Plant Movements

29

Rama Sisodia and Satish C Bhatla

Terrestrial plants are sessile and are incapable of changing their location. Yet, plants can sense their environment and can respond to sensory information through visible movements to optimize their survival, growth, and reproduction. The earliest findings published in this field were from Charles Darwin in 1880 in his book entitled *The Power of Movement in Plants* that explored the phenomenon of phototropism. Plant movements can be defined as the changes in the spatial orientation or conformation of an organ or its parts. Plant movements include movements toward light, opening and closing of flowers, growth of developing roots in search of water and nutrients, etc. In fact, inflorescence, fruits, and shoots are all capable of moving by sensing changes in environment, thereby adjusting their position, function, and behavior accordingly. Plant movements are extremely slow and often undetectable. Classical examples of visible plant movements include the response of sensitive plants like “touch-me-not” (*Mimosa pudica*) and the carnivorous Venus flytrap (*Dionaea muscipula*). In addition to whole organ, the movement of single cells is also possible which includes, for example, the movement of guard cells (which regulates the stomatal pore size), as well as growth of the pollen tube through the style. Such movements are caused by motor cells, driven by changes in pressure from within the cells exerted against the cell walls. Pressure causes changes in the dimensions of individual cells or tissues which results in distinctive movements. Plant movements are classified as:

1. **Tropic movements**: These movements occur in response to environmental signals. The direction of these movements is determined by vectorial signals, such as gravity and light.
2. **Nastic movements**: These predetermined movements occur independent of the direction of the stimulus. The location and structure of the motors driving these movements determine the direction of these movements.

S. C Bhatla, M. A. Lal, *Plant Physiology, Development and Metabolism*,
https://doi.org/10.1007/978-981-13-2023-1_29

29.1 Tropic Movements

Tropic movements are initiated by external directional signals that are perceived by the sensory receptors. These tropic responses are described as positive and negative tropisms based on whether the movement is toward or away from the signal, respectively. **Gravitropic** movements are directed by the perception of gravity by specialized sensory cells and **anisotropic** response of motor cells. **Phototropism** is guided by the direction of light. These include the movements of leaves and flowers that track the position of the sun. Such movements are also called as **heliotropic** movements, and the phenomenon is referred to as heliotropism. Climber plants have tendrils that wrap around their support in response to friction when they encounter mechanical support. Such touch (actually friction)-generated responses are called as **thigmotropic** responses. External signals can also be chemical signals that direct plant movements. Such movements are termed as **chemotropic** movements. They include movement of pollen tube toward the egg cell in response to chemical signals released from synergids. **Hydrotropism** refers to the growth movements in response to unilateral stimulus of water.

29.1.1 Phototropism

Several plant movements are driven by the necessity of plants to maximize capture of sunlight for driving photosynthesis. Light-directed movements, termed as phototropism, have been a subject of investigation since Charles Darwin published his book *The Power of Movement in Plants* in 1880. Among all environmental signals, light is one of the most versatile signals and varies along four parameters, namely, quality (wavelength), quantity (fluence, i.e., photons m^{-2}), direction, and duration (photoperiod). Phototropic responses can be termed as positive or negative depending upon whether the plant responds by growing toward or away from the light source. Aerial plant parts, including coleoptiles, hypocotyls, etc., are positively phototropic, while the tendrils of climbing plants are negatively phototropic. Interestingly leaves are **plagiotropic** organs orienting themselves at angles intermediate to the direction of light. Growth of roots is mostly non-phototropic, i.e., not directed by light. The stem of *Hedera helix* is negatively phototropic in the juvenile stage and prefers shade, while the mature plant is positively phototropic. The light-driven movements include subcellular movements as well as those of organs and whole plant. The opening and closing of stomata in the presence or absence of light are examples of light-driven movements at cellular level. Light is also known to direct the growth of seedlings toward photosynthetically active radiation (PAR) as seedlings transit from the use of stored reserve food (heterotrophic mode of nutrition) to becoming autotrophic. This is exemplified by the growth pattern of etiolated seedlings grown in dark and light (Fig. 29.1). Stem of an etiolated seedling is long and spindle-like as it grows out in search of light. Upon exposure to light, de-etiolation triggers reduction in shoot length and increase in radial growth. Shade growing plants are also known to accelerate their shoot growth towards

Fig. 29.1 (**a**) An etiolated sunflower seedling with elongated stem and persistent apical hook. (**b**) A de-etiolated seedling with reduced stem growth and straightening of apical hook

ambient light. Nascent leaves are also affected by the intensity of light and reorient themselves to maximize the interception of light. Thus, most terrestrial plants use sunlight as signal to direct their growing organs for optimal utilization of light source. Phototropism is a growth response to a light gradient. Under laboratory conditions the growing plant organ bends toward unilateral light (Fig. 29.2). However, under normal light, as plant receives light from all sides, the bending is still seen as the fluence rate varies from one side to the other, creating a gradient. Differences in fluence rate influence phototropic response of bending of plant organ. The light gradient across a plant varies according to the optical properties of the tissue as well as the variation in incident light. The former properties relate to complex interactions between light and the pigments which cause scattering, reflection, or diffraction of light as it passes through the cells. The pulvinus located at the leaf base plays an important role in perception of the light signal for directing movement of lamina to face the light. Relocation of chloroplasts within the mesophyll cells in relation to light is also mediated by light. In high light intensities, plants prevent potential damage of the chloroplasts by aligning along the anticlinal walls, i.e., parallel to the incident light. In low light, on the other hand, chloroplasts are aligned along the periclinal walls, i.e., perpendicular to the incident light, in order to maximize absorption (Fig. 29.3). The relationship between fluence and response is best understood on analyzing fluence-response curves obtained by analyzing plant response to varying amount (fluence) of total light (Fig. 29.4). A classical phototropic response to unidirectional light shows an initial positive response (fPIPP—first pulse-induced positive phototropism) represented by a peak called the first peak or first positive curvature, and it occurs in response to a pulse of low fluence of light.

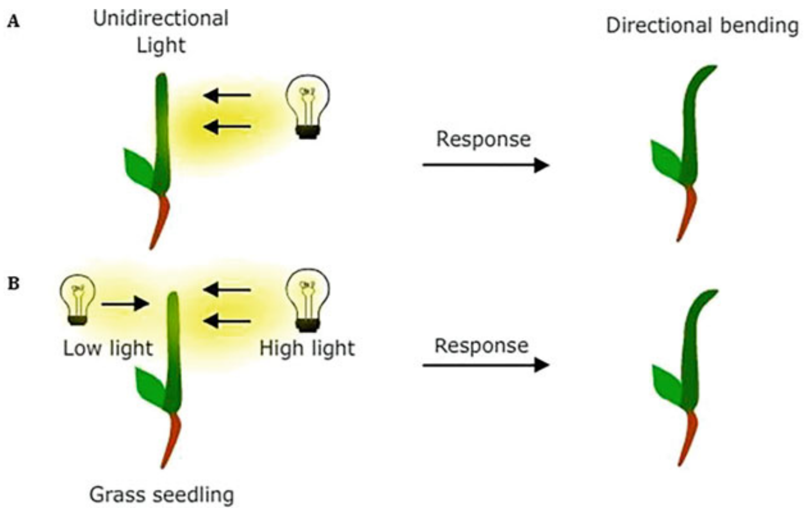

Fig. 29.2 (**a**) Illumination by unilateral light causes the grass coleoptile to bend toward it; (**b**) illumination provided from all sides, but higher intensity of light from right also results in bending toward greater illumination

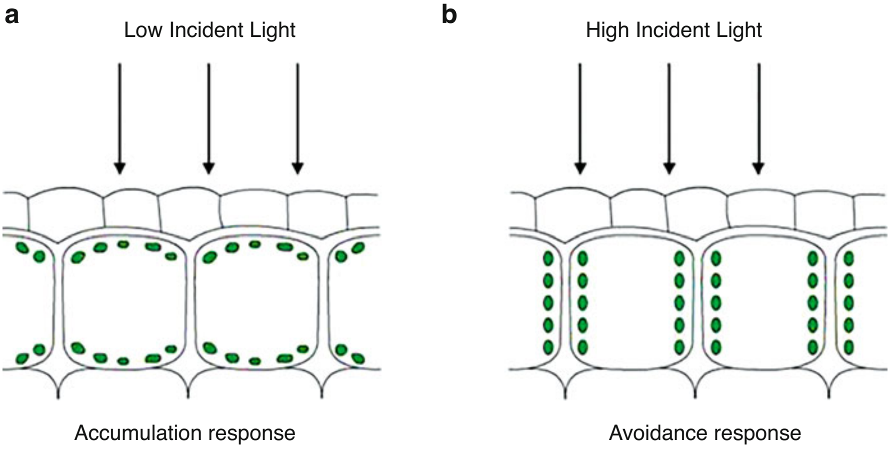

Fig. 29.3 (**a**) In low light conditions, chloroplasts orient along the periclinal walls perpendicular to the incident light. (**b**) Under high light, the avoidance response involves chloroplast alignment along the anticlinal walls, parallel to the incident light, thereby minimizing exposure to light

There is again a rise in the response curve that forms a second positive response (sPIPP—second pulse-induced positive phototropism) on exposure to light of higher fluence. The third phase of phototropic bending response (time-dependent phototropism; TDP) occurs when the growing shoot is exposed to moderate to high

