

G1 PHYTOCHROME, PHOTOPERIODISM AND PHOTOMORPHOGENESIS

Key Notes

Photomorphogenesis

Photomorphogenesis is the direct influence of light on growth and development. It involves responses to certain wavelengths of light which are perceived by photoreceptor pigments.

Photoperiodism

Photoperiodism is the response of a plant to length of day. It governs processes such as dormancy and flowering. Species may be either long-day, short-day or day-neutral in their response to day length.

Phytochrome

Phytochrome is a photoreceptor protein. It is synthesized as Pr that absorbs red light (666 nm) and is converted to Pfr which absorbs far-red light (720 nm), and initiates cell signaling events leading to photomorphogenesis. Many phytochrome responses initiated by red light are reversed by far-red light. Five phytochrome genes, *PHYA-PHYE*, have been identified. *PHYA* is expressed at high levels in etiolated tissue. In red light its expression is switched off and the protein rapidly degraded. *PHYB-E* are constantly expressed at low levels in tissue and are involved in other phytochrome responses.

Phytochrome responses

Phytochrome responses include: etiolation/de-etiolation, circadian rhythms such as leaf and petal movement, and seed germination.

Phytochrome mechanisms

Phytochrome regulates processes which involve changes in cell turgor (e.g. leaf movements) by altering proton and potassium transport at the cell membrane. Long-term phytochrome responses involve phytochrome activated genes.

Related topics

Features of growth and development (F1) Tropisms (G2)

Photomorphogenesis

Plants use light for photosynthesis. They also respond to light in other ways. For instance, a germinated seedling grows rapidly to reach light suitable for photosynthesis before its food reserves are exhausted. During this rapid elongation growth, chlorophyll and some chloroplast proteins are not synthesized and the seedling remains **etiolated** (pale and lacking developed chloroplasts) until light is reached. Then immediately, patterns of gene expression are initiated and the seedling begins to form mature, photosynthetically active chloroplasts and its growth form alters from rapid elongation to the production of leaves and a stem capable of supporting them. This is **photomorphogenesis** – change of form in

response to light; there are many other examples, including seed germination (some seeds will only germinate after being exposed to red light), leaf morphology and control of flowering. Photomorphogenesis involves specific responses to certain wavelengths of light, different to those needed for photosynthesis. These are usually either responses to blue or red light; responses to blue light include growth to unilateral light (**phototropism**), the mechanism for which is discussed in Topic G2. Growth in response to red light involves the pigment **phytochrome**.

Photoperiodism

Photoperiodism permits seasonal responses in temperate species that are independent of temperature. Plants may be classified according to whether flowering is induced by short days (**short-day plants** [SDPs]), long days (**long-day plants** [LDPs]) or is day length independent (**day-neutral species**). Flowering in LDPs occurs only when day length is greater than a given value (depending on species); in SDPs when day length is less than a given value. LDPs and SDPs in fact respond to the length of the night, as introducing a brief period of illumination (a **night-break**) overcomes the effect of long nights. Photoperiodism results from two processes: **perception of light** by the photopigment phytochrome in leaves, and an endogenous circadian rhythm (see below). Genetic control of flowering has been indicated by the description of mutant LDPs which are day-neutral and mutant day-neutral plants which are SDPs.

Phytochrome

Phytochrome is synthesized as a protein, **Pr**, able to absorb red light (666 nm). When it absorbs red light, it converts to a **Pfr** able to absorb far-red light at **730 nm** (that converts it back to Pr; Fig. 1). Many phytochrome responses show '**red-far red reversibility**' – when a process has been activated by a short period of red light, it will be stopped or reversed by a subsequent pulse of far-red light.

Phytochrome is a protein made up of two identical sub-units, in total sized 250 kDa. Each monomer (sub-unit) has a pigment (**chromophore**) molecule attached to it through an -S- (thioether) bond to the amino acid cysteine. When the chromophore absorbs red light, its structure alters slightly (Fig. 2) and this alters the conformation of the protein initiating events which ultimately results in altered gene expression.

A multi-gene family of phytochromes has been identified in arabidopsis (Topic E1), with five members, *PHYA*, *PHYB*, *PHYC*, *PHYD* and *PHYE*. These can be subdivided into two types of phytochrome: *PHYA* encodes **type 1 phytochrome**, which is the most abundant form in etiolated seedlings; *PHYB-E* encode the **type II phytochrome** which is synthesized at much lower rates. Transcription of the *PHYA* gene is regulated by **negative feedback** in red light (which causes the formation of Pfr); so when an etiolated seedling (with high levels of type 1 phytochrome) is exposed to light, production of type 1 is greatly reduced as one part of photomorphogenesis (Fig. 3). In addition, type 1 Pfr phytochrome is very sensitive to proteolysis, so the level of the protein quickly reduces when it is not being newly synthesized. Transcription of the *PHYB-E*



Fig. 1. Formation of phytochrome and its interconversion between Pr and Pfr by red and far-red light.

