8.2??Plant and organ orientation

Vascular plants orient themselves in space to optimise shoot exposure to radiant energy and CO_2 in the atmosphere, and to maximise root access to water and nutrients in the soil. To achieve this, there is a range of directional control systems, which change as a plant proceeds through its life cycle. Regardless of how a seed falls to the ground, on germination a seedling root grows downwards and the shoot grows upwards. What controls these opposite directions of growth?

First, seedling shoots are very sensitive to low-intensity *light*, curving strongly towards any directional light which may indicate a break in the leaf canopy that the shoot can utilise. In mature plants, leaf orientation can follow the sun during the day to maximise light capture, but if midday radiant energy becomes excessive the leaf blade may instead orient at right angles to the sun's rays. Flower buds are usually bent downwards, but on opening the stem straightens and holds the flower upright to maximise exposure to insects and other pollinating agents.

Second, *gravity* is an all-pervasive and constant orienting signal. However, roots and shoots generally show opposite responses to gravity, reflecting the intrinsic polarity in all higher plants. One half, the root system, is adapted for life in dense dark soil, while the other half, the shoot system, has evolved to exist in the fragile atmosphere, and harvests sunlight for photosynthesis. Conforming with this dichotomy, main roots exhibit a positive directional response to gravity, whereas shoots generally show a negative reaction.

Table 8.6   Characteristics of four types of plant tropism. Positive means growing towards a directional stimulus, and negative means growing away. Plagiotropism is growth at an angle to gravity

| Tropism	Stimulus	Response	Examples
Gravitropism	Gravity	Positive	Primary roots
		Negative	Shoots
			Leaves
			Coleoptiles
		Plagiotropism	Axillary branches
			Lateral roots
			Some leaves
			Runners
			Rhizomes
Phototropism	Light	Positive	Shoots
			Leaves
			Coleoptiles
		Negative	Some types of shoot
			Some types of root
			Tendrils
Heliotropism	Light	Following the sun	Leaves
Thigmotropism	Touch	Positive	Tendrils of climbing plants
			Stems of vines

[1]

Table 8.6

Directional growth responses to directional stimuli are called tropisms. There are three main kinds:

1. Gravitropism — gravity sensing

2. Thigmotropism — touch sensing

3. Phototropism — light sensing

The characteristics of the major tropisms are shown in Table 8.6. All these responses are due to different growth rates on two sides of a responding organ, resulting in curvature either towards or away from the stimulus. The positioning, or orientation in space, of many plant organs can be due to several tropisms and nastic (non-directional) responses acting together.

8.2.1??Gravitropism
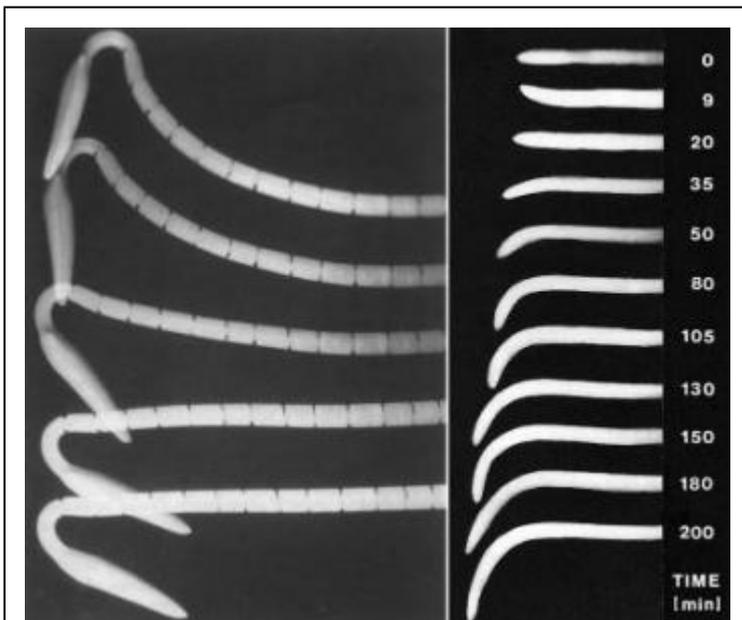
[2]

Figure 8.8 Time-lapse photographs showing gravitropism responses in horizontally placed roots and shoots. (a) Negative shoot gravitropism of a dark-grown cucumber seedling photographed at 15 min intervals. The ink marks on the hypocotyl are 2 mm apart. Upward curvature commences by 30 min due to simultaneous initiation of differential growth along the whole hypocotyl. (b) Positive gravitropism in a maize root. The initial slightly upward curvature is not unusual. Downward curvature commences around 30 min and continues as the tip grows forwards. By 150 min, the root tip has been restored almost to vertical.