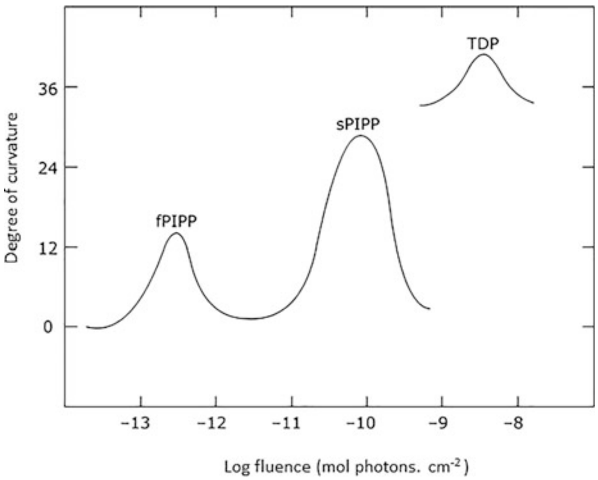

Fig. 29.4 A typical phototropic fluence-response plot. fPIPP first pulse-induced positive phototropism, sPIPP second pulse-induced positive phototropism, TDP time-dependent phototropism

illumination (unidirectional) over an extended period. It is important to note that the photoreceptor responsible for transducing this light signal is located in the cytoplasm and the chloroplast movement is mediated by cytoskeleton. Analysis of action spectra for light mediated movement of coleoptile of plants such as *Avena sativa*, *Zea mays*, etc. has revealed that they share a common photoreceptor—a flavoprotein called **phototropin**. The absorption spectrum of phototropins shows a peak in the blue and UV-A regions of the spectrum. Phototropins mediate a number of blue light-induced responses such as phototropic movements, stomatal opening-closing, and redistribution of chloroplast in response to intensity of light. Phototropins have been studied in details in several plants including *Arabidopsis thaliana*, *Avena sativa*, and *Pisum sativum.* Initially, phototropin was characterized in an *Arabidopsis* mutant *non-phototropic hypocotyl* 1 or *nph I*, which is unable to respond to the phototropic stimulus and lacks the 120 kDa membrane protein. It was later renamed as phototropin 1 (phot1) because of its role in phototropism. *Arabidopsis* contains two phototropins—phot1 and phot2—that have partially overlapping roles in regulating phototropism. Phototropins have two segments (Fig. 29.5): the N-terminus has the photosensory domain that contains two LOV domains that bind with flavin mononucleotide (FMN) making the phototropin sensitive to light. LOV domains share sequence homology to a number of eukaryotic and prokaryotic protein motifs involved in sensing light, oxygen, and voltage (hence the name LOV). The LOV domains consist of five antiparallel β-sheets and two α-helices that bind to FMN. The C-terminus has a serine-threonine kinase activity. In dark phototropin is unphosphorylated and inactive. The light signal initiates a photochemical reaction which is perceived by phototropin. This sets up a signal transduction chain beginning with the autophosphorylation of phototropin and initiates a phosphorylation cascade. In addition to phototropin, another photoreceptor called **neochrome** has been isolated from the fern *Adiantum capillus-veneris* that has the properties of both

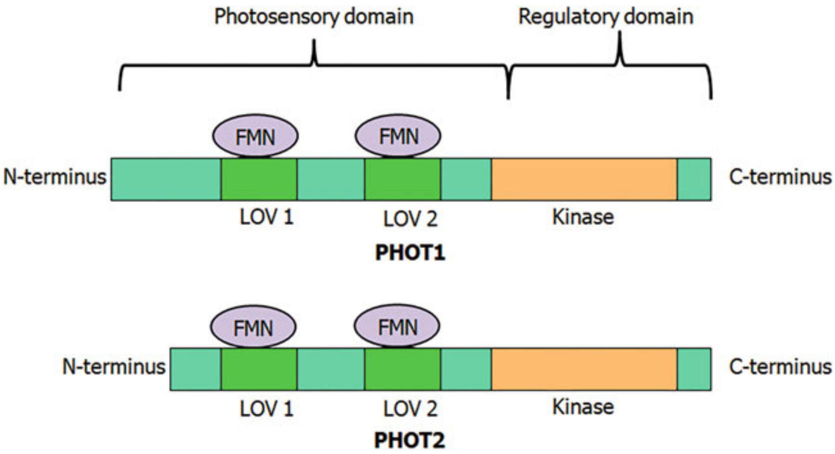

Fig. 29.5 PHOT1 and PHOT2 of *Arabidopsis* contain two LOV (light, oxygen, voltage) domains. These bind to the cofactor flavin mononucleotide (FMN). C-terminal contains a kinase domain

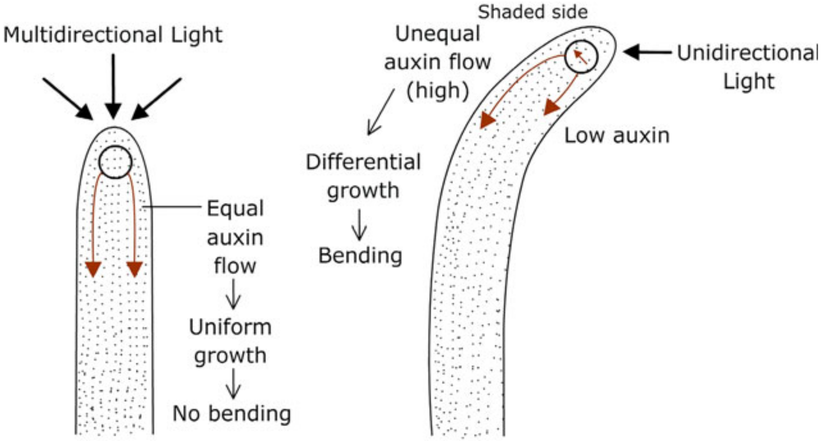

Fig. 29.6 Differential auxin distribution as a response to unidirectional light leading to bending response. Increased auxin accumulation on the shaded sides enhances growth and consequent bending of the coleoptile toward light

phytochrome and phototropin and is regulated by both red and blue light. Both neochromes and phototropins are known to operate in ferns, mosses, and algae.

The phototropic response involves differential growth on one side of organs that responds to the light signal. The differential growth is mediated by lateral distribution of auxin as it moves from the apex basipetally to other areas. Upon unilateral illumination, an unequal distribution of auxin ensues and causes auxin accumulation and subsequent enhanced growth at the shaded side (Fig. 29.6). In *Zea mays*, the immediate tip area of the shoot apex (1–2 mm) is involved in auxin production, and the phototropic redistribution of the auxin occurs in the subapical region. The asymmetric distribution of auxin by phototropin is mediated by disrupting the distribution of auxin efflux facilitator protein called PIN. The latter is usually located at the basal end of cells associated with xylem cells and facilitates the vertical transport of auxin. Following phototropic stimulus, it has been experimentally shown that the basal location of PIN is disrupted in the cortical cells on the shaded side leading to accumulation of auxin and subsequent unequal growth and phototropic bending. As much as 20% higher concentration of auxin is known in *Brassica oleracea* hypocotyl on the shaded side with accompanying increase in auxin-regulated genes including those that code for α-expansins that regulate cell expansion.

29.1.2 Gravitropism

Gravity represents an omnipresent, constant force that acts on all organisms including plants, directing their growth and movements (Fig. 29.7). These movements are guided by gravity vector and are differentiated on the basis of vertical growth as **orthogravitropic**, as exhibited by primary root and shoot, or by the angle with which the organ grows (**plagiotropic**). The subterranean rhizomes exhibit a horizontal two-dimensional movement and are termed **diagravitropic**. The orthogravitropic movement in a single dimension facilitates the movement of the primary root vertically downward in search of water and minerals. Similarly, the young shoots grow vertically upward for optimal absorption of light and carbon dioxide for photosynthesis, and they are termed negatively geotropic in contrast to roots (positively geotropic). As the plant matures, the growth pattern shifts to plagiogravitropic mode allowing the plant to expand three-dimensionally, increasing

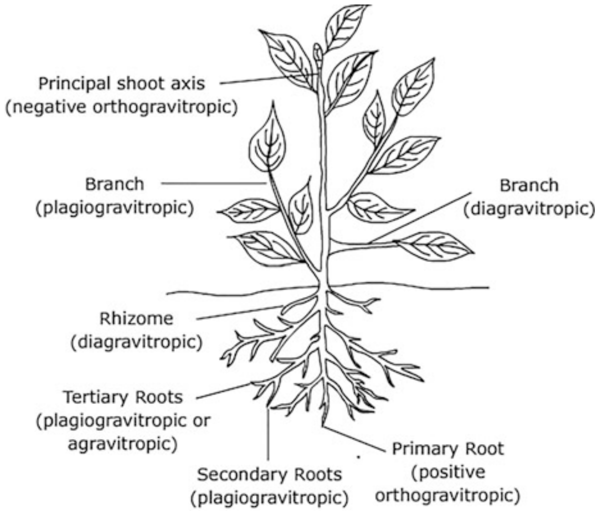

Fig. 29.7 A variety of gravitropic responses direct growth and movements of plants

the supply of resources exponentially. The diagravitropic portions of the plants allow movements in two dimensions with the outgrowth of buds and leaves in case of shoots and adventitious roots growing out and thus expanding in the plant territory. Gravitropic movements are also modified by light with both the presence or absence of light and the direction of light modifying the response. Thus, young roots of *Zea mays* seedlings exhibit horizontal or diagravitropic response in dark. However, in the presence of red light, its roots grow vertically down changing their response to positive geotropic. In other cases, red light may increase or decrease the gravitropic response. Direction of light also modifies the gravitropic response. Unidirectional illumination from a direction opposite to the gravity signal results in an intermediate response curvature that depends on the magnitude and direction of the two vectors—light and gravity. In roots, the gravitropic response is also modified by the water potential gradient (hydrotropism) and also by mechanical stimulation (thigmotropism). The ability to perceive gravity signal resides in specialized cells called **statocytes**, which contain sedimentable starch grains called **statoliths**. Tissues that contain statocytes are called as statenchyma. These are located in the columella cells inside the root cap or calyptra. In stem and other aerial plant parts, the statocytes are located in the starch sheath. Statoliths consist of a group of starch grains enclosed within amyloplasts (Fig. 29.8). Usually amyloplasts are not mobile within the cell. However, they can move in the direction of gravity in columella cells of the root cap as well as in the starch sheath or endodermal cells. Amyloplasts' mobility is evident in the cells of the inner cortex of stems and the pulvini as well as in the motor tissue located at the nodes of grass stem. Starch grains are heavier than the cytoplasm and therefore tend to cluster under the influence of gravity near the lower surface (inner) of the statocyte (force sensor hypothesis). The weight and size of starch grains disturb the subcellular organization of the cytoskeletal elements and organelles such as endoplasmic reticulum, creating a physiological asymmetry in the cell or