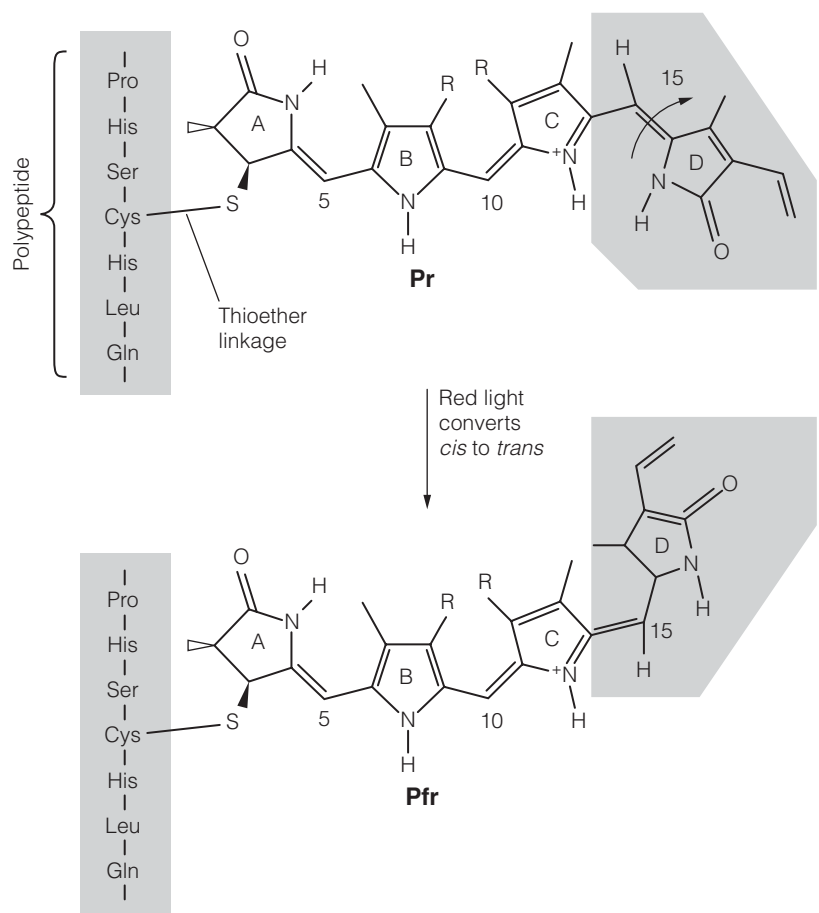
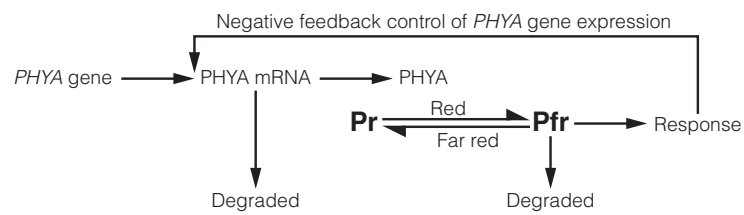


Fig. 2. The structure of Pr and Pfr forms of phytochrome. (Redrawn from L. Taiz and E. Zeiger, Plant Physiology 2nd edn, 1998, Sinauer Associates. © 1998 Sinauer Associates.)



PHYB-E: low level of production, not sensitive to degradation, no negative feedback from response

Fig. 3. PHYA is the form of phytochrome active in the etiolation response of dark-grown seedlings. The PHYA gene is expressed at high levels, producing Pr; when the plant is exposed to red light and Pfr is produced, the plant responds by producing functional chloroplasts and altered growth. PHYA production is stopped by a negative feedback control of the expression of the gene and any Pfr already formed is degraded. PHYB-E are involved in other phytochrome responses and are produced at much lower levels. They are not sensitive to degradation and do not show decreased gene expression after exposure to red light.

genes is not sensitive to light, and type II phytochrome is much less sensitive to proteolysis, so it remains more or less constant in the plant.

Phytochrome responses

The **red:far red ratio** of light changes in different environments and through the day. Daylight, for instance, has an R:FR ratio of 1.19, while at sunset it is 0.96 and under a leaf canopy can be 0.1. Light intensity also varies throughout the day. Phytochrome is involved in a wide range of plant responses to light, including:

- **Etiolation**, in which a seedling or organ rapidly elongates without the production of chloroplasts until it receives red illumination, whereupon **de-etiolation** occurs and functional chloroplasts are produced.
- **Circadian rhythms**. A number of plant processes, including metabolism and leaf positioning follow a periodic cycle of 24 h. The phytochrome response ensures synchrony of the rhythm with daylength.
- **Seed germination**. Many seeds are stimulated to germinate by light in a phytochrome-mediated response. This may require only brief irradiation or prolonged illumination, depending on species. Other seeds (such as wild oat) show germination inhibited by light, though this requires intense irradiation over long periods, and is unlikely to involve phytochrome.

Phytochrome mechanisms

In some processes, changes induced by phytochrome involve changes in **cell turgor**. The circadian (day/night) movement of leaves and petals in some plants are examples (Topic G3). Such **turgor** movements are rapid and involve altered proton pumping and K^+ movement through the plasma membrane (Topic I3).

Phytochrome also regulates changes in **gene expression**. The gene for the small subunit of ribulose biphosphate oxygenase (Rubisco) is a phytochrome-regulated gene involved in the de-etiolation of dark grown seedlings. Red light perception by Pr activates a protein activator of the Rubisco small subunit gene. This activator (called a **trans acting factor**) binds to the promoter region of the gene (the **cis regulator region**) and activates it. Phytochrome regulates a number of genes in de-etiolation and this results in the change from non-photosynthetic plastids (etioplasts) to fully functional, photosynthetic chloroplasts.

G2 TROPISMS

Key Notes

What are tropisms?	Tropisms are plant responses to environmental stimuli including unilateral light and gravity which involve altered growth. They may be positive involving growth towards the stimulus, or negative, away from the stimulus.	
Phototropism	Phototropism is the response of the plant to unilateral light. The photoreceptor is likely to be a plasma membrane protein (NPH-1 in arabidopsis) which is phosphorylated in the presence of blue light. The signal is transmitted to the growing region by auxin redistribution between the light and dark sides of the tissue. Auxin stimulates elongation growth resulting in curvature.	
Gravitropism	Gravitropism is the response of the plant to gravity. Roots are positively gravitropic, while shoots are negatively gravitropic. The stimulus is perceived either by amyloplasts in specialized statocytes in root caps and around vascular tissue or by stretch-activated ion channels and transmitted by auxin redistribution to the growth zone.	
Related topics	Biochemistry of growth regulation (F2)	Phytochrome, photoperiodism and photomorphogenesis (G1)
	Molecular action of growth regulators (F3)	

What are tropisms?