As the primary root emerges from a germinating seed, it shows strong positive gravitropism leading to rapid downward curvature (Figure 8.8a). This enables the root tip quickly to penetrate the soil, giving anchorage and access to water, the latter being a vital factor in successful establishment. Root gravitropism has been investigated for over a century, but its mechanism is still not fully understood. However, we do know that gravity is detected in the root cap, and that normally both root cap and root tip need to be present for straight growth and curvature to occur. Because the elongation zone is situated behind the tip, information about the root's position must be transferred from the sensing site in the cap to the elongation zone.

Shoots sense gravity differently. Both the shoot tip and the growing zone behind it can detect and respond to gravity (Figure 8.8b), so that even decapitated shoots retain an ability to curve upwards when displaced from the vertical. The shoot tip, unlike the root tip, is therefore not essential for gravitropism.

Gravity perception

Detecting the direction of gravity is the essential ?rst step in gravitropism. Plant organs achieve this by sensing the move-ment and position of starch grains contained within amyloplasts of specialised cells called statocytes (Figure 8.9a).
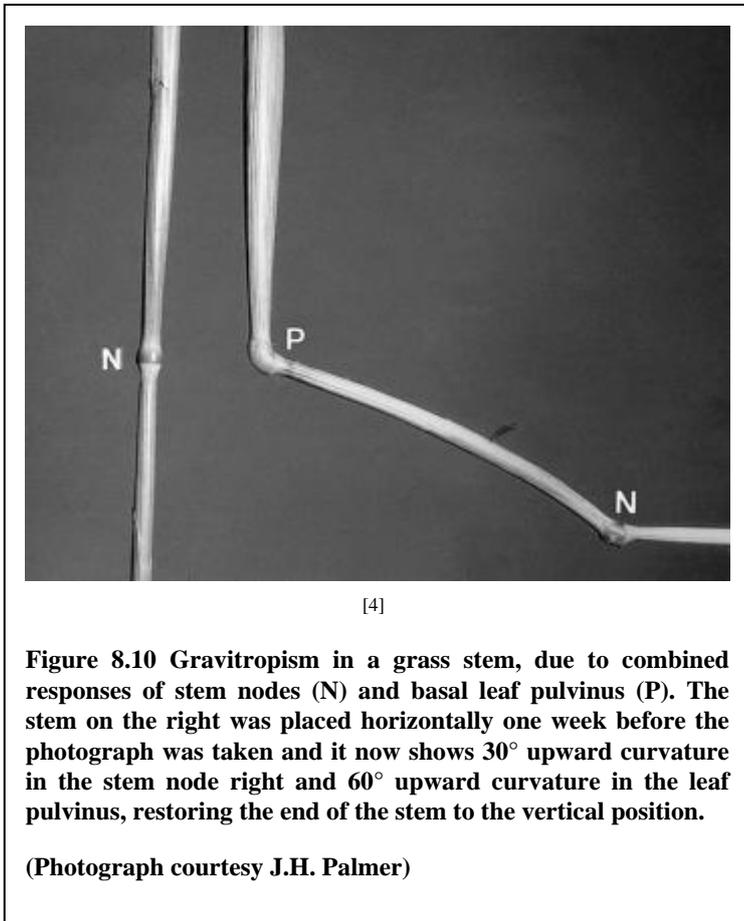