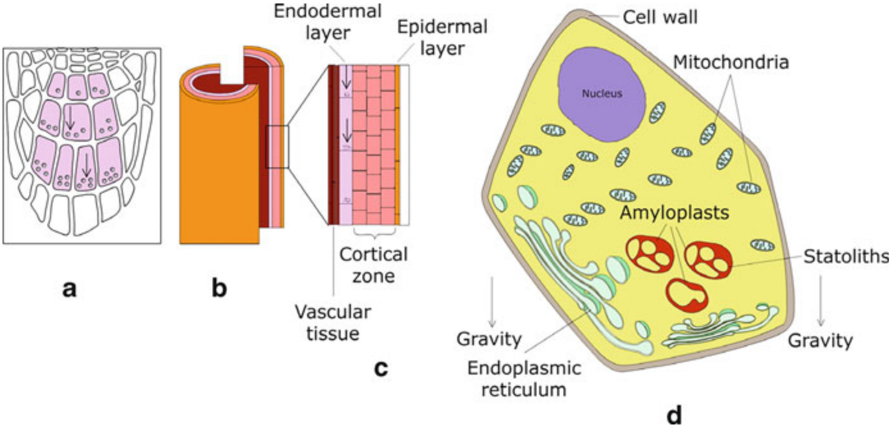

Fig. 29.8 Schematic illustration of root tip (**a**) and shoot (**b**, **c**) in longitudinal section showing the direction of sedimentation of starch grains in response to gravity. (**d**) Statocytes containing amyloplasts that have established a cytoplasmic asymmetry in the cell in response to gravity

tissue. It has been shown that position (or inclination) of statoliths (and not their mass) is responsible for gravity perception in plant cells. Statoliths respond to gravity like liquid, and not like a granular material. They respond to the slightest change in angle as a liquid would do to attain a horizontal position. Thus, the hypothesis of statocytes as "force sensors" is now replaced by "position sensor" hypothesis. The gravity signal is perceived, transduced, and transmitted to generate a response in the zone of elongation of growing root and shoot (Fig. 29.9). The transmission and response of the gravitropic signal involve lateral redistribution of auxin in the elongation zone. The horizontal orientation of the plant shoot or root causes redistribution of auxin toward its lower side. This causes relatively more growth toward the lower side in comparison to the other side causing the negatively geotropic organ, such as the shoot or the coleoptile, to turn upward. In contrast, in positively geotropic organs, such as roots, the higher concentration of auxin in roots

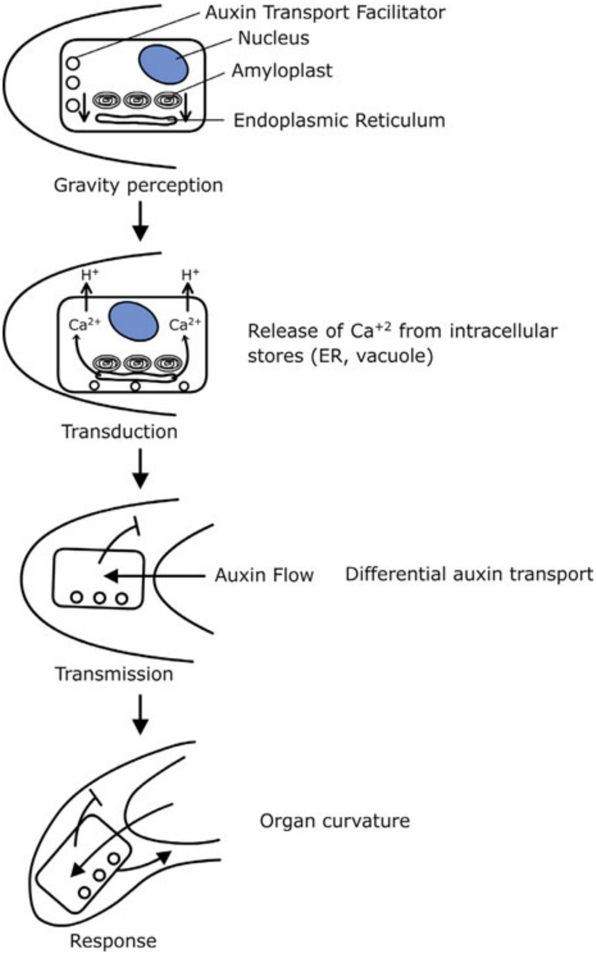

Fig. 29.9 Phases of generation of gravitropic response: perception, transduction, transmission, and physiological response

inhibits elongation on the lower side in comparison to the upper side causing the root to grow downward. The path of auxin transport in root is often explained with the "auxin fountain model." Auxin synthesized in the shoot is transported basipetally down through the vascular tissue into the root and then acropetally toward the root tip. In the columella, the direction of the auxin flow is reversed, and it moves basipetally in a uniform manner into the cells of the root cortex in the zone of elongation. However, when roots are displaced horizontally, the auxin flow in the columella is redistributed laterally toward the lower side of the root. The higher concentration of auxin in the lower side inhibits elongation relative to the upper side, thus causing roots to turn down.

29.1.3 Chemotropism

External signals, including certain chemicals, are also known to drive plant movements. The growth of the pollen tube through the style is guided by the chemical secreted by the cells lining the style. Within the ovary the pollen tube moves toward the egg steered by the chemical cues provided by the degenerating synergids. These chemical signals include proteins like stigma/style cysteine-rich adhesion (SCA)—a lipid transfer protein that is secreted by the epidermal cells lining the style and is known to play a role in growth and adhesion of the tube in the stylar tract. Another protein that plays a role in directing the growth of the tube is **chemocyanin** (a member of the phytocyanin family of blue copper proteins). Pollen-attracting peptides have been identified in *Torenia* as cysteine-rich polypeptides, called **LUREs**, as attractants derived from synergid cells.

29.2 Nastic Movements

Nastic movements are nondirectional movements that are driven by growth or turgor changes and are genetically predetermined. Autonomic internally directed nastic movements include those shown by developing buds as they swell and open up. Paratonic nastic motions are externally directed such as those of the leaves and flowers in responses to changing light and temperature. **Nyctinastic** movements or night movements involve folding of flowers and leaves with the onset of night. Other nastic movements include rapid **seismonastic** movements and **thigmonastic** movements in response to touch. **Photonastic** movements such as folding and unfolding of leaves, opening and closing of flowers, etc. are synchronized by dark to light transition. In contrast, the **skotonastic** movements are synchronized by the light to dark transition. **Thermonastic** movements occur in response to temperature fluctuations. For example, flowers of the plant *Crocus* (Iridaceae) open under ambient temperature and close with lowering of temperature. **Chemonastic** movements such as opening and closing of guard cells in response to the carbon dioxide in the substomatal cavity are mediated by changes in the guard cell osmoticum. Signals may also be generated by growth processes, like movement of root hairs through the soil, seed germination, initiation of leaf primordia, and shoot development.

29.2.1 Epinasty and Hyponasty

Nastic movements are also displayed by developing organs, such as leaves, petals, and sepals, which exhibit structural and physiological differences between their adaxial (upper) and abaxial (lower) sides. As these organs develop, they may exhibit unequal growth expansion on the two sides, resulting in upward (**hyponastic**) or downward (**epinastic**) growth (Fig. 29.10). Such bending movements are mediated by unequal growth and are part of normal development of the plant. For example, leaves of tomato plant growing in soil flooded with water exhibit epinastic movement of leaves. These are under endogenous control, and though the growth is irreversible, the bending of the organ is reversible. It has now been proved that hyponastic and epinastic movements are controlled by the differential distribution of auxin and ethylene. Similar epinastic and hyponastic movements are also exhibited by developing vegetative and floral buds. The dome-shaped vegetative apex initially produces leaf primordia by more rapid growth on the lower side, which becomes convex, while the upper side becomes concave. Such unequal growth results in the developing leaf primordia forming a sheath around the young shoot primordium, resulting in a compact bud formation (Fig. 29.11). As the growth proceeds, the lowermost leaves change from hyponastic to epinastic growth. Expansion of the upper side changes the leaf architecture from convex/concave to a typical flat leaf lamina. Elongation of the internode results in the separation of the newly flattened leaf lamina, which now becomes a part of the shoot. The sequential change of the leaf growth from hyponasty to epinasty is under endogenous control and enables leaves to expand and photosynthesize. Similarly, the transition from vegetative to reproductive growth results in the vegetative shoot apex transforming into floral bud