Tropisms are responses to environmental stimuli which involve altered growth. Plants are able to respond to a range of environmental stimuli in order to make optimal use of their environment. *Table 1* describes a range of tropisms and their functions. Tropisms may be **positive** (towards the stimulus) or **negative** (away from the stimulus). All tropisms involve a **receptor** to sense the stimulus involved (a **gravireceptor** or **photoreceptor**, for instance) and a mechanism to transmit that stimulus to the region of the plant in which the altered growth will take place.

Roots are generally positively **gravitropic** (i.e. grow downwards with

Table 1. Tropisms

Tropism	Function
Phototropism	Orientation towards/away from a unilateral illumination
Gravitropism	Growth towards/away from gravity
Hydrotropism	Growth towards water
Thigmotropism	Growth towards touch (e.g. in a tendril curling around a support)
Chemotropism	Growth towards a chemical stimulus

gravity), but non-phototropic. Shoots are generally positively **phototropic**, but either non- or negatively gravitropic. Leaves, orientated at an angle to catch sunlight are **plagiotropic**.

Tropisms have attracted a lot of interest since they were first studied by Charles Darwin in the 1870s. Much of the work has concentrated on the responses of the coleoptile of grasses. The **coleoptile** is a sheath of cells which covers and protects the primary leaf, and shows rapid extension growth (Topic D3).

Phototropism

The photoreceptor

When a **coleoptile** is exposed to unilateral light for a short period (1–2 h) it bends towards the light. The action spectrum of phototropism shows sensitivity to blue light. Early experiments showed that it was located at the tip of the coleoptile, as removal or covering the tip prevented the response. A protein photoreceptor has been identified by studying arabidopsis mutants that do not show phototropisms. These mutants lack **NPH-1**, a plasma membrane receptor protein phosphorylated in response to blue light. The action spectrum of NPH-1 and phototropism correspond almost exactly.

Transmission of the signal

Auxin (Topic F2) has been suggested as the transmitted signal in phototropism. The **Cholodny-Went hypothesis** states that unilateral light causes **auxin redistribution** near the apex, with more auxin on the shaded side. The Cholodny-Went hypothesis was criticized for many years, as it was hard to prove auxin redistribution using the techniques that were available. However, transgenic plants expressing **promoter-reporter gene constructs** (Topic E2) have been used to show that measurable changes in auxin concentrations do occur (*Fig. 1*). It is therefore likely that auxin is one of the regulators that transmits the signal from perception to the growing tissue.

The growth response

Auxin causes increased growth on the dark side of the shoot or coleoptile stimulating acidification of the cell wall, resulting in loosening of the **wall matrix**. Turgor pressure against the loosened wall results in elongation (Topic F2).

Gravitropism

The gravireceptor

The perception of gravity requires the presence of an object that responds (e.g. by movement) to the gravitational field. Such objects are named **statoliths**. Starch-filled plastids (**amyloplasts**) are good candidates, as their density means that they move readily within the cytoplasm in a gravitational field. Amyloplasts move against endoplasmic reticulum (ER) at the cortex (outer edge) of specialized cells termed **statocytes**. *Figure 2* illustrates how statocytes function. The statocytes are in the root cap (in primary roots) or in a layer (the **starch sheath**) adjacent to the vascular tissue. Removal of the root cap results in a loss of sensitivity to gravity in primary roots. The *scr* (*scarecrow*) mutant of arabidopsis, which has no layer of starch-containing cells around its vascular tissue, does not respond to gravity.

There are some plants (the alga, *Chara*, for instance) which appear to have no starch grains and still show responses to gravity. An alternative hypothesis is that plant cells have specialized ion channels that are activated by stretching. Such **stretch activated channels** would sense movement of the protoplast

