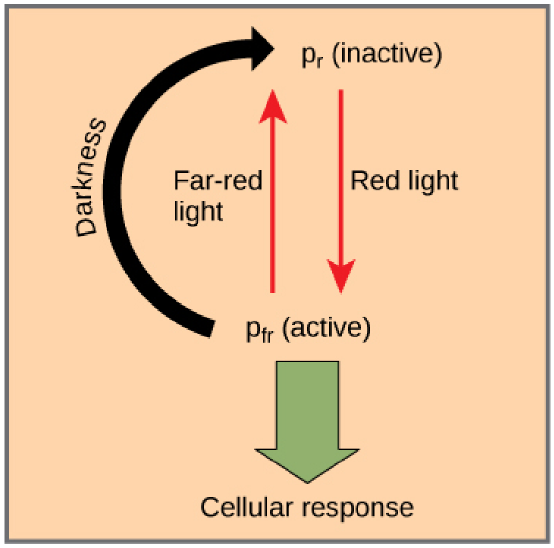

Figure 8: P_r and P_{fr}. (Credit: Biology LibreTexts)

5.2 Phytochrome Control of Circadian Rhythms and Photoperiodism

A plant naturally has a **free-running period** of 21-27 hours. This free-running period was determined experimentally by placing plants in a constant-light environment. There is still a consistent rhythm, but it's not exactly 24 hours. The sudden P_{fr} increase at sunrise (stimulated by red light) resets the **biological clock**, keeping the circadian rhythm on track.

Different plants also have different **photoperiods**, which determine if a plant flowers or not. Although these plants are named after day length, it is actually **night length** that is critical for flowering. It is important to note that this critical length is unique for each plant.

- **Short-day plants** are actually **Long-night plants**. Thus, they flower when the night is *longer* than a critical length.
- **Long-day plants** are actually **Short-night plants**. Thus, they flower when the night is *shorter* than a critical length.
- **Neutral-day plants** flower no matter how long the night is.

If night length is interrupted by a flash of light, the plant's flowering potential will be messed up. Experiments involving flashes of red (simulating day) and far-red (simulating night) lights have shown that only the *last* flash of light matters. In general, if night is interrupted by a significant period of *red light*,

- short-day (long-night) plants WILL NOT flower.
- long-day (short-night) plants WILL flower.

On a side note, **vernalization** is when a plant is exposed to cold temperatures to induce flowering (another control of flowering).

Example 5.1 (USABO 2013 Open Exam) Lettuce seeds receive flashes of far red and red light in this order: far red, red, far red, red, red, red, red, far red. The seeds will...

A. Germinate since far red light induces germination.
B. Germinate since the first flash of light determines germination.
C. Germinate since there are more flashes of red light.
D. Not germinate since the flashes of light have destroyed the seeds.
E. Not germinate since only the last flash of light determines germination.

Solution: Critical night length is determined by the last flash of light. Since the last flash was far red light, the night length will not be affected and most of the phytochromes will be in the P_r state. Thus, since P_r inhibits germination, the lettuce seed will not germinate since only the last flash of light determines germination **(E)**.

5.3 Gravity and Gravitropism

Positive gravitropism means growth downwards (in gravity's direction), while negative gravitropism means growth upwards (against gravity). It's hypothesized that **statoliths**, specialized plastids with starch inside, indicate the direction of gravity (and induce gravitropism) by sinking to the bottom of each cell. Though gravitropism can occur without statoliths, they're thought to be major contributors to the gravitropic response.

5.4 Touch and Thigmomorphogenesis

Plant growth in response to touch is called **thigmotropism**. For example, vines can latch onto another structure to grow higher after contacting that structure. This phenomenon also explains why plants in windy environments grow shorter (if they grow taller, the wind will knock them over). Also, plants such as the **mimosa** and **venus flytrap** rapidly fold their leaves in response to touch through a rapid loss of **turgor pressure** inside the cell through potassium ion loss followed by water loss.

Figure 9: The sleeping mimosa plant displays a thigmonastic response after making contact with a human finger. (Credit: Nagwa)

5.5 Responses to Stressful Conditions

5.5.1 Drought

A plant's goal during drought conditions is to **reduce transpiration**. The plant can alter its physical structure, undergo wilting or shedding, or close its stomata. As previously mentioned, abscisic acid synthesis is increased during a drought, closing the stomata and preventing excessive water loss.

5.5.2 Flooding

In a flood, the plant has to adapt to low-oxygen conditions (due to water blocking oxygen flow in the soil). In some cases, **Ethylene** synthesis increases to kill cells in the root cortex, producing "snorkel" air tubes to provide oxygen to the roots.

Figure 10: A plant in flooded conditions. (Credit: The Spruce)

5.5.3 Salinity

High-salt conditions increase the water potential difference between the plant and its surroundings. To reduce this difference, plants will produce many solutes, reducing the water potential difference with the plant's surroundings.

5.5.4 Temperature

In normal conditions, transpiration regulates plant temperature with evaporative cooling. However, when it gets too hot, the plant cannot afford to lose more water necessary for survival, so it produces **heat-shock proteins** which help protect the plant.

On the other hand, plants need to prevent membrane solidification in cold temperatures, so they change the composition of their membranes to increase fluidity (e.g., adding unsaturated fats). To prevent freezing, plant cells increase solute concentration in their cytoplasms to prevent water loss. Special **antifreeze proteins** can also be synthesized for plants to be able to live under 0°C.

Figure 11: A frozen plant. (Credit: Cypress Creek Landscape Supply)

6 Conclusion

Thank you for reading to the end – I hope you learned some useful information! In my opinion, plant hormones are relatively simpler than animal hormones (even just numbers-wise), but their interactions are still really interesting. Doing practice problems will also increase your analytical skills, which can be applied to other sections of the USABO. DM me on Discord if you have any questions (username is ".ochre").