Fig. 29.10 Epinastic movement in tomato leading to downward bending of leaves in response to stimulus (flooding)

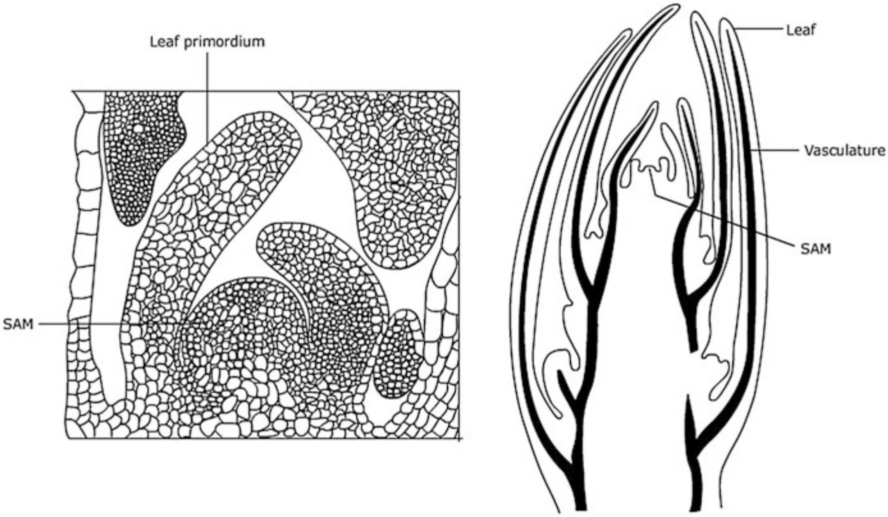

Fig. 29.11 Developing shoot bud with ensheathing leaf primordia that transit from epinastic to hyponastic growth. *SAM* shoot apical meristem

Fig. 29.12 Geotropic movement of flower stalks during development in *Papaver rhoeas* L.

primordium, and instead of leaves it produces flower parts: sepals, petals, stamens, and carpels. Since the function of flowers is to cause pollination, exposure of the stamens and ovary, which is a prerequisite to the process, occurs with the epinastic growth leading to unfolding of the calyx and corolla. In addition to these floral parts, other structures also exhibit epinastic movements. These include the epinastic movement of flower stalk of poppy plant as it curves down by differential growth forming a hook (Fig. 29.12). As the flower opens, growth is reversed resulting in hyponastic movement and straightening of the flower. Interestingly, the poppy flower responds to rain by downward bending of peduncle and loss of petal turgor which, therefore, causes closure of the flower, thereby preventing pollen loss.

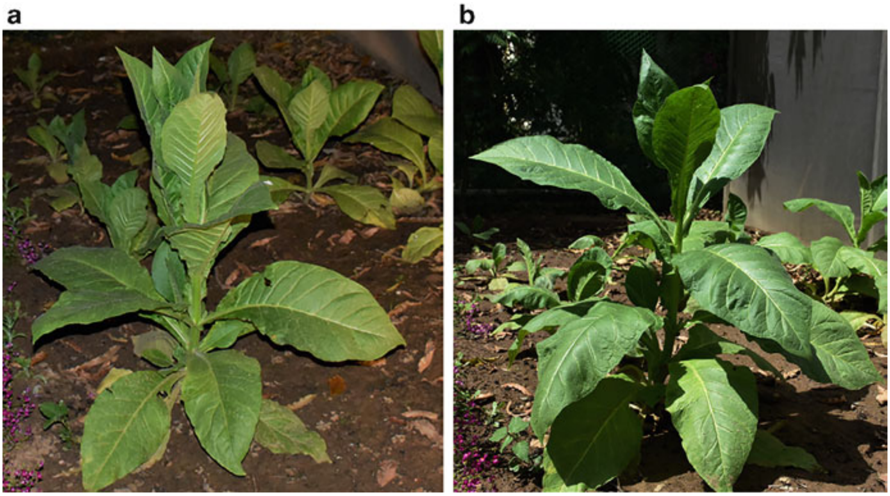

Fig. 29.13 (**a**) Nyctinastic movement of leaves in *Nicotiana tabacum*. Expanded/opened leaves during daytime. (**b**) Clasping of upper leaves at night

29.2.2 Nyctinasty

Nyctinastic movements (Gr. *nyctos*, night + *nastos* = closure) refer to the rhythmic sleep movements driven by reversible turgor pressure changes. During the day, plant leaves are typically in the horizontal or open position. The position changes during the night with the leaves acquiring a closed position. Leaves of plants like tobacco, clover, mint, etc. exhibit such movements (Fig. 29.13).

29.2.3 Thermonasty

Plant movements controlled by temperature fluctuations are called as thermonastic movements. Flowers of *Tulipa* sp. (Liliaceae) and *Crocus* sp. (Iridaceae) open on increasing the temperature and close on lowering the temperature by as less as 1–3 °C around the ambient temperature (Fig. 29.14). Closure of perianth is mediated by changes in the extension growth of the abaxial and adaxial surfaces of the perianth itself in response to temperature fluctuations.

29.2.4 Thigmonasty

"Touch-me-not" (*Mimosa pudica*) plant with its pinnately compound leaves is a popular example of a plant that exhibits thigmonastic movements, i.e., movements in response to touch (Fig. 29.15a, d). The touch stimulus is perceived by the **pulvinus** located at the base of each leaflet and is transmitted through sieve tubes. The

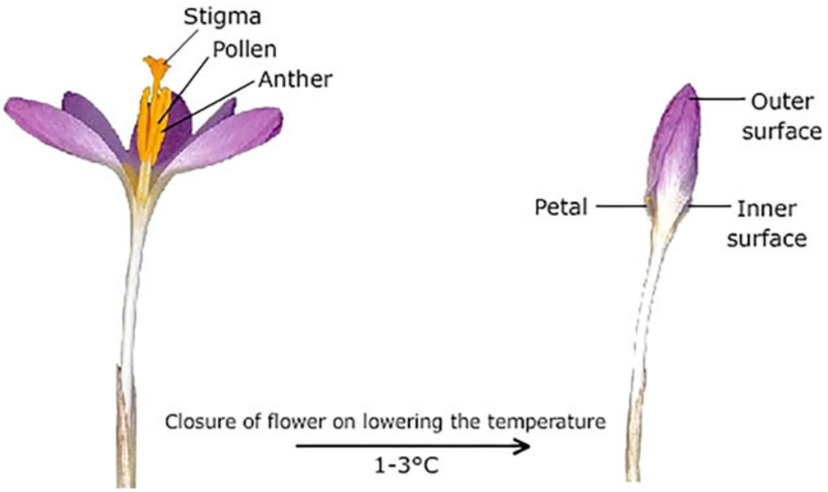

Fig. 29.14 Thermonastic movement of *Crocus sativus* flower in response to temperature fluctuation. Flower petals close upon lowering the ambient temperature by 1–3 °C

stimulus includes ABA (abscisic acid), and ABA controlled ion transport leading to their diffusion into the upper region of the pulvinus causing efflux of K^+ ions and water into the intercellular space. The resulting loss of turgidity of the cells in the upper region of pulvinus causes the downward (closure) movement of the leaflets. The opening of the leaves takes place by the gain of turgor with active pumping of K^+ back into the cells (Fig. 29.15b, c). The inability of dark-grown plants to exhibit seismonastic responses suggests that these movements are ATP-dependent. K^+ efflux is regulated by Ca^{+2} ions stored in vacuoles. An action potential is propagated from cell to cell causing neighboring leaves to respond in a similar manner. In *Arabidopsis*, four genes have been identified that are upregulated when the plant is touched (TCH1–4). Three of these encode proteins linked to Ca^{+2} signaling, but TCH4 encodes xyloglucan endotransglucosylase, which modifies the structure of the xyloglucan components of the cell wall. It has been shown that treatment of tendrils with specific jasmonates causes them to coil in an identical manner to the touched tendrils. This effect was shown to be independent of ethylene and auxin.

29.3 Autonomous Movements

Interestingly there are few plant movements that are guided by both external and internal signals. These include movements that are under the control of circadian clock that are defined by the 24-hour diurnal rhythms of light and dark periods. Examples of such movements include the unfolding (and refolding) of flowers during the day, which synchronizes the opening of flowers for optimal periods of pollination. The circadian movements are synchronized and rephrased by environmental signals such as light or temperature.