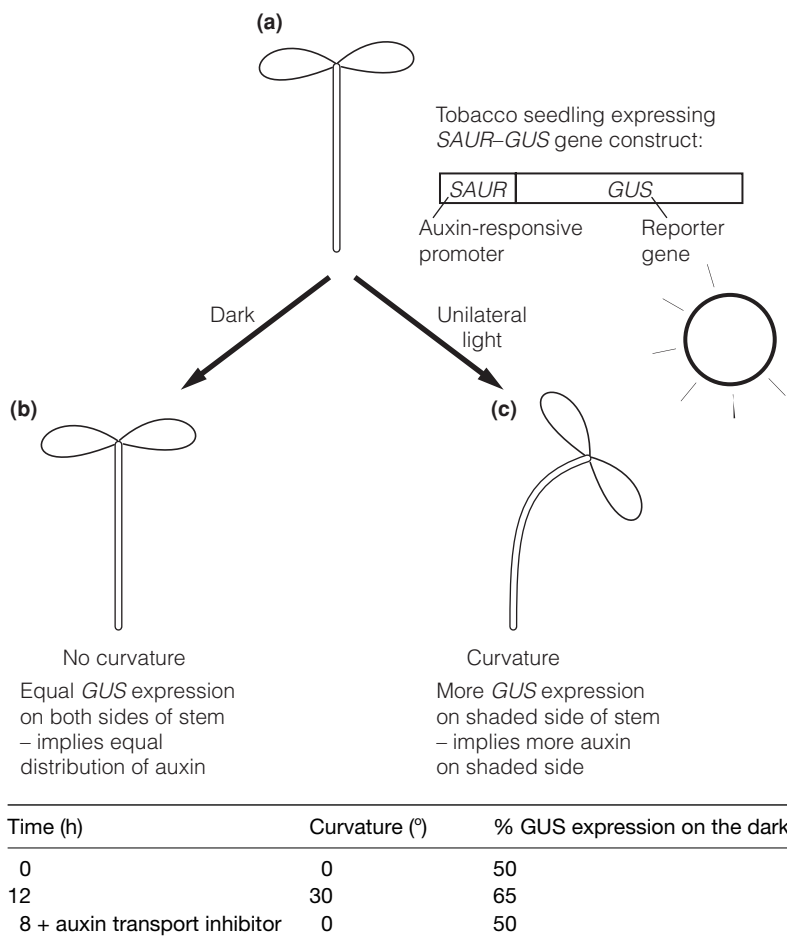


Fig. 1. Use of tobacco seedlings transformed with a construct of SAUR (small auxin up-regulated) promoter (which responds to auxin) and a β -glucuronidase (GUS) gene to detect altered auxin concentrations in phototropism (a). The transgenic plants created were either kept in darkness (b) or exposed to unilateral light (c) and the concentration of auxin measured by estimating the amount of purple-colored product formed when the seedlings were soaked in the substrate for GUS. As the GUS gene is regulated by the SAUR promoter, its expression is proportional to the concentration of auxin; so high auxin ultimately results in a more intense purple coloration.

under gravity and respond by allowing a calcium gradient to be set up. It may also be that stretch activated channels in the ER respond to moving amyloplasts.

Transmission of the signal and growth response

Auxin is suggested to transmit the signal from the statocytes to the growth zone. In roots, high levels of auxin on the lower side inhibit growth, while lower levels on the upper side permit it; in shoots, higher levels on the lower side stimulate growth while lower levels on the upper side inhibit it. Experiments using plants with promoter-reporter gene constructs (Fig. 1; see also Topic E2)

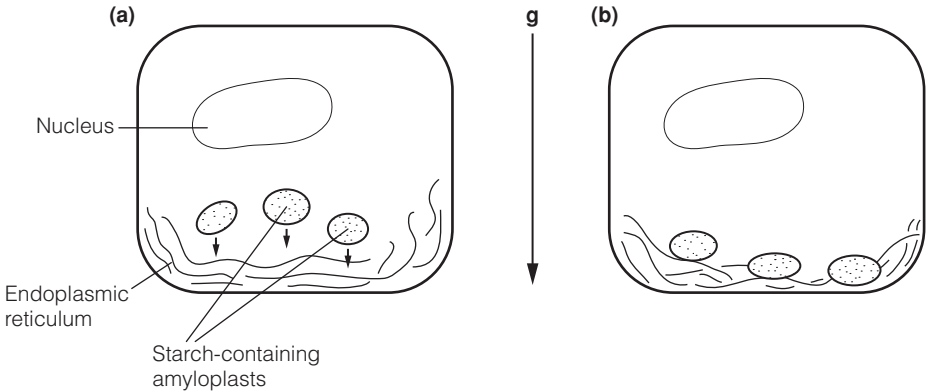


Fig. 2. The starch sedimentation theory of graviresponse. Statocyte cells within the root cap or in a starch sheath around the vascular tissue contain amyloplasts (starch filled plastids) which sediment in the cytoplasm under a gravitational field (g) (a). When the amyloplasts interact with ER in the cell cortex, they initiate a signaling chain resulting in altered growth (b).

have confirmed a redistribution of auxin in seedlings experiencing altering gravitational forces. The mechanism of action of auxin in stimulating growth is described in Topic F2. Calcium has also been suggested to be involved in graviresponse, as transport of calcium from the upper side to the lower side of roots has been shown, and roots will bend towards an agar block containing calcium.

G3 NASTIC RESPONSES

Key Notes

Nastic responses

Nastic responses are movements in which the direction of the stimulus is unimportant. Most nastic movements involve turgor changes in specialized cells, such as thermonastic movements in response to temperature or thigmonastic curling in response to contact.

Nyctinasty

Nyctinasty is movement of leaves or petals in a diurnal rhythm resulting in opening during daytime and closure at night. Movement results from turgor changes in the motor cells of specialized pulvini, where the flexor cells are turgid while the extensors are not and *vice versa*. The movements frequently occur in a circadian rhythm.

Seismonasty

Seismonastic movements are rapid movements of leaves and petioles in response to touch. They involve turgor changes in specialized pulvini triggered by a depolarization of the cell membrane propagated through the phloem tissue.

Related topics

Molecular action of hormones and Tropisms (G2)
intracellular messengers (F3)
Phytochrome, photoperiodism and
photomorphogenesis (G1)

Nastic responses

Nastic responses are plant movements in response to stimuli in which the direction of movement is not related to the direction of the stimulus; this differentiates them from the tropisms (Topic G2). Most nastic movements do not involve growth (i.e. they are not permanent), though the terms **epinasty** and **hyponasty** are used to describe bending of an organ which does involve growth. The others are commonly also called **turgor movements**, as the mechanism of movement is usually a change in turgor of the tissue involved.

A wide range of nastic movements have been described which include:

- **epinasty**, downward curvature of an organ;
- **hyponasty**, upward bending of an organ;
- **thermonasty**, plant movements in response to temperature changes. The petals of some flowers show thermonasty, opening or closing the flower, in response to temperature;
- **thigmonasty**, curling in response to contact with a support. Tendrils of some plants curl around supports with which they contact;
- **seismonasty**, rapid movements in response to touch. The leaves of the sensitive plant, *Mimosa pudica*, fold rapidly when touched;
- **nyctinasty**, 'sleep' movements of petals and leaves in which leaves fold or close at night and open again next morning.

