Reprinted from G. Russell, B, Marshall and P. G. Jarvis (eds.) (1988)
Plant canopies: Their Growth, Form and Function.
SEB Seminar Series, 31

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7. Diurnal leaf movements and productivity in canopies

Introduction

Over the past 15 years a number of studies have focused on characterising diurnal leaf movements that occur in a variety of plants in response to the sun's movement across the sky. It is now clear that these solar tracking leaf movements are triggered by a directional light stimulus and that these movements result in at least a partial regulation by the leaf of the intensity of the incident photon irradiance. The purpose of this chapter is to review what is known about the different kinds of leaf solar tracking movements, their impact on primary productivity, and the potential ecological roles of these phenomena.

Solar tracking is an expression applied to describe the heliotropic movements of both leaves and flowers; it denotes the ability of these structures to move in response to the diurnal change in the sun's position in the sky. Heliotropic movements are distinguishable from other directional types of growth by their rapidity, the reversibility and by the overnight resetting to face the morning sun (Yin, 1938). Two main kinds of diurnal movements are recognised: diaheliotropic movements in which the leaf lamina remain oriented perpendicular to the sun's direct rays and paraheliotropic movements in which the leaf lamina are oriented obliquely to the sun's direct rays (Ehleringer & Forseth, 1980). In the extreme cases of paraheliotropism, the leaf lamina may change from nearly perpendicular to the sun's rays to an orientation parallel to the sun's rays.

The first and most immediate consequence of leaf solar tracking is to regulate the level of the incident photon irradiance from the sun. This means that solar tracking movements can be used to maximise or minimise photon irradiance incident on the leaf (Fig. 7.1). Since only the direct component of photon irradiance can be regulated, the minimum incident photon irradiance in Fig. 7.1 represents the incident component of diffuse solar radiation. Through such leaf movements, exposed canopy leaves are not only able to regulate the intensity of the peak photon irradiance, but also its diurnal timing and the daily receipt of photons. Fig. 7.1 shows that, depending on the water stress levels imposed on the plant (as will be discussed later), the peak photon irradiances on a paraheliotropic leaf (*a*,*b* or *c*) can occur at any time between early morning and late afternoon.

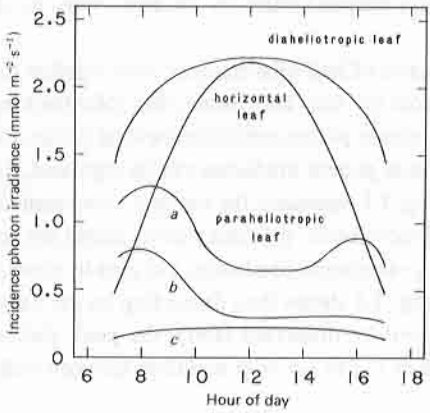
Solar tracking movements may be quantified by calculating the cosine of the angle between the normal to the leaf lamina and the direct solar beam, i.e., the angle of incidence. The cosine varies between 0 and 1 depending on the relative geometrical positions of the leaf lamina and the sun, and is calculated as

$$\cos(i) = \cos(\alpha_l)\sin(\alpha_s) + \sin(\alpha_l)\cos(\alpha_s)\cos(\beta_s - \beta_l) \quad (1)$$

where α_l is the angle above the horizontal of the long axis of the leaf lamina, α_s is the angle of the sun from the horizontal and β_l and β_s are the azimuthal positions of the leaf and sun respectively (Gates, 1962). A value of cos(i) close to 1.0 throughout the day indicates a leaf with a strong diaheliotropic ability. If the leaves in a canopy do not move and have a random leaf azimuth distribution, the average cos(i) should vary sinusoidally through the day as the sun passes across the sky.