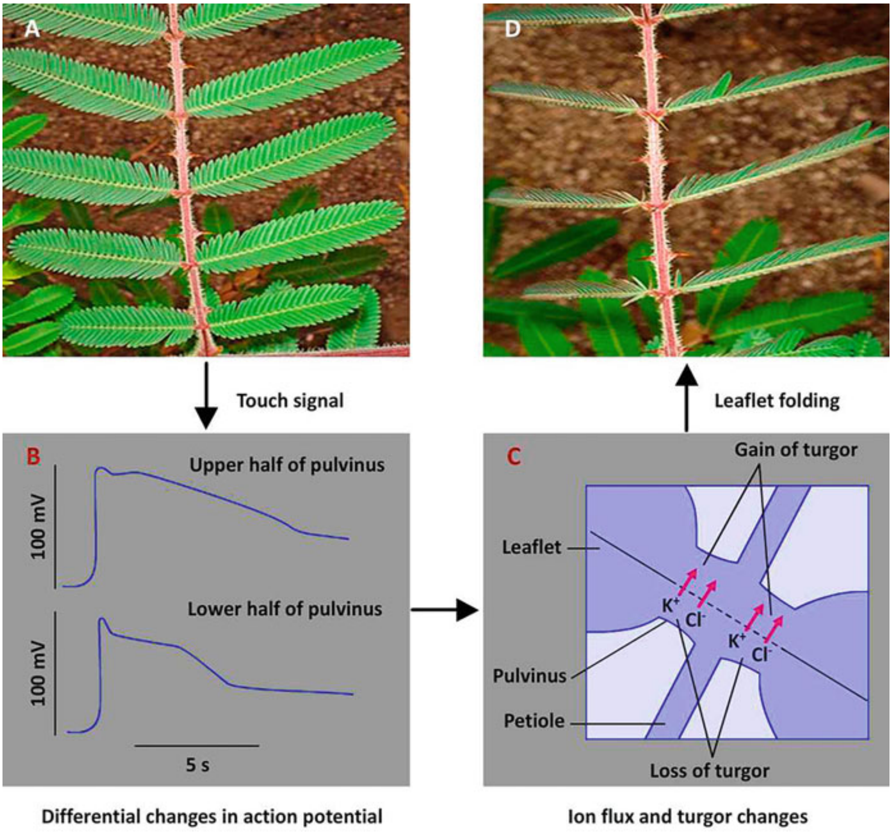

Fig. 29.15 (**a**, **d**) Thigmonastic movements of leaflets of "touch-me-not" (*Mimosa pudica*) plant. (**b**, **c**) Mechanical stimulation activates ion channels that cause differential changes in action potential and closure of the leaflets

29.3.1 Diurnal Movements and Circadian Rhythms

Plants are routinely exposed to diurnal cycles of light and dark and exhibit rhythmic behavior in association with these changes. These include rhythmic movements of leaves and petals and opening and closing of stomata that influence the metabolic processes of photosynthesis and respiration. Flowers in the members of Onagraceae, Cactaceae, Convolvulaceae, and Oxalidaceae exhibit spectacular diurnal movements. Such flowers close by inward curvature of the perianth leaves and open by reversing the curvature. These movements are mediated by growth and take place as the flower/inflorescence develops. The rhythms alternate with a regular periodicity of 24 h and are called as **circadian rhythms** (derived from Latin, circa *diem* meaning approximately a day). Circadian rhythms are expressed continuously even in the absence of external controlling factors, e.g., upon transfer of plants from daily light and dark cycles to uniform conditions of either continuous dark or light. The rhythms are governed endogenously by an oscillator or a biological clock that is coupled to a variety of physiological processes. The biological clock is unaffected by temperature and can function normally under a variety of climatic conditions. It is, therefore, known to exhibit temperature compensation. In nature, the period of the circadian rhythms tends to be closer to 24 h (Fig. 29.16). Characteristic features define circadian rhythms. These include the period which refers to the time between two points in the repeating cycle, e.g., between consecutive peak (or maxima) and trough (or minima). Phase refers to any point on a cycle recognizable by its relationship to the rest of the cycle. Amplitude is the degree to which the observed response varies from the mean, and the range is the difference between the maximum and minimum values. The amplitude of a biological rhythm can change, but the period remains unchanged. Under constant conditions the length of the plant cycle is not influenced by any environmental factor and is called as the free-running period. Under such conditions the rhythms depart from the typical 24-hour period, either gaining or losing time, depending on whether the period is shorter or longer than 24 h. However, under natural conditions, the plants are exposed to a fluctuating environment, and, therefore, the rhythms also exhibit the same period and are said to be **entrained** to its environment. The **entrainment** can be brought about by a number of factors with light being the strongest modulator. The environmental signals or cues are called as **zeitgebers**, a German term for "time givers." The environmental zeitgebers are required to initiate the expression of the internally generated rhythms. In case the rhythms damp out with time, an exposure to a zeitgeber is required to restart them. It is important to note that the biological clock itself does not damp out, rather a coupling between the endogenous oscillator and the physiological response occurs. A single oscillator is often coupled to more than one circadian rhythm, which are themselves often out of phase with each other. In circadian rhythms, the operation of endogenous oscillator initiates response at a particular time of the day. A single oscillator can be coupled to multiple circadian rhythms, which may even be out of phase with each other. The entrainment of the molecular clock is mediated by specific photoreceptors. Both blue and red lights are effective in entrainment, indicating the role of both phytochromes and

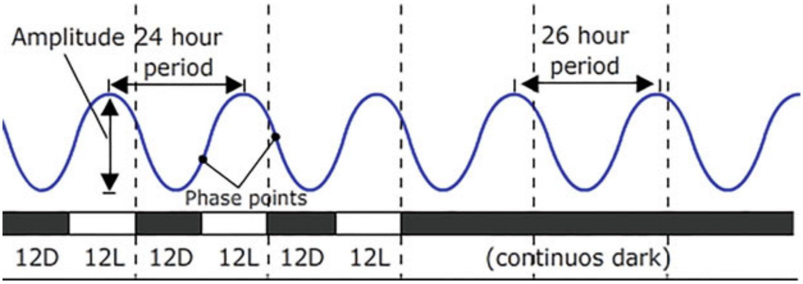

Fig. 29.16 A typical circadian rhythm entrained to a 24-h light-dark cycle

cryptochromes in this process. In *Arabidopsis*, phytochrome C is involved in clock entrainment, whereas CRY1 and CRY2 proteins function as intermediates during the signaling of phytochrome-mediated clock entrainment.

29.3.2 Photoperiodism

The endogenous circadian clock of the plant enables it to monitor the time of the day and determines the specific time of the day at which a specific physiological or molecular event has to occur. This ability of a plant to detect day length and thus allow a seasonal response to occur is called as **photoperiodism**. Circadian rhythms and photoperiodism are modulated by cycles of light and dark periods. Geographic locations determine the length of the day and night. At equator, the length of the day and night is equal, and as one moves toward the poles, the days become longer in summer and shorter in winter (Fig. 29.17). Plants detect these seasonal changes and influence their photoperiodic responses. The understanding of plant photoperiodic responses was initiated with the work of Wightman Garner and Henry Allard in the 1920s as they conducted a series of experiments at the US Department of Agriculture, Beltsville, Maryland, on a mutant variety of tobacco Maryland Mammoth. The plants grew up to a height of about 5 m but failed to flower in the summer. However, the plants produced flowers in winter or on artificially providing short-day conditions during summer. It was, therefore, concluded that the length of the day was critical in determining the flowering response and later this could also be confirmed for a number of other plant species as well. Extensive experimentation

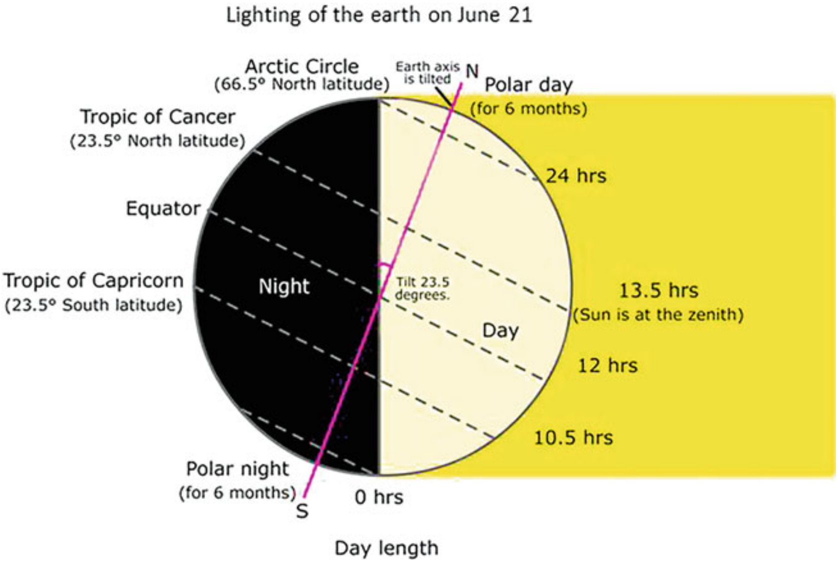

Fig. 29.17 The relative length of day changes from equator to poles

lead to the establishment of the idea that flowering in plants is modulated by photoperiod and plants can be classified under different categories. 1. Short-day plants or SDPs: Plants flowering only under short days are called as qualitative SDPs. Incase flowering is accelerated by short days these plants are called quantitative SDPs. 2. Long-day plants or LDPs: Plants which flower only under long-day conditions are called as qualitative LDPs. Incase flowering is accelerated by long days the plants are called quantitative LDPs. Flowering in LDPs is promoted only when the length of the day exceeds a certain duration called as critical day length. The critical day length determines the flowering response in both LDPs and SDPs. Long-day plants flower when the day length exceeds or the night length is less than a critical duration in a 24-hour cycle. Short-day plants flower when the day length is less than or the night length exceeds a critical duration in a 24-hour cycle. LDPs, for example, many varieties of wheat (*Triticum aestivum*), monitor the lengthening of the day as spring progresses toward summer, and as the critical day length is reached, the plant flowers. SDPs, for example, *Chrysanthemum morifolium*, on the other hand, flower in fall when the day length is less than a critical day length. The absolute value of the critical day length, however, varies among plant species. A detailed account of photoperiodism has already been provided in Chap. 25.

29.4 Mechanisms of Movement

Plant movements can be caused by a variety of mechanisms mediated by turgor pressure changes, changing growth dynamics, movement by contraction, and change in conformation.