Nyctinasty

Flowers of many species close at night and leaves of some, including the prayer plant (*Maranta*), *Coleus* and French bean (*Vicia faba*) fold together at night and open out in daylight. This rhythm is maintained by an endogenous clock, as it persists even when the plant is placed in continuous light or continuous darkness for several days. The rhythm is therefore said to be **circadian** – an endogenous rhythm of about 24 h reinforced by regular exposure to light and darkness.

Leaf movement occurs at a **hinge region** in the petiole, the **pulvinus**. Pulvini appear as swellings in the petiole that contain **motor cells** surrounding central vascular tissue which drive the movement. Motor cells may be divided into two groups: **extensors** and **flexors** (Fig. 1) which lie opposite to one another. Turgor driven swelling and shrinkage results in movement; thus when the extensors are fully turgid, the flexors are flaccid and *vice versa*. These turgor changes are driven by movement of K^+ and associated cations (Cl^- , organic acids). The ion movements are driven by the *trans*-membrane electrical gradient set up by the plasma membrane proton pump and occur through ion channels in the plasma membrane (Topic I3).

While the mechanism of movement is well understood, the mechanism governing the circadian rhythm is less so, although it is known that

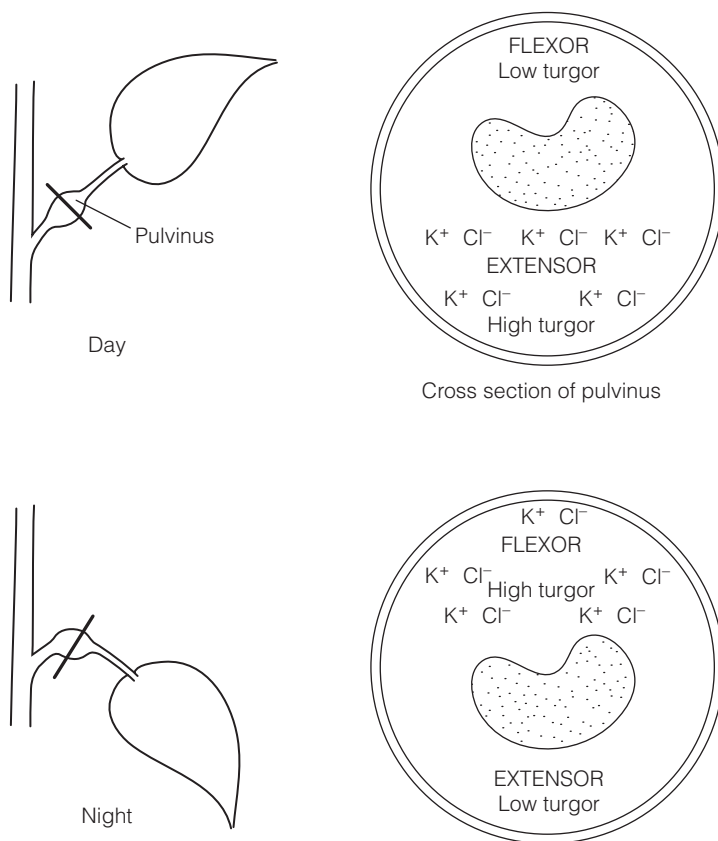


Fig. 1. The role of extensor and flexor motor cells in the pulvinus of a plant (e.g. a bean) undergoing nyctinasty. Note the movement of K^+ and anions into the highly turgid extensor cells in daytime and from these cells into the flexor cells at night, resulting in leaf folding.

phytochrome is involved in entraining ('setting') the endogenous clock to coincide with light and dark in the 24 h period (Topic I1). It is likely that intracellular messengers are also involved. Understanding the clock is likely to be achieved through analysis of mutants of *Arabidopsis* which show altered circadian rhythms.

Seismonasty

Seismonasty is most dramatically seen in sensitive plants, such as *Mimosa pudica*, in which touch will cause leaflets and then leaves to progressively collapse and fold (Fig. 2). It is believed that this deters herbivory, as insects either fall off, or are presented with a less palatable meal. The mechanism of folding is identical to that of nyctinasty – turgor changes in motor cells in pulvini in the petioles of the leaves. However, the trigger is different and a circadian rhythm is not involved. As the leaf collapse is progressive, i.e. it occurs near the point touched initially, then spreads to other pulvini as the leaf is touched more vigorously, there must be a mechanism for the signal to be transmitted across the leaf. An electrical signal has been measured flowing from the point of contact to the petiole. This resembles the action potential of a nerve and may involve the opening and closing of potassium channels that depolarize the plasma membrane of the phloem.

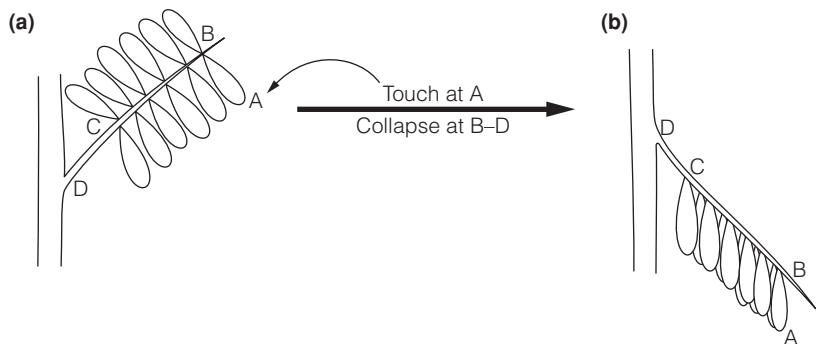


Fig. 2. The leaf structure of the sensitive plant, *Mimosa pudica* includes many pulvini. (a) Touch at point A results in progressive collapse due to turgor changes in these pulvini (b). A measurable electrical potential flows along the phloem between each pulvinus propagated by potassium channels.