The mechanism responsible for solar tracking movements appears to be turgor-mediated and is similar to that involved in other types of rapid leaf movements such as seismonasty and nyctinasty (Schwartz & Koller, 1978; Satter & Galston, 1981; Vogelmann & Björn, 1983). However, the receptor sites that detect direct sunlight appear to differ between species. For example, in two species from the Malvaceae (*Malva neglecta* and *Lavatera cretica*) orientation is controlled by turgor changes in a pulvinus located at the junction of the lamina and the petiole, while the light perception sites appear to be in the major veins of the lamina (Yin, 1938; Schwartz & Koller, 1978). In contrast, *Lupinus succulentus* from the Fabaceae exhibits both light perception and turgor changes in the pulvinus (Vogelmann, 1984). One hypothesis advanced to explain the first type of sensing mechanism involves differential carbon assimilation patterns of mesophyll cells on either side of major veins due to

Fig. 7.1. The diurnal courses of incident photon irradiance (400–700 nm) on a diaheliotropic leaf (cos(i)=1), two paraheliotropic leaves exhibiting diurnal decreases in cos(i), a paraheliotropic leaf, (cos(i)=0.1), and a horizontal leaf. Based on Shackel & Hall (1979) and Ehleringer & Forseth (1980).



microtopographical shading effects. This differential production of carbohydrates would then result in the transmission of some signal to the cells of the pulvinus, initiating reorientation (Fisher & Fisher, 1983). The tracking photoreceptor in both types is activated by blue light (Yin, 1938; Koller, 1981; Vogelmann & Björn, 1983; Sheriff & Ludlow, 1985), making it more effective for fully sunlit leaves than for those within the canopy.

There is currently little information as to the extent of solar tracking among higher plants, but those data that are available clearly suggest that it is frequent among the annual and herbaceous vegetation of arid and semi-arid habitats (Begg & Torssell, 1974; Wainwright, 1977; Ehleringer & Forseth, 1980; Sheriff & Ludlow, 1985). Solar tracking also occurs in plants from temperate and sub-tropical habitats, especially among legumes and other compound leaved species (Gates, 1916; Herbert, 1984; Herbert & Larsen, 1985; Forseth & Teramura, 1986). Its occurrence among crop plants has been noted for many species, including bean (*Phaseolus vulgaris*) (Dubetz, 1969; Wien & Wallace, 1973), cotton (*Gossypium hirsutum*) (Lang, 1973; Ehleringer & Hammond, 1987), soybean (*Glycine max*) (Meyer & Walker, 1981; Wofford & Allen, 1982; Oosterhuis, Walker & Eastham, 1985), sunflower (*Helianthus annuus*) (Shell, Lang & Sale, 1974; Shell & Lang, 1976; Lang & Begg, 1979) and alfalfa (*Medicago sativa*) (Travis & Reed, 1983). Undoubtedly, many more examples exist and our biogeographic understanding of this phenomenon is far from complete.

Solar tracking and photosynthesis

The maintenance of a high cosine of incidence throughout the day in diaheliotropic leaves will result in relatively constant high photon irradiances (near 2.0 mmol m^{-2} s^{-1}, 400–700 nm). For paraheliotropic leaves, the incident photon irradiances will also remain nearly constant but at a reduced level. What are the photosynthetic characteristics of such leaves?

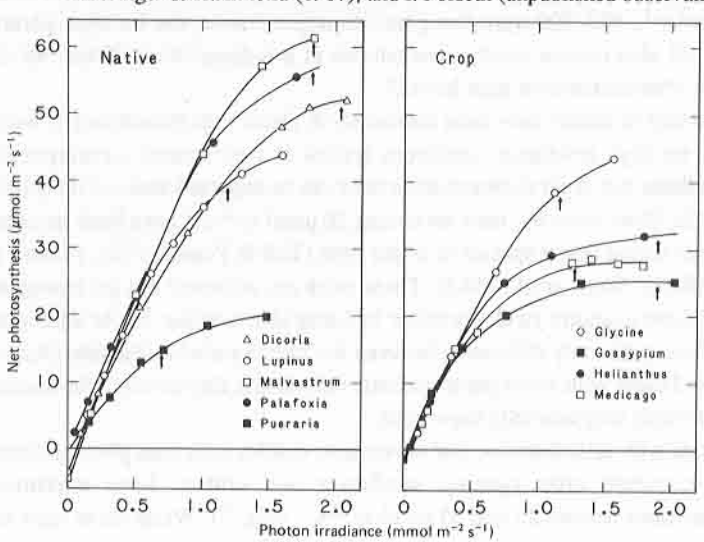
A small number of studies have been conducted on plants with diaheliotropic leaves grown under the high-irradiance conditions typical of their natural environments. These data indicate that rapid photosynthetic rates can be expected under midday light levels (Fig. 7.2). Photosynthetic rates exceeding 50 μmol m^{-2} s^{-1} have been recorded for a number of native desert species in bright light (Toft & Pearcy, 1982; Forseth & Ehleringer, 1983a; Werk *et al.*, 1983). These rates are achieved not by having an intrinsically higher quantum yield, but rather by being able to utilise bright light more efficiently. That is, the only difference between the photosynthetic characteristics of these plants and those with lower photosynthetic rates is that they do not light saturate under the conditions they normally experience.