29.4.1 Turgor-Mediated Movement

Plant movements are caused by a group of cells and tissues referred to as motors. Motors may be single-celled and are responsible for movements, for example, that of the guard cells, growth of the root hairs, and pollen tubes. Multicelled motors operate to move entire leaves, roots, apical buds, flowers, fruits, and entire shoots. The motor tissue is either separate from the organ that it moves or it is part of the moving and growing tissue. For example, motor tissues driving heliotropic and sleep movements are specialized and distinct from the organs they move. Cells of such motor tissues extend reversibly to mediate such movements. In contrast motor tissues driving the pollen tube growth are made up of cells that expand irreversibly. A common feature of all motor-driven movements is that these are based on physical force exerted against the cell walls, i.e., these movements are driven by changes in turgor pressure within the motor cells. However, turgor-driven movements in immature cells occur with the irreversible extension of cell walls and increase in cell volume and growth, while in mature cells these movements result in reversible and elastic extension of their cell walls. The variations in plant movements arise due to differences in the signals that initiate them as well as due to the location of the motor cells and the mechanisms by which they respond. These movements rely on the turgor-mediated changes in a specialized motor organ called pulvinus that occurs at the base of the compound leaves in the families Leguminosae and Oxalidaceae. The motor cells of pulvinus are made up of large thin-walled parenchymatous cells that use turgor-mediated reversible changes in size and shape to alter the position of the leaf. The opposite sides of the pulvinus are called as flexor (upper) and extensor (lower) regions. At night, the extensor cells lose their turgor, while the flexor cells gain turgor resulting in the petiole turning toward the stem leading to closure of the leaf. During the day, the extensor cells regain their turgor, while the flexor cells lose their turgor resulting in the petiole turning away from the stem axis and leaf opening up. The relative swelling and shrinkage of the flexor and the extensor regions of the pulvinus thus regulate the movement of the leaves or leaflets. The relative position of the flexor and the extensor regions in the pulvinus is dependent on whether the closure movement is acropetal or basipetal. Nyctinastic movements are defined by blue light, phytochrome, as well as endogenous rhythms. The changes in the turgor pressure within the pulvinus are mediated by massive redistribution of potassium ion (K^+) between the symplast and apoplast regions of both the extensor and the flexor regions of the pulvinus. Depolarization of the membrane results in the K^+ channels to open and cause an influx of K^+ ions into the extensor cells, thereby increasing their turgor. A model integrating the role of phytochrome and secondary messengers, like inositol triphosphate, has been proposed to explain leaf movements of nyctinastic plants. Light signal activates the phytochrome and enhances the level of secondary messengers, inositol 1,4,5-triphosphate (IP_3) and diacylglycerol (DAG). The latter stimulates the release of Ca^{+2} into the cytosol and causes phosphorylation of several cytoplasmic proteins that further causes the extrusion of protons from the cell. A proton motive force is generated thereof and causes the diffusion of K^+ ions into the cell.

29.4.2 Growth-Mediated Movement

Plants, being immobile, maximize their growth and survival by directing their growing active parts toward available resources. The growing root and shoot tips move forward through the soil and aerial environment, respectively, by means of motor tissues located in the elongation zone just behind the apex, with newer cells continually being added by the dividing cells of the apical meristems. Change in direction of the actively growing plant organs can also be achieved by growth-mediated curvature of the elongating shoot apex. Differences in growth rates in the opposite sides of the motor tissue as well as acceleration and inhibition of cell elongation in one region of the organ vs. the other side result in curvature and thereby bring about change of spatial orientation of the organ. Forward movement of root hairs, as it directs its growth around the soil particles, is affected by a shift in the pattern of growth of root tip toward the side opposite to the one that encounters the soil particles, thus growing around the obstacle and moving forward.

29.4.3 Movement by Change in Conformation

Change in the architecture and conformation also leads to movements such as those exhibited by the stomatal guard cells. The anisotropic structure and differentially thickened cell walls of the guard cells cause changes in their volume, thereby leading to opening and closing of stomata. The guard cells thus represent single-celled motors that operate by conformational changes. Multicellular motors, such as those that operate in the leaves of grasses, cause extensive changes in leaf conformation. These include motors located on the sides of the midribs along the major veins and which consist of a single row of large bulliform cells. As the grass leaves dry up, these bulliform cells dry up and cause the leaf lamina to roll along its length. When water becomes available, the cells inflate and thus flatten the leaves.

29.4.4 Movement by Contraction

In addition to movement effected by change in conformation, some movements are caused by contraction, for example, the movement of bulky storage organs, such as bulbs and corms, through the soil caused by specialized contractile roots. The contractile roots are characterized by the presence of an upper unbranched non-absorbing, thick fleshy part and a lower branched distal part. The radial expansion of the fleshy part of the roots caused by the growth of the parenchyma cells of the cortex creates a space in the soil facilitating the movement of the storage organ (Fig. 29.18).

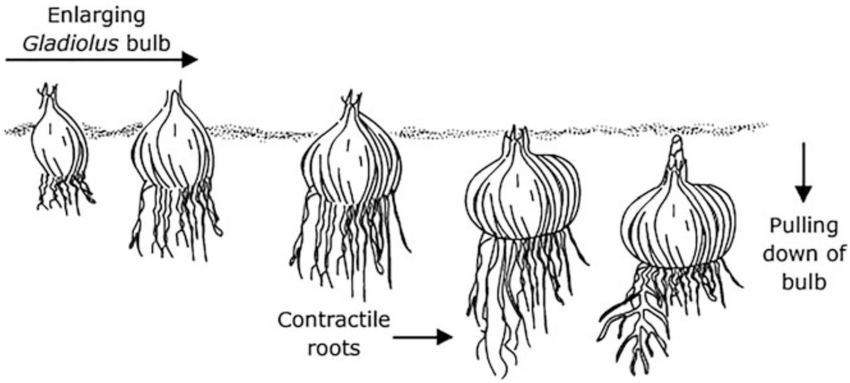

Fig. 29.18 Enlargement-associated movement of the *Gladiolus* bulb through the soil. The contractile roots contract to pull down the attached bulb through the soil

29.4.5 Twining Plants

Other interesting examples of motors are those that operate in twining plants in which tendrils locate and attach to suitable support by forming extensive circumnutations. The tendrils may be modified branches as in *Bryonia* (Cucurbitaceae) and *Passiflora* (Passifloraceae) or even leaves as in *Lathyrus aphaca* or *Pisum sativum* (Fabaceae). The leaf lamina is highly reduced in such cases and is, in fact, limited to the midvein that functions as a tendril. The photosynthetic function of the leaves is performed by stipules. The tendrils resemble the torsion spring of mechanical watches, and differential contraction and expansion along the two sides of the tendril establish a dorsiventral asymmetry between the two flanks of the tendril resulting in progressive coiling of the tendril. Contraction of the tendril below the support results in drawing the plant toward the support. The thigmonastic response of the tendrils is rapid and highly selective. The epidermal protuberances found in Cucurbitaceae members, such as *Luffa cylindrica*, represent the receptors that elicit thigmonastic responses. The epidermal cells of the tendril are interconnected by plasmodesmatal connections that integrate the protoplasts into a symplast, thus allowing rapid transmission of the thigmonastic response.

29.5 Prey-Driven Movements

Several plants that lack chloroplasts are unable to follow an autotropic life and survive as parasites on autotrophic plants or are carnivorous that derive nutrition from their entrapped insect preys. These can be classified as:

- Holoparasites that are dependent on host plants for their organic nutrition, e.g., dodder (*Cuscuta*)
- Hemiparasites that have the ability to produce their own organic assimilates but are dependent on the host for absorbing water and solutes from the soil, e.g., mistletoe (*Phoradendron*)

Carnivorous plants are generally found in nitrogen-deficient habitats and obtain their nutrition by capturing and killing insects and absorbing the digested proteins of those insects.

29.5.1 Parasitic Plants

Parasitic plants locate their prey using a variety of mechanisms. For example, plants like the Santalaceae members—the mistletoes (*Viscum album* and *V. cruciatum*) and *Loranthus acacia* and *L. europaeus* from Loranthaceae—produce brightly colored and tasty fruits attracting birds. The birds eat the fruit, but the indigestible seed sticks onto their beaks and is generally wiped off against a tree branch where it gets deposited. On germination, the seedling invades the host tissue and uses a

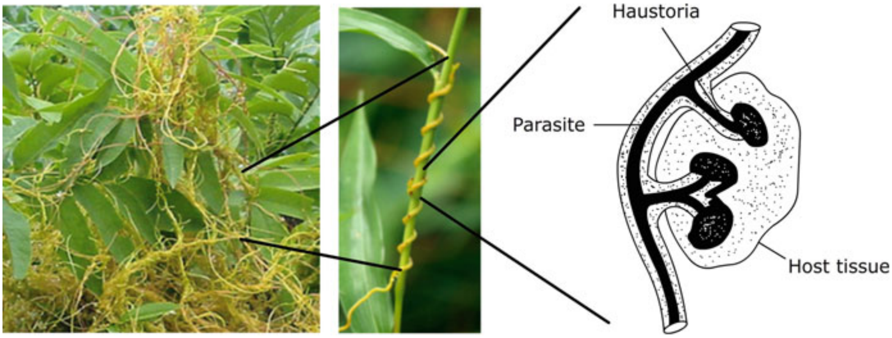

Fig. 29.19 *Cuscuta* or dodder plant coils around its host plant, drawing nutrition using a haustorium

haustorium to absorb nutrition. The parasitic dodder plant (*Cuscuta*, Convolvulaceae) is an obligate holoparasite that is dependent on its host plant to complete its life cycle. It produces innumerable seeds that germinate, and the seedling grows initially using the limited supply of nutrients available in the seed. The seedling twines around a suitable host attracted by the smell of a volatile compound or chemoattractants emitted by the host itself (Fig. 29.19). These chemical cues are volatile terpenoids such as α-pinene, β-myrcene, and β-phellandrene. As a contact is established, the parasitic epidermal and parenchymatous cells differentiate to form a secondary meristem and prehaustoria called as adhesive disk. Signals, like mechanical pressure, osmotic potentials, and phytohormones, such as auxins and cytokinins, initiate and control prehaustoria formation. Secretion of adhesive substances like pectins and other polysaccharides by the prehaustoria enhances adhesion which is further reinforced by the secretion of sticky substances such as arabinogalactan proteins by the host plant. Host cells also respond by an increase in the cytosolic calcium concentration initiating a signal transduction cascade. The prehaustoria develops into parasitic haustoria that penetrate the host stem by exerting mechanical pressure supported by degradation of host cell walls by the hydrolytic enzymes such as pectinases and cellulases. The haustoria invade the host tissue, establishing functional connections to the xylem and phloem of the host. *Cuscuta* forms a continuous symplastic connection with its host. The haustoria form an interface where nutrients, solutes, and carbohydrates as well as macromolecules, such as mRNA, proteins, and viruses, are exchanged between the host and parasite.