G4 ABSCISSION

Key Notes

Biological
importance

Abscission is a controlled process resulting in the removal of plant parts either when they have completed their development or function (e.g. flowers) or in response to adverse conditions (e.g. leaves). The process permits the plant to achieve efficient fruit dispersal and to survive an unfavorable period, particularly drought.

Mechanism

An abscission zone forms at the point of attachment of the organ to the plant. Initially, high auxin levels from young tissue keep the zone inactive; later, the abscission zone develops and becomes sensitive to ethylene as auxin levels decline. Finally, ethylene triggers the release of cell wall degrading enzymes into the wall and the tissues separate at separation layers within the abscission zone.

Related topics

Features of growth and development (F1)
Biochemistry of growth regulation (F2)

Molecular action of hormones and intracellular messengers (F3)

Biological
importance

Abscission describes the removal of plant parts (leaves, flowers, fruit) either in response to environmental stimuli or at specified points in the life cycle in a controlled and ordered manner. In different species, abscission permits survival in temporary adverse conditions, e.g. drought, cold, survival during regular or adverse conditions, fruit and seed dispersal; shedding of damaged organs or those which have completed development such as flowers and fruit.

Leaf abscission occurs in a number of circumstances. Most familiar in temperate climates is the abscission of leaves before winter in perennial deciduous species. Many of the nutrients within the leaf are reabsorbed by the plant and removal of the leaf reduces water loss during the winter when photosynthetic gain would be low and leaf damage (due to frost or pathogens) great. Controlled loss of the leaf and the sealing of the point of separation prevents pathogens from penetrating. Leaf abscission also occurs in many species in drought, thus reducing water loss and enhancing survival. It occurs in older leaves in plants in temperate zones throughout the growing season, and throughout the year in the tropics.

Fruit and flower abscission occur at the end of their development. Loss of the remains of the flower prevents necrosis and pathogen accumulation at the plant surface and removes organs no longer needed after pollen shedding or when no possibility of pollination remains. Fruit abscission results in the dispersal of seeds.

Mechanism

The abscission process ensures two things: the separation and sealing of the point of separation of the abscized organ and the appropriate timing of the abscission event.

The **abscission zone** is recognizable as a slight swelling in the petiole or stalk

attaching the organ to the plant (Fig. 1). Within it, one or two layers of cells, the **abscission layer**, forms as the zone develops. These layers become sensitive to ethylene and develop the secretory machinery necessary to deposit cell-wall-digesting enzymes into the wall space between them. It is the separation of these layers that results in abscission at a well-defined location resulting in a ‘clean break’ of minimal surface area.

Young leaves produce large amounts of auxin (Topic F2); this diminishes as the leaf matures, or if it is damaged (Fig. 1). Drought (wilting), damage, short days or declining temperatures stimulate ethylene production and diminish auxin production in the leaf. With high auxin and low ethylene, the cells of the abscission zone remain inactive. As the leaf production of auxin diminishes, the abscission zone becomes sensitive to ethylene and begins to develop. Finally, when ethylene levels are sufficient, the layer is activated and enzymes (e.g. polygalacturonases, cellulases) are secreted and digest the cell walls holding the leaf to the stem. The break is then sealed preventing water loss and pathogen penetration. While abscisic acid (ABA; Topic F2) was named because of a supposed involvement in abscission, it is now known that it acts only indirectly in this process by accelerating ethylene production.

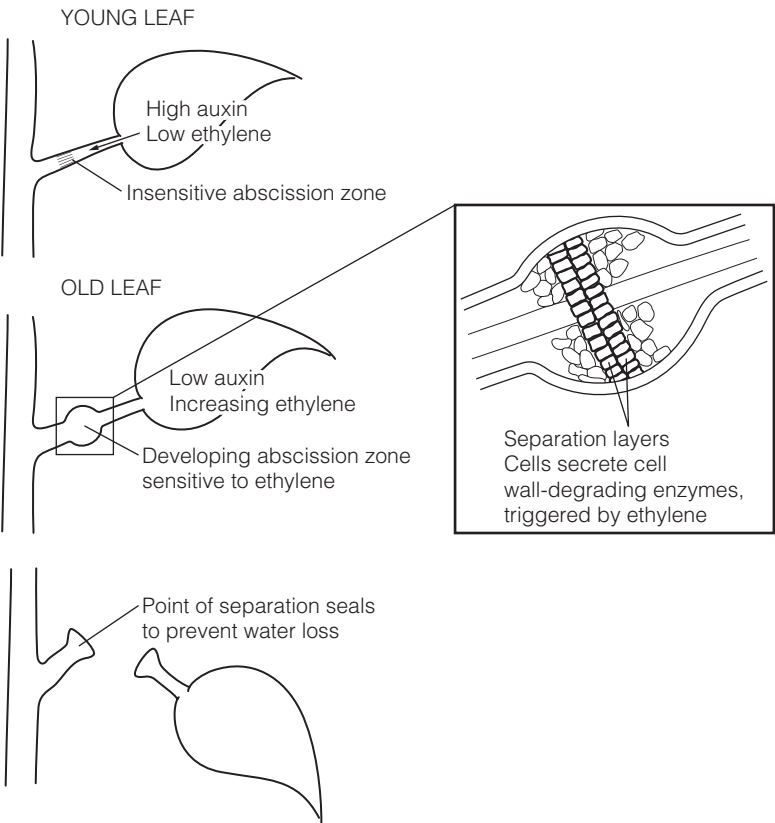


Fig. 1. Development of an abscission layer. In young leaves, high auxin keeps the abscission layer insensitive to ethylene. Later, auxin production declines and the abscission layer develops and becomes sensitive to ethylene. Finally, rising ethylene triggers the secretion of cell wall hydrolytic enzymes into the separation layers and the two layers separate.