Not all plants with diaheliotropic leaf movements exhibit such high photosynthetic rates. Two common crop species, sunflower and cotton, have maximum photosynthetic rates betwen 25 and 35 μmol m^{-2} s^{-1} (Fig. 2). While these rates are

indeed high compared with other C_3 species (Black, 1973; Bazzaz, 1979) they are substantially lower than in native plants that exhibit solar tracking. Photosynthesis in both sunflower and cotton appears to be light saturated at irradiances less than those typically incident on the leaf through the day. In fact, Ehleringer & Hammond (1987) demonstrated that solar tracking cotton leaves were light saturated by a photon irradiance of 1.2 mmol m^{-2} s^{-1}, so that during the day leaves were experiencing irradiances 40% beyond what they were able to utilise in photosynthesis. The significance of a reduced photosynthetic rate and photosynthetic light utilisation in these crops is unclear. It is, however, important to note that both of these species have undergone significant selection during breeding so that some aspects of current plant performance may differ from those found in more primitive forms. In addition, solar tracking movements do not occur in all cultivated cotton varieties (Ehleringer & Hammond, 1987) and leaf movements in domesticated sunflowers decrease through time in mature plants (Lang & Begg, 1979).

In both native and crop species with paraheliotropic leaf movements, the gas exchange data indicate that leaves are operating near the upper end of the linear portion of the photosynthesis–light response curve (Fig. 7.2; *Lupinus*, *Pueraria*, *Glycine* and *Medicago*). This indicates that while the absolute photosynthetic rate of paraheliotropic leaves may be lower than that of diaheliotropic leaves, the efficiency of utilisation of incident light appears to be higher. The arrows in Fig. 7.2 indicate the average midday photon irradiance incident on the leaves. In all cases, it appears that paraheliotropism has resulted in a modification of the incident light so that leaves are operating over a

Fig. 7.2. The dependence of net CO_2 uptake by leaves of species exhibiting solar-tracking leaf movements. Based on Werk *et al.* (1983), Travis & Reed (1983), Ehleringer & Hammond (1987), and I. Forseth (unpublished observations).



portion of the response curve where changes in incident photon irradiance have a pronounced effect on photosynthetic rates.

Diurnal leaf movements have two principal effects on environmental aspects of photosynthesis: (1) they provide a mechanism whereby the plant is able to achieve favourable photosynthetic rates at specific times during the day, and (2) they allow the leaf to avoid high incident photon irradiances at times of the day that are not favourable for photosynthesis. In particular, since stomata are sensitive to humidity and close under reduced humidities (Schulze & Hall, 1982), solar tracking movements result in higher incident light levels, and thus faster photosynthetic rates, early in the morning and late in the afternoon when humidity levels are typically highest (Bonhomme, Varlet Grancher & Artis, 1974; Mooney & Ehleringer, 1978; Forseth & Ehleringer, 1983*b*). When the availability of soil water is limited, paraheliotropic leaves appear to have an advantage over strictly diaheliotropic leaves because they are able to vary the fraction of the direct solar beam that is incident. This allows the leaves to capitalise on early morning sunlight and to minimise midday and afternoon sunlight if soil water conditions are unfavourable (Shackel & Hall, 1979). In general, it appears tht paraheliotropic leaves move diurnally to adjust incident irradiances so that photosynthetic rates are not light saturated (Shackel & Hall, 1979; Travis & Reed, 1983; Forseth & Teramura, 1986).