[3]
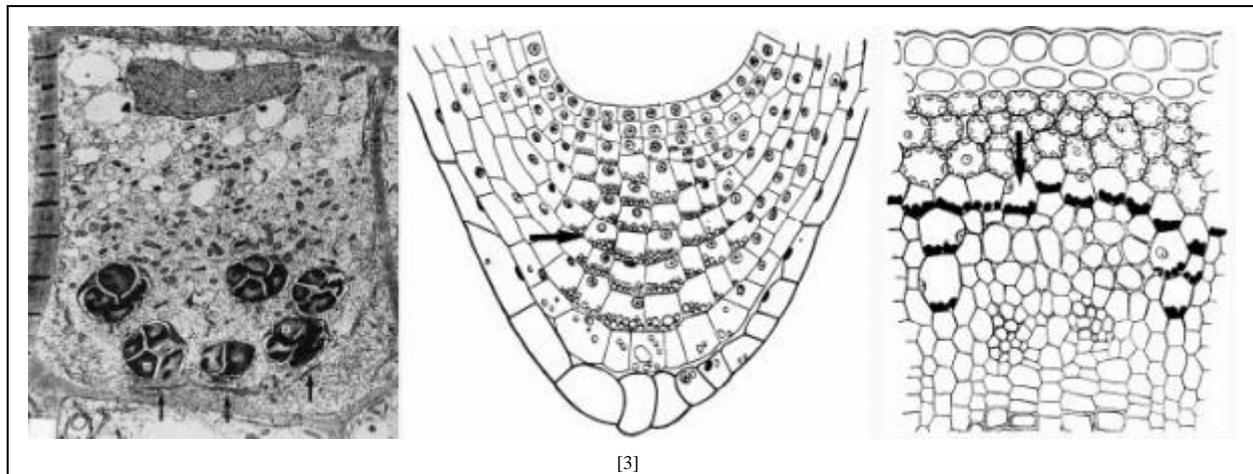
Figure 8.9 Sites of gravity perception. (a) Transmission electron micrograph of a statocyte cell in a root showing six statoliths (amyloplasts) each with a boundary membrane and containing two to four starch grains. Characteristically, the statoliths are resting on a network of endoplasmic reticulum (arrowed), which may be able to sense their movement. n, nucleus. (b) Longitudinal section through a root cap showing statocyte cells (arrowed) near the centre. (c) Transverse section of a primary stem showing layer of starch-containing cells (arrowed)which make up the starch sheath.

Roots

In roots, statocytes are located in the root cap (Figure 8.9b) which also serves to protect the root

meristem from abrasion by soil particles as it grows through the soil. Root cap involvement was ?rst demonstrated in maize, when a needle was used to prise off the root cap. This procedure did not inhibit growth, but ability to sense and respond to gravity were completely lost until a new cap grew over the root tip about one day later. Subsequently, a gravity-insensitive mutant of maize was found that does not secrete the mucilage which normally covers and protects the root cap and tip. Mucilage arti?cially applied to mutant roots immediately restored the gravity response indicating that the root cap transmits infor-mation through the mucilage. This information is probably in the form of a small diffusible molecule, moving either in the mucilage or through the root apoplasm. Researchers have not yet been able to identify this chemical.

[4]

Figure 8.10 Gravitropism in a grass stem, due to combined responses of stem nodes (N) and basal leaf pulvinus (P). The stem on the right was placed horizontally one week before the photograph was taken and it now shows 30° upward curvature in the stem node right and 60° upward curvature in the leaf pulvinus, restoring the end of the stem to the vertical position.

(Photograph courtesy J.H. Palmer)

Shoots

In dicotyledonous shoots, statocytes form a cylindrical tube one cell thick, which surrounds the vascular tissue (Figure 8.9c). This cylinder is known as the 'starch sheath', because numerous starch grains show up very clearly in stem sections stained with starch-speci?c iodine solution. These statocytes are distributed along the length of the shoot and so can sense gravity in the absence of the apex. In grasses and cereals, stem statocytes are restricted to the stem node and leaf sheath pulvinus. Consequently, only the nodes and pulvini respond to gravity (Figure 8.10).

Statocyte operation

The involvement of statocyte starch grains in gravity perception was proved by keeping barley plants in the dark for 5d, which resulted in disappearance of starch grains as the starch was consumed in respiration. These starchless plants completely lost their gravity response, but feeding with sucrose

resulted in starch grains reforming and restoration of gravity sensing. Additional evidence comes from a maize mutant known as *amylomaize*, which has abnormally small starch grains and very slow gravitropic response.