G5 STRESS AVOIDANCE AND ADAPTATION

Key Notes

Plants as sessile organisms

Plants are sessile – they cannot move to avoid adverse environments or predators. They show adaptations to permit survival without movement. These include plasticity of development, ability to regenerate new organs and a range of defences to deter herbivory and pathogenesis.

Herbivory and pathogenesis

Plants deter herbivores by physical barriers such as a cellulose cell wall, waxy cuticle, lignification, hairs and stinging hairs, and also by chemical deterrents including compounds which make the plant unpalatable or poisonous or disrupt digestion.

Toxic ions

Many nutrient ions become toxic at high concentrations, others are almost universally toxic. Plants tolerate toxicity by one of four mechanisms: tolerance permits growth and metabolism in the presence of the toxin; exclusion where barriers at the root surface or root/shoot interface prevent uptake; amelioration, the dilution or chelation of the toxin; and phenological escape, where growth only occurs in favorable seasons.

Gaseous toxicity

Gaseous toxins include oxides of sulfur and nitrogen and ozone. Gaseous pollutants have the direct effects of cell and membrane damage and the indirect effects of soil acidification and inhibition of nutrient uptake.

Waterlogging

Plant roots growing in waterlogged soil become anoxic and growth is inhibited. Some species form aerenchyma, either constitutive or induced by ethylene. The root meristem develops anaerobic metabolism.

Salinity

Salinity causes both toxicity and osmotic problems. Most plants have little or no salt tolerance. Salt tolerant species may produce non-protein amino acids as compatible solutes to overcome osmotic problems, some form salt glands that excrete the salt.

Related topics

- | | |
|---|---|
| Features of growth and development (F1) | Movement of ions across membranes (I3) |
| Abscission (G4) | Uptake of mineral nutrients by the plant (I4) |
| Plants and water (I1) | |

Plants as sessile organisms

The vegetative form of many higher plants is sessile; they cannot respond to changing environments by moving to new locations. Therefore, they must be able to tolerate adverse conditions. The range of adaptations varies between species: some characteristics are shown by almost all plants, but many others are only present in a few plants that tolerate particular environments. Plant devel-

opment is plastic; in other words, it is not predetermined to a rigid path as mammalian development is. The presence of persistent embryonic tissue (meristems; Topic C1) and the fact that new meristems can be induced, means that plants can respond to a changing environment, wounding, etc, by altered growth. The form of growth may also alter, for instance to a lower, more compact form in response to high wind speeds. Plant hormones (Topic F2) are essential to plasticity as they integrate environmental stimuli with development.

Herbivory and pathogenesis

Plants are exposed to many herbivores, ranging from mammals to insects. Defenses include:

- **Physical barriers and defenses.** Cellulose cell walls; waxy cuticles; spines, hairs and stinging hairs; bark and secondary thickening; silica deposition.
- **Chemical defenses.** Formation of toxic or unpalatable secondary products (*Table 1*; see also Topic J5). Many of the compounds indicated are synthesized rapidly in response to herbivory or pathogen attack and plants may acquire resistance to further attack. **Salicylic acid** is produced by infected tissue and induces **defense genes** elsewhere in the plant. Fragments of the pathogen and the plant cell wall produced during the initial stages of infection by hydrolytic enzymes from the pathogen, called **elicitors**, also act to initiate cell signaling pathways resulting in the activation of defense genes, including those for the enzymes responsible for the production of many of the compounds included in *Table 1*.

Table 1. Compounds involved in defenses against herbivory

Type of compound	Examples	Effects
Phenolic compounds	Coumarins	Cytotoxic and irritant
	Lignin	Indigestible
Terpenes	Pyrethrin	Insecticidal
Tannins	Various	Bind proteins and inhibit digestion
Isoflavonoids	Phytoalexins	Fungicidal/bacteriocidal
Alkaloids	Cocaine, morphine, nicotine, caffeine	Toxic and/or physiologically active drugs
Non-protein amino acids	Various	Inhibit protein digestion
Proteinase inhibitors	Various	Inhibit proteinases in the herbivore, preventing digestion of the plant material

Toxic ions

Most nutrient ions, at high enough concentrations, become toxic to plant growth. Others, such as **Cd** and **Al** are almost universally toxic, even at relatively low concentrations. *Table 2* lists some major toxic ions in soil. Toxic ion concentrations may arise when the toxin is added to the soil (e.g. by atmospheric pollution or in industrial waste) or when soil conditions change (e.g. acidification will release **Al** from non-toxic complexes to free solution).

In general terms, toxicity occurs when growth is inhibited or a plant is prevented from completing its life cycle. Toxicity may result from (i) inhibition of **resource acquisition** (e.g. water uptake, the uptake of essential nutrients or of photosynthesis), or (ii) inhibition of the **utilization of resources** (e.g. inhibition of enzymes, damage to cell membranes, etc.).