Leaf movements to regulate incident solar radiation

While paraheliotropic leaf movements regulate the diurnal patterns of incident light, the significance of this phenomenon depends on the availability of soil water. Under conditions of adequate soil water, plants with the potential for paraheliotropic movements appear to be reacting to short-term midday conditions of high evaporative demand in such a way as to regulate light interception, so that a balance is struck between light level and gas exchange activity.

Some native and cultivated leguminous species growing in conditions of adequate soil water show constant diurnal values of cos(i) (Kawashima, 1969*a*, *b*; Forseth & Ehleringer, 1980; Forseth & Teramura, 1986). The value of this constant cos(i) varies between 0.4 and 0.6 and results in little variation in incident irradiance for these species throughout the day. This regulation of incident radiation will have several effects. First, since transpiration is likely to increase with increasing incident irradiance while photosynthesis shows a saturating response, water use efficiency will tend to be enhanced (Rawson, 1979). Radiation not necessary for photosynthetic carbon gain is thus not intercepted, reducing heat loads. Secondly, the maintenance of this constant cos(i) by outer canopy leaves will allow much greater light penetration into the lower canopy. This may enhance the contribution of leaves lower in the canopy to the overall carbon fixation of the canopy (Travis & Reed, 1983). Finally, the coincidence of peak irradiance levels and evaporative demand at midday experienced by horizontally displayed leaves is not experienced by these

paraheliotropic leaves (Fig. 7.4(*b*)). This results in the avoidance of short-term water stress conditions that may be induced by high transpiration rates even under conditions of high soil-water availability.

There are numerous reports of plant species being able to adjust leaf angles in response to limited soil moisture conditions (Dubetz, 1969; Wien & Wallace, 1973; Begg & Torssell, 1974; Shackel & Hall, 1979; Forseth & Ehleringer, 1980; Meyer & Walker, 1981; Herbert, 1984; Oosterhuis *et al.*, 1985). These studies indicate that under soil water stress, the leaves or leaflets increase their leaf angle such that they are near vertical at midday. Most of these species have compound leaves, and the "cupping movements" that result in these steep leaf angles involve leaflet folding

Fig. 7.3. Leaflet orientations in *Lupinus arizonicus* under well-watered (left), and droughted (right), soil conditions with the sun's position being in the upper left.

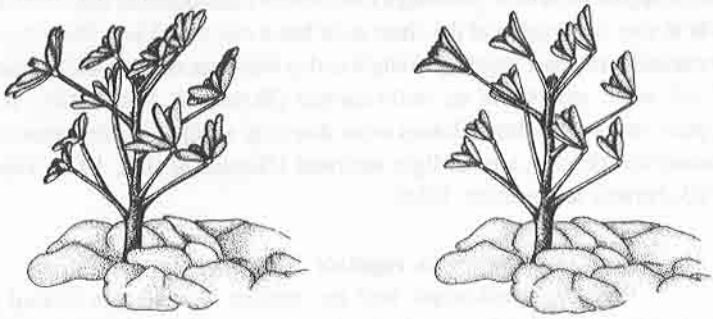
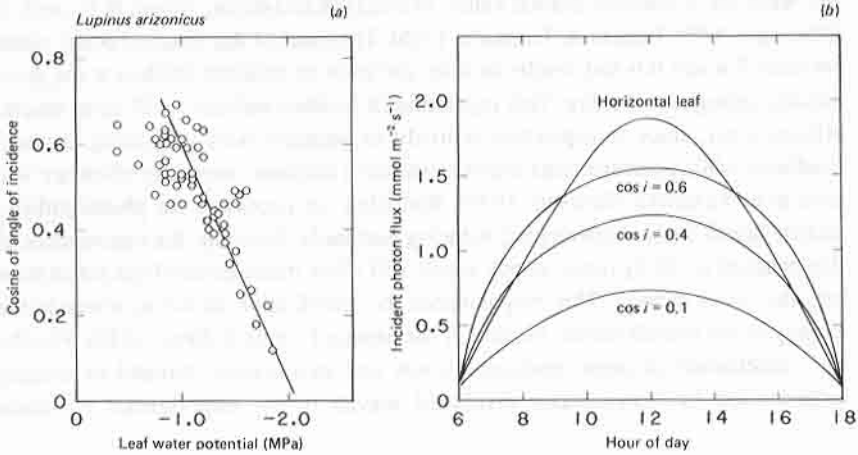