Proof that the controlling force is gravity, and not, for example, lines of magnetic ?eld, comes from experiments in which a centrifugal force was substituted for gravity. If a germinating bean seed was placed at the axis of a horizontal centrifuge rotating at one revolution per second, to give an acceleration of $4 \times 10^{-3}g$, this effectively counteracted gravity. The starch grains in the root cap developed in the centre of the cell and were unable to generate a displacement message. Consequently, the root remained straight. At two revolutions per second, equivalent to $2 \times 10^{-2}g$, the starch grains were forced against the outside wall of the statocytes. As a result, the root commenced to curve, bringing the tip parallel with the centrifugal force, that is, growing radially outwards. Now the centrifugal force acted along the length of the root and the starch grains were displaced onto the normally lower sides of the statocyte cells in the root cap, leading to straight growth. Experiments on plants under 'micro-gravity' conditions in space orbit have con?rmed much of what was previously deduced from experiments on earth (Halstead and Dutcher 1987).

How do amyloplasts enable gravity sensing? Because of their high density and relatively large mass, they normally occupy the lowest part of the statocyte. When a root is dis-placed from the vertical, statocyte orientation is changed and the starch grains roll or slide 'downhill' through the cytoplasm to reach the new low point. Statocytes, possibly through stretch or displacement receptors in the plasma membrane, are able to recognise that starch grains have moved to new positions. An asymmetric message is then transmitted from the root cap to the growing region and a correction curvature is initiated until the cap returns to vertical. Similar events occur in shoots.

Plagiotropism

Many organs naturally grow at an angle to gravity. This is a type of gravitropism termed plagiotropism and occurs in lateral shoots and roots, and also in some prostrate primary shoots, for example runners of strawberry and subterranean rhizomes of some grasses and sedges (Figure 7.18). The lateral growth angle is variable but is at least partly under genetic control, giving every plant a recognisable architecture. In shoots, the angle is also influenced by the vertical primary stem and by environmental factors. For example, exposure to bright sunlight tends to increase the angle to the vertical, while shade reduces it. Couch grass illustrates the requirement for exposure to direct sunlight. When their runners grow into shade, the plagiotropic tendency disappears and stems grow vertically in search of higher light intensity. The primary shoot apex also influences direction of growth of lateral shoots, which often changes to vertical if the primary shoot tip is removed. This response is probably linked to apical dominance.

8.2.2??Thigmotropism
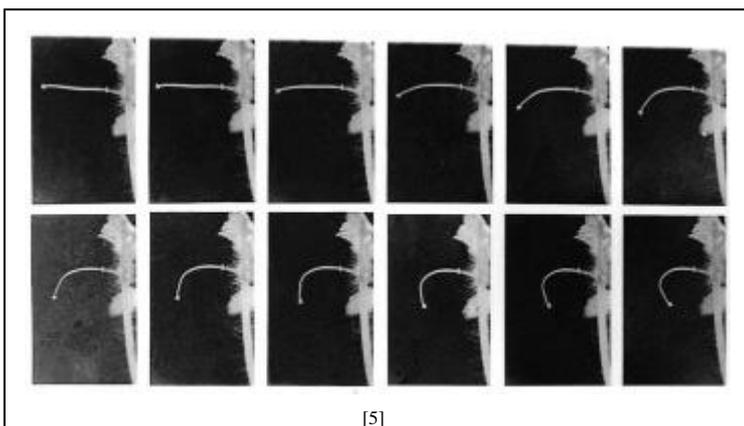
[5]

[6]

Figure 8.12 Thigmotropic twining of a tendril around a supporting stem, after touch contact by one side of the tendril. Later, tension coiling within the tendril has dragged the stem towards the support.

(Photograph courtesy J.H. Palmer)

Tendrils are specialised thread-like structures that can grasp objects with which they come into contact. They are modi?ed leaves or stems sensitive to sliding and/or repeated touch, such as occurs when a tendril contacts a neighbouring stem. Tendrils enable climbers and vines which have slender non-self-supporting stems to access sunlight at the top of the vegetation cover with less investment in shoot biomass per unit height gain. In effect, tendrils search for surrounding objects because the end of the tendril makes wide spon-taneous sweeping movements as it grows. On contact, the touch stimulus induces the tendril to coil around the object as a result of the cells on the non-stimulated side expanding more rapidly than those on the side making contact (Figure 8.11). Coiling is a tropic response, since direction of curvature relates to the direction of touch. Touch stimulation is con-tinued during coiling so that tendrils ultimately twine several times around the object. The rest of the tendril may then show spontaneous coiling which effectively pulls the stem nearer to the contacted object, giving mechanically superior support (Figure 8.12). This second phase is often in the opposite helical direction and may be initiated by tension.