29.5.2 Carnivorous Plants

Carnivorous plants have developed strategy to entrap their mobile prey. The preys are attracted to the traps by means of sight or smell. Traps are made up of modified leaves and can be passive traps or active traps driven by mechanical triggers. Plants with mobile-active traps are the snap traps of Venus flytrap (*Dionaea muscipula*) and

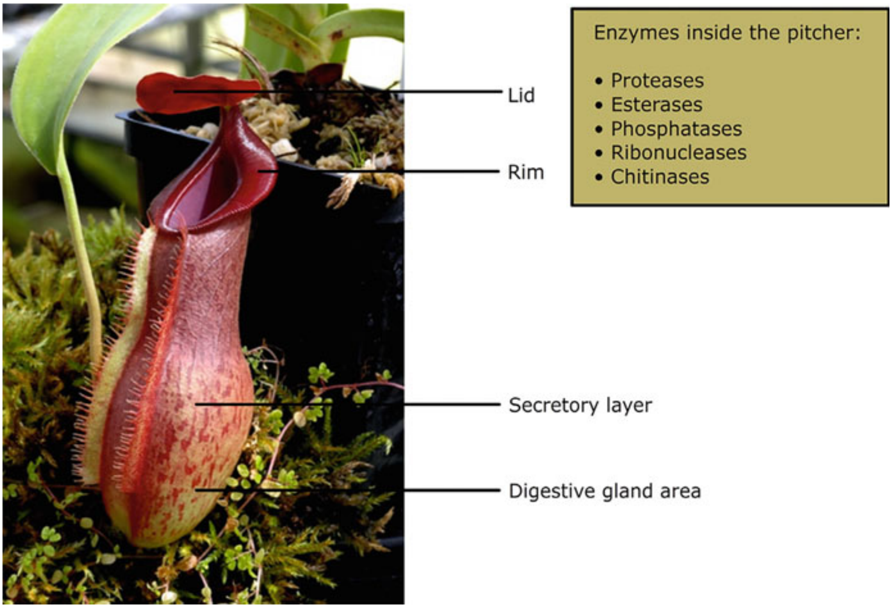

Fig. 29.20 Pitcher plants (*Nepenthes* sp.) entrap the prey in the pitcher-like traps filled with digestive enzymes

the suction traps of bladderworts (genus *Utricularia*). These are triggered by the prey and are activated by electrophysiological signaling processes. Passive traps do not move and use slippery surfaces, sticky secretions, etc. to trap their prey. Passive traps include those used by pitcher plants *Nepenthes* sp. (family Nepenthaceae), which has a pitcher-like container, formed by leaf lamina, and is filled with digestive enzymes secreted by specialized glands (Fig. 29.20). The prey attracted by the pitcher plant slips into the slippery neck of the trap and with its exit blocked by the stiff epidermal hairs pointing in one direction drowns into the enzyme soup and is digested away. Such traps are stationery and do not involve movements. However, carnivorous plants like *Pinguicula grandiflora* (family Lentibulariaceae) involve the use of movements of the leaves to entrap the prey in a cagelike structure formed by the folding of the leaf lamina as its cells loose turgor forming a bowl-like structure. Similarly, the sundew plant (*Drosera* sp. Family Droseraceae) uses traps capable of large-scale movements. The upper surface of the leaves in these plants bears long flexible tentacles each of which has a mucilage and enzyme-secreting gland at the top. The tentacles are arranged in concentric circles in the center of the lamina and are inclined at an angle to the surface. Those that are in the center are the ones that function to produce digestive enzymes, while those away from the center form the trap. Mechanical stimulation generated by the trapped prey in the tentacles is transmitted within seconds enabling rapid curvature of the tentacles toward the center where the prey drowns in the digestive enzymes secreted by the central tentacles forming mucilage-filled bowl. The trap of the Venus flytrap (*Dionaea* *muscipula*) is driven by turgor-mediated changes in lamina of specialized leaves that have two identical lobes on either side of the midrib. These lobes have long stiff bristles located perpendicular to the laminar surface (Fig.29.21a, b). Mechanical stimulation of the bristles by the prey activates mechano-sensitive ion channels. This causes induction of electrical signaling involving action potential, the transient depolarization of the plasma membrane (Fig. 29.21c). The action potential mediates the movement of the two lobes of the trap to move toward each other with the midrib functioning as a hinge and the bristles on the opposite lobes precisely interlocking to

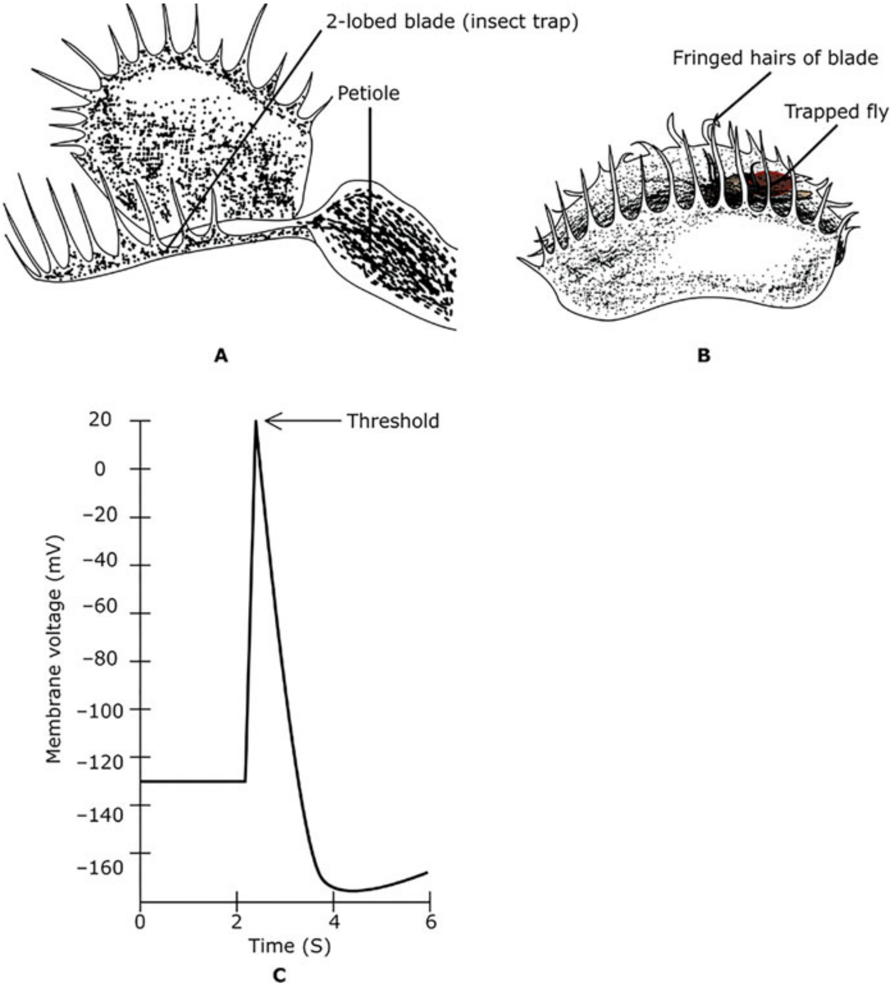

Fig. 29.21 (**a**, **b**) Venus flytrap (*Dionaea muscipula*) has leaves modified to act as traps with bristles on edges that interlock upon excitation to entrap the prey. (**c**) Mechanical stimulation of bristles causes generation of action potential that mediates the movement of the two lobes toward each other trapping the prey

form a trap for the prey. For activation, the hairs must be touched within 20 s of each other. Each movement generates an action potential and is recorded by the plant. Induction of action potential causes the two lobes of the leaf to close and secrete digestive enzymes. Aquatic plant—*Utricularia* (Lentibulariaceae)—is known to possess traps with hinged trap doors. These traps are formed by leaves modified to form flattened pear-shaped bladders attached to the submerged branches of the plant by tiny stalks. At the entrance to the trap opening is a flap-like tissue that forms an inward opening door. Several bristle-like hairs surround the submerged trough, which entraps the prey preventing their exit.

