

8.2.3??Phototropism

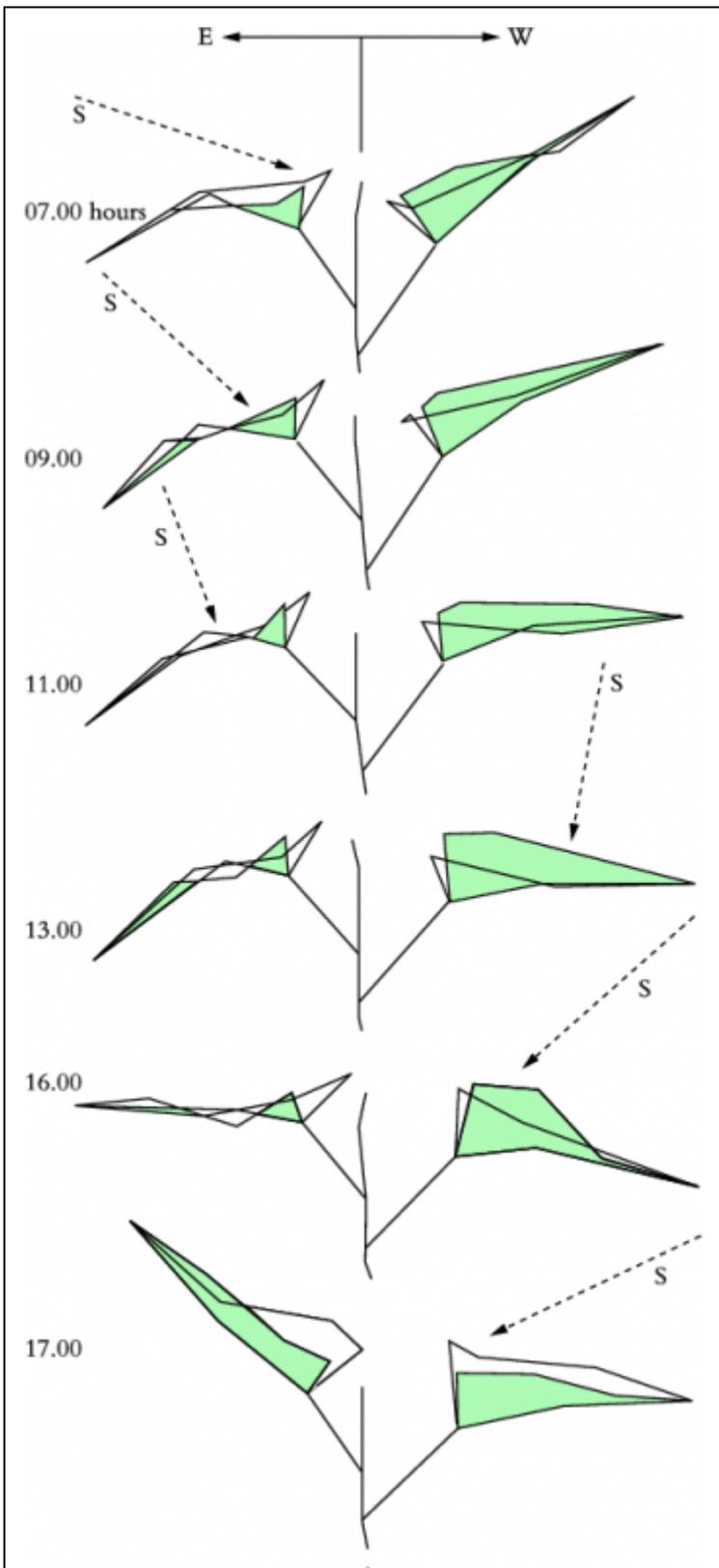


Figure 8.13 Diagrams of heliotropic movement of sunflower leaves from 7 am to 5 pm. Lamina inclination changes for leaves on the east (E) and west (W) sides of the plant, so that they maintain a relatively constant angle to the solar beam (S), as the sun moves from east to west during the day. During 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, filamentous 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 efficiently absorb blue light and resulted in carotenoids and flavins being proposed as possible phototropic sensors. Rapid progress in the 1990s has led to identification 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.

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