Tendrils detect contact via sensory epidermal cells called tactile blebs. These cells are rich in microtubules and actin ?laments, suggesting an involvement of the cytoskeleton. Touch sensing by the sensory bleb is converted to a signal which results in coiling commencing only a few seconds after contact. Coiling is due partly to changes in cell turgor and partly to differential growth along opposite sides of the tendril.

8.2.3??Phototropism
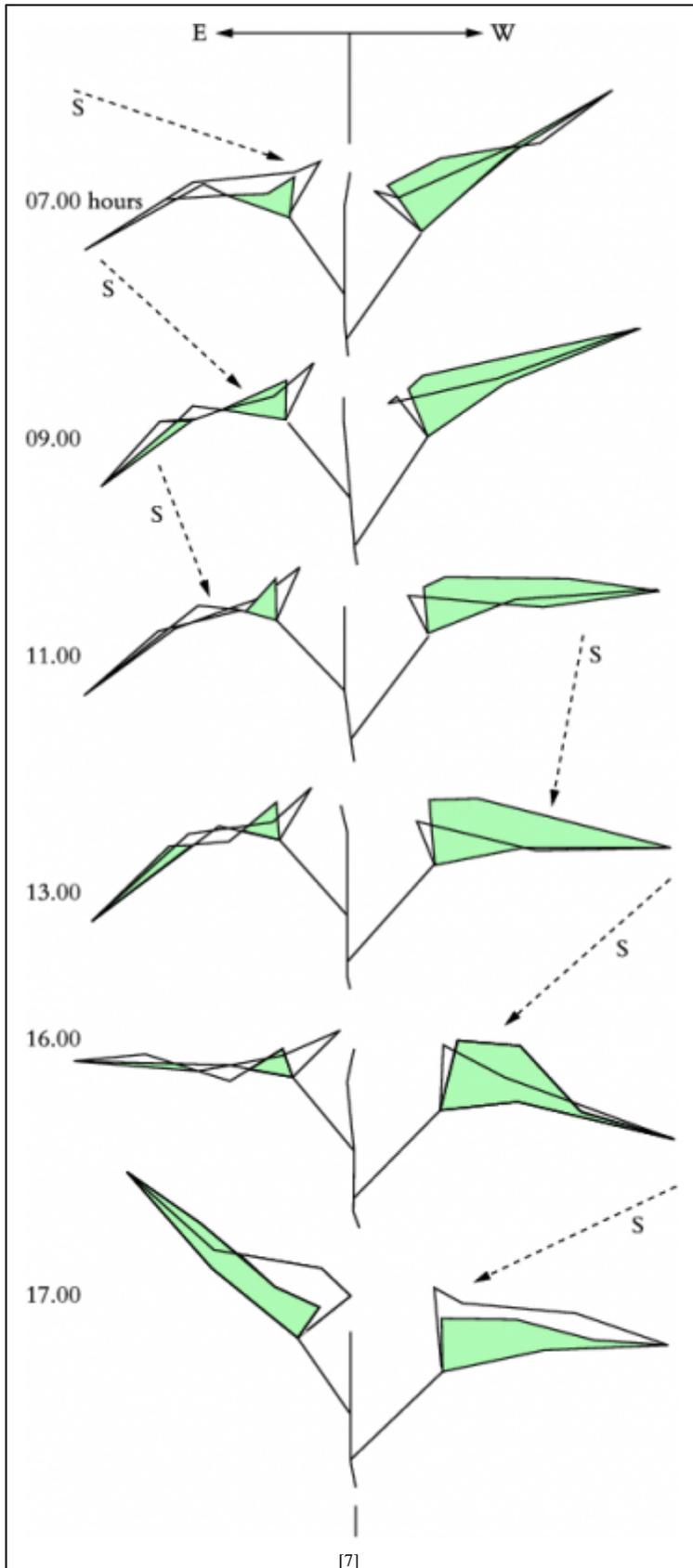
Figure 8.13 Diagrams of heliotropic movement of sunflower leaves from 7 am to 5 pm. Lamina inclination changes for leaves on the east (E) and west (W) sides of the plant, so that they maintain a relatively constant angle to the solar beam (S), as the sun moves from east to west during the day. During the night, leaf positions recover to their starting point. Lamina inclination is controlled by curvature of the petiole, which is not shown in these drawings.