Table 2. Some toxic ions and their effects

Toxic ion	Circumstances in which toxicity occurs	Effect
Aluminum	Acid soils below pH 4	Inhibition of root growth; binds to phosphate, DNA, RNA, disrupts membranes and ATP-metabolism
Boron ^a	Soil contaminated with fuel ash	Chlorosis and necrosis of tissue
Copper ^a	Mine-spoil contaminated land	Damaged root cell membranes; inhibition of growth
Magnesium ^a	Soils with high Mg/low Ca	Causes Ca deficiency
Manganese ^a	Acid soils	Causes Ca and Mg deficiency; inhibits shoot growth
Sodium	Saline soils; irrigated soils	Competes with potassium for uptake and osmo-regulation; osmotic effects; stomata remain open
Chloride	Saline soils; irrigated soils	Osmotic effects; competes with other anions for uptake giving deficiency

^a Essential at low concentrations, toxic at high.

Tolerance to toxicity

Plants may respond to the presence of a toxic ion in a number of ways. For many plants, severely inhibited growth and death will occur, but others show adaptations that permit them to survive. Such plants may only grow slowly, but because they can occupy an environment that other plants cannot, they are able to benefit from that lack of competition. Plants may tolerate toxicity in one of four ways presented in Table 3. Hyper-accumulator species that are able to tolerate and accumulate large amounts of toxic ions are considered in Topic N5 (Bioremediation).

Gaseous toxicity

Gaseous toxicity may occur when plants are exposed to toxic gases from industry or volcanoes. Pollutants include **ozone**, **sulphur dioxide**, **nitrogen oxides** and **carbon monoxide**. Their effects may be direct, e.g. inhibited stomatal action, damage to surfaces, inhibition of enzymes; or indirect, e.g. altered soil properties preventing nutrient uptake. Table 4 gives the direct and indirect effects of some major atmospheric pollutants.

Table 3. Adaptations to toxicity

Tolerance	Adaptations which permit normal growth and metabolism in the presence of the toxin, even when in the tissues. This includes modified enzymes which are not inhibited by the toxin. Species which take up the toxin are termed includers
Exclusion	The toxic ion is not taken up by the plant. This may be because of an effective barrier at the root surface (through the possession of very specific ion transport systems) or internally, particularly at the root–shoot interface. Species which take up the toxin into the root tissue and prevent it from moving to the shoot (e.g. at the root endodermis) are termed ‘includer/excluders’
Amelioration	Some ‘includer’ plants minimize the effects of a toxic ion by modifying or storing it away from the key enzymes of growth and metabolism, usually in the vacuole. Amelioration may involve: compartmentation of the ion in the vacuole; chelation, in which the ion is complexed with an organic compound (for instance citrate or malate) and then deposited in the vacuole; and dilution in which the ion is diluted to below toxic concentrations
Phenological escape	A species may escape a seasonal stress by growing in the other seasons when the stress is minimal, for instance species growing in zones only covered by extreme tides in a salt marsh

Table 4. Effects of atmospheric pollutants

Pollutant	Direct effect	Indirect effect
Sulfur dioxide (precipitates from the atmosphere in rain as sulfates, including sulfuric acid)	Interveinal chlorosis (yellowing between leaf veins); death of leaves of forest trees	Acidification releases toxic aluminum in soils giving aluminum toxicity; Uptake of other nutrients inhibited
Oxides of nitrogen (precipitates from atmosphere in rain as nitric acid)	Black, necrotic lesions on leaves	Acidification releases toxic aluminum in soils giving aluminum toxicity; Uptake of other nutrients inhibited; Formation of NO in light from NO ₂ results in release of O which reacts with O ₂ to form ozone (O ₃)
Ozone	Weakens palisade cell walls and results in necrosis, particularly near stomata; damages plasma membranes and thylakoids; inhibits photosynthesis	Produces reactive chemicals that cause genetic mutation

Waterlogging

Waterlogged soils contain low concentrations of oxygen which inhibit the growth of roots. Some species of plants contain aerenchyma, gas spaces in the root which both reduce the overall root oxygen demand and may supply oxygen to the growing tip. Aerenchyma may be formed constitutively, i.e. is always present, for instance in paddy rice. In other species, such as maize, it is induced by ethylene, produced in response to low oxygen. It is formed by the death of cells of the root cortex. Cells at the meristem do not die, but respond to lack of oxygen by the induction of anaerobic metabolism (fermentation). This involves induction of a number of enzymes, including alcohol dehydrogenase, which removes ethanol, a toxic product of fermentation, from the tissues.

Table 5. Salt tolerance in plants

Type and examples	Sodium concentration tolerated	Examples of mechanisms shown by some species
Glycophyte (beans, maize)	<50 mM	None
Salt-tolerant glycophyte (barley, wheat)	<200 mM (tolerated but growth retarded)	Limited salt accumulation to shoot; Production of solutes to provide osmotic balance with external solution of NaCl
Halophytes (sugar beet) (<i>Suaeda maritima</i>)	<500 mM (tolerate, but growth retarded) <700 mM (tolerated and growth stimulated up to 350 mM)	Make solutes like non-protein amino acids and accumulate ions in the vacuole to balance external osmotic effects; Endodermis restricts transport from root; Absorption of ions from xylem flow; Succulence; Salt glands actively secrete salt from the leaves

Salinity

Toxicity due to NaCl has considerable impact on agriculture. Both Na^+ and Cl^- are toxic and occur in excess where land is exposed to sea water, in many arid zones and on irrigated land where evaporation exceeds precipitation or irrigation. Declining water tables due to deforestation and intensive agriculture and resulting salinization are an increasing agricultural problem.

The chief causes of damage by salt are: osmotic stress and dehydration; inability to regulate stomata (as Na^+ replaces K^+); nutrient ion deficiency; and Cl^- toxicity. Plants show a wide range of salt tolerance, from **glycophytes**, able to tolerate small amounts of NaCl, to **halophytes** able to tolerate ≥ 500 mM. Plants able to grow in high salt conditions show a number of adaptations which are summarized in *Table 5*.