29.6 Movements for Dispersal

Ability to undergo sexual reproduction and production of offsprings has been the primary reason why angiosperms have been able to dominate earth. Plants have devised their developmental programs to produce offsprings under optimal conditions to ensure their survival. Also, these offsprings, comprising of either seeds or spores, are packaged and dispersed using remarkably diverse mechanisms. Life cycle of all terrestrial plants comprises of a sexual generation that begins with unicellular spores produced within sporangia borne on specialized leaves called sporophylls. The sporangia of all seed plants, i.e., angiosperms and gymnosperms, are heterosporous, bearing numerous small male spores or microspores, also called as pollen grains borne within microsporangia (pollen sacs), and usually a single female spore, called megaspore located in the megasporangium. The megaspore develops into the female gametophyte and is enclosed within the protective megasporangium tissue and integument/s that forms the ovule. Upon fertilization, the fertilized egg develops into the diploid embryo, and the ovule becomes the seed enclosed within the ripened ovary now referred to as fruit. The fruit performs the dual function of protecting the seed and also aids in the dispersal of seed. A remarkable diversity of fruits is seen in angiosperms, and these are classified on the basis of characteristics such as whether it is dehiscent or indehiscent, dry or fleshy, etc. These features enable the fruits to facilitate seed dispersal.

29.6.1 Cohesion-Mediated Seed Propulsion

Passive dispersal of seeds is observed in plants that have dry dehiscent fruits such as capsules of *Lilium* (Liliaceae) and *Iris* (Iridaceae). The seeds in these plants are liberated by gravity along with the help of wind, rain, or animals. In many plants belonging to the families Acanthaceae, Balsaminaceae, and Euphorbiaceae, ballistic explosive movements of fruit coat at the time of dehiscence are responsible for dispersal of seeds. Other examples include *Alstroemeria* (Alstroemeriaceae), *Lotus* (Papilionaceae), and *Bauhinia* and *Cytisus scoparius* (Fabaceae). In *Ricinus communis* the capsules dehisce explosively as the fleshy exocarp dries and the endocarp dehisces along the three one-seeded valves with transverse fibers.

Progressive dehydration causes the capsule to recurve and split open catapulting the seeds to about 3–3.5 m away. Explosive dehiscence is also seen in the family Acanthaceae as the two-valved capsule that is enclosed tightly within two lignified sepals explode as they dry up. After rainfall, these sepals open up exposing the capsule. The capsule valves are under increasing strain as they dehydrate after maturation because of the structural differences between the outer and inner layers. On imbibing the moisture, the valves split open explosively, and the seeds are catapulted out of their capsules.

29.6.2 Turgor-Mediated Seed Propulsion

Plants, such as *Ecballium* (Cucurbitaceae), *Impatiens parviflora* (Balsaminaceae), *Cardamine impatiens* (Brassicaceae), and *Oxalis acetosella* (Oxalidaceae) have fruits that remain fleshy and turgid until they dehisce explosively. In such plants, the changes in the turgor mediate the explosive dehiscence of the fruits to propel the seeds out. Using this mechanism, the parasitic plant *Lathraea clandestina* (Orobanchaceae) can catapult its seeds to a considerable distance of 12–20 m. The fruits of the plant *Impatiens* are elongated capsules that have a fleshy pericarp with several valves joined margin to margin. The subepidermal cells of the capsule are large parenchymatous cells that are elongated in anticlinal orientation. During maturation, turgor pressure builds up in these cells exerting pressure along the fault lines (where the walls are weak) in the sutures. Eventually the strain splits the sutures, and the separation is immediate resulting in explosive inward curvature of the valves, thereby throwing the seeds to long distances.

Summary

- Movements in plants that occur in response to external stimuli are called as tropic movements. Based on the nature of the stimuli, these movements can be classified as phototropism, in response to light, and geotropism—in response to gravity. Other tropic movements include hydrotropism and chemotropism in response to water and specific chemicals, respectively.
- Nastic movements are independent of the direction of the stimuli and can be internally (autonomous) or externally directed (paratonic). These include nyctinasty or sleep movements; thermonasty, i.e., movements induced by temperature variations; and seismonastic movements that require a touch stimulus to occur.
- Central to the concept of movements in plants is the presence of cellulosic plant wall and the positive hydrostatic pressure that builds up in the cell. Movements can be attributed to change in growth or changes in turgor. Growth-mediated movements are caused by changes in the length of the opposite sectors. Relocation of auxin to a sector results in variation in growth on one side relative

to the other directing specific movement of the organ. Turgor-mediated movements on the other hand take place by contraction of one sector and the expansion of its opposite sector.

- In phototropism, the exposure to unilateral light affects the activity of auxin transporters activating in preference those farthest away from the light, and the resulting lateral transport of auxin causes the acceleration of the growth on the shaded side.
- Several plant movements are guided on a circadian cycle monitored by the length of the day. The universal biological oscillator functions as a "clock" and can be easily monitored in plants grown under constant environmental conditions of light, temperature, and humidity. Such plants exhibit autonomous movements with a remarkable constant rhythm. Examples of circadian movements include the sleep movements of leaves, the opening and closing of stomata, and the diurnal opening and closing of flowers.
- Parasitic plants exhibit many types of movements for trapping prey. The active traps of such plants have mobile elements that entrap the prey upon stimulation. The touch-induced closure of the traps involves induction of electrical signaling in the form of action potentials as voltage-gated ion channels cause transient depolarization of plasma membrane. Several plants also have passive traps that use slippery surfaces and sticky secretions to entrap their prey.
- Propulsion of seeds for dispersal is caused by passive cohesion as well as active turgor-mediated mechanisms.

Box 29.1 Transcription Regulation of Circadian Clock in Plants

The circadian clock system of plants operates with three essential processes—perception of the external stimulus, setting of the central clock or oscillator, and induction of specific physiological response. The perception of the external signal is mediated by photoreceptors such as phytochrome and cryptochrome. These modulate the phase of the oscillator in response to the external cues such as the day length. The final response is generated by the plant mediated by clock-controlled genes. Several clock-controlled genes have been investigated including *CAB* genes encoding chlorophyll a/b binding proteins of the light-harvesting complex, those for small subunit of Rubisco, etc. Transcription of *CAB* genes shows a cyclic increase at the beginning of the day and peaks few hours later, and the expression later goes down as the day proceeds. The *CAB* transcript level has been used to monitor circadian rhythms at the molecular level. The use of a *CAB2::luc* (luciferase) reporter gene cassette has been used to create a rhythmic light emission system facilitating genetic analysis of the clock. Several clock-associated genes have been isolated. These include the *TOC1* (*timing of CAB*), *CCA1* (*CIRCADIAN CLOCK ASSOCIATED 1*) and *LHY* (*LATE ELONGATED HYPOCOTYL*), *CAT3* (a gene encoding enzyme catalase), and *ELF3* (*early flowering 3).*

(continued)

Box 29.1 (continued)
CCA1 is an important transcriptional regulator that binds to *CAB* promoter and links phytochrome with the expression of *CAB*. The biological clock is based on negative feedback system that relies on the mutual reciprocal feedback inhibition of *CCA1* and *TOC1*. The relative concentrations of the two rise and fall alternately during the day. These oscillations are kept in phase by the external light cue. The final physiological response is generated by the switching on and off *TOC1* and *CCA1* regulated genes. One of the important genes regulated by *TOC1* includes the *CO* (*Constans*) gene that regulates the flowering response.

Multiple-Choice Questions

1. Pea tendril coiling around a support is an example of:
   (a) Thermotaxis
   (b) Thigmonasty
   (c) Thigmotaxis
   (d) Thigmotropic
2. Curving of plant toward light is called:
   (a) Thigmotropism
   (b) Gravitropism
   (c) Phototropism
   (d) Thigmonasty
3. Sleep movements are mediated by turgor changes in specialized motor cells located in:
   (a) Pulvinus
   (b) Stem
   (c) Leaf blade
   (d) Root
4. Roots perceive gravity by a mechanism that involves sedimentation of:
   (a) Chloroplasts
   (b) Statoliths
   (c) Ribosomes
   (d) Mitochondria
5. Which of the following is *not* true for nastic movements?
   (a) Depend on the direction of the stimulus
   (b) Are independent of the direction of the stimulus
   (c) Genetically predetermined
   (d) Driven by growth or turgor changes

6. Circadian rhythm is a biological rhythm with a cycle of:
   (a) 12 hours
   (b) 24 hours
   (c) 36 hours
   (d) 48 hours.
7. Curvature of the stem due to phototropic movement is due to uneven distribution of:
   (a) Cytokinin
   (b) Auxin
   (c) Phytochrome
   (d) Gibberellin
8. Folding of leaflets of *Mimosa pudica* is associated with the efflux of:
   (a) Calcium ions
   (b) Magnesium ions
   (c) Potassium ions
   (d) Chloride ions
9. ___________ cells function as multicellular motors in the leaves of grasses cause extensive changes in leaf conformation.
   (a) Guard cells
   (b) Bulliform cells
   (c) Subsidiary cells
   (d) Lenticels
10. Carnivorous plants entrap their prey in traps driven by:
    (a) Turgor-mediated changes
    (b) Growth
    (c) Contraction
    (d) Locomotion

Answers

1.b 2.c 3.a 4.b 5.a 6.b 7.b
8.c 9.b 10.a

Suggested Further Readings

Darwin C (1898) The power of movements in plants. D. Appleton, New York
Koller D (2011) The restless plant. Harvard University Press, Cambridge, MA/London
Trewavas A (2014) Plant behaviour and intelligence. Oxford University Press, Oxford