(Based on Lang and Begg 1979)

Phototropism is a curvature in relation to directional light. In ferns, conifers and flowering plants, positive phototropism, that is, curvature towards the light source, is the dominant response. Phototropism assists cotyledons and emerging leaves to maximise light interception for photosynthesis, before a seedling's food reserves are exhausted. Seedlings of some tropical vines, for example *Monstera* and *Philodendron*, are instead negatively phototropic and direct their stems towards the shadow cast by tree trunks, which these vines need for support. Among lower plants, ?lamentous algae can grow towards or away from a light source and in bryophytes sporophyte stalks show positive phototropism.

Phototropism appears to occur in three stages: light perception, transduction and curvature. Illuminating a seedling from one side establishes a light gradient across the width of the stem, because light is absorbed by various pigments. By measuring the positive phototropic response to exposure to different wavelengths of light, an 'action' spectrum can be established (Figure 8.35). In coleoptiles, this action spectrum has major peaks in the ultraviolet (370 nm) and in the blue region (420–475 nm). This stimulated a search for chromophores which ef?ciently absorb blue light and resulted in carotenoids and flavins being proposed as possible phototropic sensors. Rapid progress in the 1990s has led to identi?cation of a flavin, in the form of FAD (flavin adenine dinucleotide), as the chromophore which is coupled to a soluble protein to generate the complete flavoprotein photoreceptor (Cashmore 1997). During the transduction stage in etiolated grass and cereal seedlings, the absorbed blue light may cause auxin (indoleacetic acid, IAA), which normally moves down the shoot from the tip, to migrate towards the shaded side. This would promote more elongation in the shaded side than in the illuminated side, causing bending towards the light during the subsequent growth response.

Evidence for redistribution of IAA, rather than its destruction on the illuminated side, comes from experiments in which stem segments were placed vertically on agar receiver blocks after the stem tip had been cut off to remove the source of naturally produced IAA. An agar block containing ^{14}C IAA was then placed on the apical end of the stem segment. When the stem segments were illuminated on one side, it was found that distribution of ^{14}C label in agar receptor blocks on the illuminated and shaded side was in the ratio of 25:75, and in the tissue was 35:65 for the illuminated and shaded halves. Of course, the label may have been converted to other compounds and endogenous auxin in intact plants may behave differently. Indeed, no IAA gradient is found in many graviresponding tissues (Mertens and Weiler 1981). We must therefore conclude that *gross* IAA redistribution is not the only cause of phototropic bending. An alternative explanation is that IAA may need only to move between adjacent tissue layers, perhaps from the cortex to the more-auxin-sensitive epidermal cells (Macdonald and Hart 1987). Because unilateral illumination does induce other rapid changes in stem cells, leading to growth inhibition on the illuminated side and curvature towards the light source, there may be no need to invoke a long-distance signal such as auxin.

Heliotropism is a variation of phototropism where the leaf lamina and apical bud respond to changes in direction of the sun's rays, and track the movement of the sun. Generally, inclination to the sun remains constant during the day and this optimises radiation interception. Sunflower leaves and flower heads provide a good example (Figure 8.13). In leaves, lamina inclination in the daytime is controlled by

diurnal petiole straightening, curvature and rotation. During the night, leaves return from a westerly inclination at sunset to face east at sunrise. Heliotropic leaf movement is dependent on continued petiole growth and ceases at leaf maturity.

8.2.4??Overall models for control of tropisms

The pioneering studies on auxin responses in coleoptiles have undoubtedly influenced present-day models, yet vigorous debate among researchers continues on the wider importance or otherwise of auxin in tropisms, especially where sensing and responding cells are the same (Trewavas *et al*. 1992). Some researchers have attempted to generate a single model to explain all the types of differential growth that are represented by tropisms. Early researchers, including Charles Darwin, measured responses by angle of curvature either towards or away from the stimulus. However, detailed kinetic analysis has revealed that, perhaps surprisingly, there are at least four versions of growth differential. Some involve growth acceleration and some, deceleration (Table 8.7; Firn and Digby 1980). It is hard to envisage a single growth-regulating chemical, whether auxin or not, being laterally redistributed and causing sometimes net growth promotion, sometimes net growth inhibition and sometimes no change at all in growth rate on one side of the organ (Franssen *et al*. 1982). Coleoptile tips are very sensitive to light and may initiate a basipetal wave of growth-regulating chemical, but it is dif?cult to reconcile this notion with the observations that (a) all growing regions of oat coleoptiles initiate a response at the same time (Figure 8.14a) and (b) virtually the same response can occur even when the coleoptile is covered with a black cap (Figure 8.14b). Overall, greater progress has been made on the signal perception systems for light and gravity than on how the signals are translated into altered growth patterns.

Table 8.7   Types of growth differential induced during tropic responses. All these tropisms result in redirection of the growing tip, but how this is achieved varies. The only option not represented here is differential acceleration of both sides, presumably because an overall increase in growth rate is more difficult to sustain in tissues that were already growing before the response started

| | | | Nature of growth differential | | |
Tropism type	Species	Organ	Faster side	Slower side	Source
Phototropism	Oat	Coleoptile	0	−	Franssen *et al.* (1982)
	Cress	Hypocotyl	0	−	Franssen *et al.* (1982)
	Cucumber	Hypocotyl	0	−	Franssen *et al.* (1982)
	Mustard	Hypocotyl	+	−	Rich *et al.* (1987)
Gravitropism (−)	Sunflower	Hypocotyl	+/0	−	Carrington and Firn (1985)
			+	−	Berg *et al.* (1986)
	Cucumber	Hypocotyl	+	−	Cosgrove (1990)
	Wheat	Node	+	0	Bridges and Wilkins (1973)
Gravitropism (+)	Pea	Root	+	−	Konings (1995)
	Cress	Root	+	−	Selker and Sievers (1987)
	Maize	Root	+	0	Barlow and Rathfelder (1985)
			−	−	Evans *et al.* (1986)
	Wheat	Root	−	−	Rufelt (1971)

(Information derived from Firn and Digby 1980 and Hart 1990)
+= stimulation of growth compared with previous rate;
0 = no change compared with previous growth rate;
− = reduction of growth compared with previous rate;
−− = reduction greater than that observed on other side of organ.
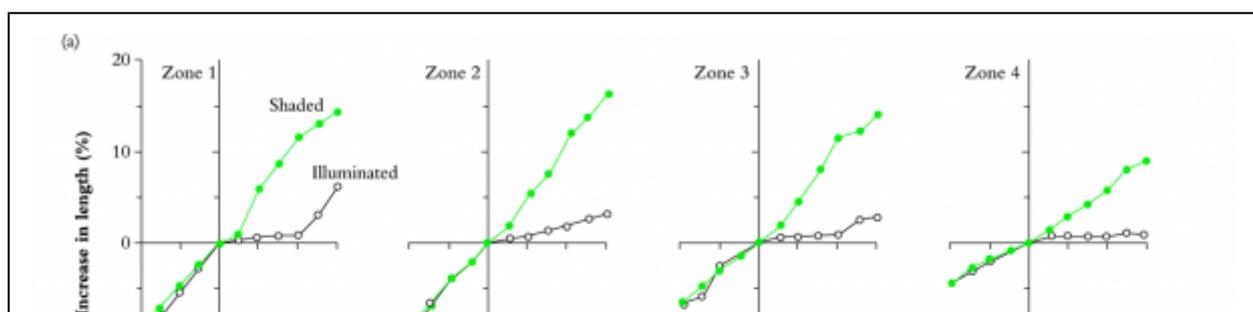
[8]

Table 8.7

8.2.5??Nastic movements

[10]

Figure 8.15 Turgor-based nastic movements of leaflets of pinnate legume leaves. Left, horizontal leaflets of *Luecaena* early in the day. Right, leaflets folded to vertical at midday, edge-on to the sun.

(Photograph courtesy C.G.N. Turnbull)

Nastic responses differ from tropisms because the direction of movement is not related to the stimulus direction but is instead dictated by the plant. Many legumes with divided leaves such as *Leucaena* (Figure 8.15), *Phaseolus* beans and the pasture species Siratro (*Macroptilium atropurpureum*), widely grown for forage in Queensland, are good examples. Early in the morning on hot days, leaflets are oriented horizontally, but as temperature and solar radiation levels rise the leaflets move to a vertical position perpendicular to the sunlight. This is helionasty, which cuts down radiation absorption and consequently reduces water use and overheating. When solar radiation declines towards dusk, leaflets return to their former horizontal position. In legumes, movement is controlled by reversible turgor changes in a small fleshy elbow, the pulvinus, located at each leaflet or pinnule base, which can flex back and forth as water flows in or out of the pulvinus cell vacuoles.

(a)??Seismonasty

Figure 8.16 Seismonastic movement of pinnae and pinnules in leaves of the sensitive plant (*Mimosa sensitiva*) (a) before and after touch stimulation.

(Photographs courtesy J.H. Palmer)

Seismonastic or thigmonastic movements are rapid responses to vibration, touch or flexure. Examples are the high-speed bending of leaf pulvini in the sensitive plant *Mimosa sensitiva* (Figure 8.16), and the curvature of hairs of insectivorous plants. In the case of the Venus fly trap, sensory hairs coupled to an electrical signalling system require stimulation at least twice within a 30 s period (Simons 1992). This appears to allow the plant to discriminate single pieces of debris from an insect crawling within the trap. Most seismonastic movements result from the explosive loss of water from turgid 'motor' cells, causing the cells temporarily to collapse and inducing very quick curvature in the organ where they are located.

(b)??Nocturnal 'sleep' movements

[12]

Figure 8.17 Leaf movements in the 'Prayer plant' (*Maranta bicolor*), an ornamental house plant. (a) Leaf inclined down into night-time position. The leaf movement is caused by turgor changes in the fleshy pulvinus at the base of the leaf blade.

Leaves and leaflets that become vertical at night are called nyctinastic. This is commonly termed a 'sleep' movement, although these plants do not actually slow down their metabolism at night. The 'Prayer Plant' (*Maranta*) is a good example (Figure 8.17). Sleep movements are either growth based, and therefore cease at leaf maturity, or are caused by reversible turgor changes in the pulvinus.

Turgor-based pulvinus flexure

Turgor-based sleep movements are exhibited by many legumes. Examples are clover (*Trifolium*), bean (*Phaseolus*), *Bauhinia*, coral tree (*Erythrina*) and many tropical legume trees, such as *Pithecelobium saman* and *Leucaena*. Turgor-based sleep movements occur mainly in compound leaves with a mechanism similar to helionasty. The daily rhythm of water movement results from a flux of potassium ions from one side of the pulvinus to the other, either increasing or decreasing the water potential of cell vacuoles in each half.

Growth-based petiole epinasty

[13]

Figure 8.18 Growth-based epinastic curvature in sunflower petioles. The plant on the right side was exposed to 20 µg of ethylene in the surrounding air for 10 h. The epinastic curvature of the petioles is due to growth of cells in the upper half of the petiole being strongly promoted by ethylene causing the upper half to increase in length and induce the observed downward curvature of the petioles. Older leaves at eh base of the plant have ceased growth and hence their petioles do not respond to ethylene.

(Photograph courtesy J.H. Palmer)

Other species follow a daily rhythm of leaf movement due to differential growth of upper and lower halves of the petiole. The day–night rhythmic curvature of the petiole is not related to a directional stimulus and is termed 'epinastic'. Like turgor-based sleep movements, magnitude varies with the amount of solar radiation intercepted. Epinastic growth movements may be caused by diurnal changes in production of the plant hormone ethylene, which promotes growth of cells on the upper side of the petiole, inducing downward curvature (Figure 8.18). Leaves constantly produce small amounts of ethylene and, according to one hypothesis, production in-creases towards the end of the day, moving the lamina from horizontal to vertical. The opposite would occur towards the end of the night, allowing the lamina to return to the horizontal daytime position. Supporting evidence comes from petiole cells where ability to respond to ethylene is blocked by silver thiosulphate, and the epinastic leaf movement subsequently disappears.

Nocturnal leaf folding may help plants to conserve water by promoting dew formation, since the air and soil beneath the canopy cool more rapidly after the canopy has folded up or become vertical. The lower temperature then promotes dew development, which falls to the ground around the base of the plant, supplementing rainfall.

Growth-based epinasty is also seen in many dicotyledonous seedlings during germination, when the end of the shoot is bent over in a plumular hook. The hook is a temporary structure which protects the apical bud as the shoot pushes through the soil. It is created by cells on one side of the plumule expanding more rapidly than cells on the opposite side, possibly in response to ethylene, which is produced by the plumule in darkness. On reaching the soil surface, the plumule is exposed to daylight which appears initially to reverse and then to cancel the differential response to ethylene, and consequently the stem straightens.

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