Fig. 7.4.(*a*). The dependence of the cosine of the angle of incidence for leaves of *Lupinus arizonicus* as a function of leaf water potential. Based on Forseth & Ehleringer (1980), and (*b*) the calculated solar radiation levels incident on leaflets of *Lupinus arizonicus* through the course of the day on 1 April (typical midpoint of growing season) as a function of the cosine of the angle of incidence. Based on Forseth & Ehleringer (1983*b*).



around the basal pulvinal region near the tip of the petiole (Fig. 7.3). While most investigators have focused their observations on the midday period, diurnal measurements of cos(*i*) values on water-stressed plants indicate that these sun-avoidance movements occur throughout the day (Shackel & Hall, 1979; Forseth & Ehleringer, 1980, 1983*a*).

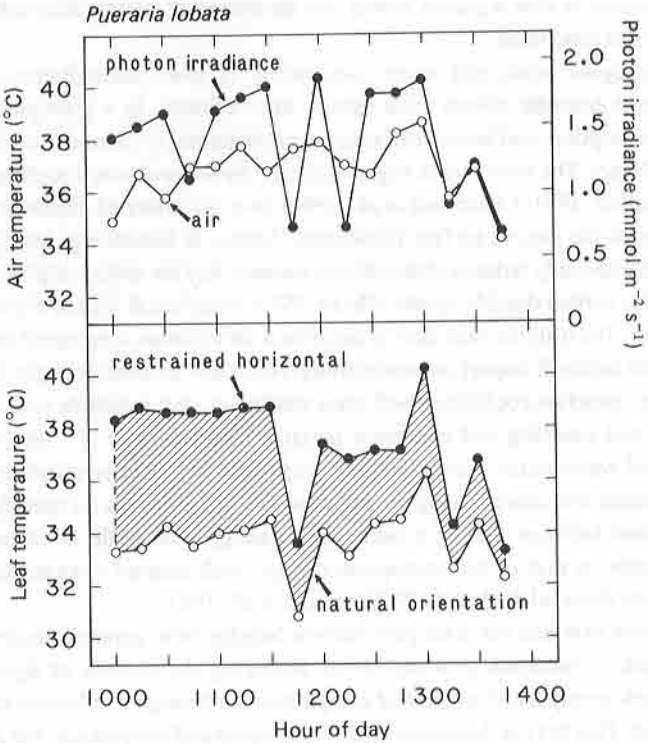
Further, instead of being an all-or-none phenomenon, cos(*i*) varies continuously with leaf water stress (Begg & Torssell, 1974; Shackel & Hall, 1979; Forseth & Ehleringer, 1980, 1983*a*). The response appears to be plastic and is rapidly reversible when the stress is alleviated. In *Lupinus arizonicus*, leaf cos(*i*) is closely related to leaf water potential (Fig. 7.4(*a*)). The responses of cos(*i*) to water stress for different field populations or for greenhouse versus field-grown materials are indistinguishable. There appears to be a tight control over leaf movements in *L. arizonicus*, so that neither leaf cos(*i*) nor leaf water potential exhibit much diurnal fluctuation (Forseth & Ehleringer, 1982). This results in less variable light levels on the leaf through the day (Fig. 7.4(*b*)). Local microsite variations in soil depth and water content in these desert soils, however, result in leaves from different plants within a single population exhibiting different values of cos(*i*). Since both leaf orientation and leaf conductance to water vapour are tightly coupled to the leaf water potential (Forseth & Ehleringer, 1982), the consequence is that adjacent plants can be operating quite differently depending on local soil conditions.

Under dense canopies when soil water availability is low, paraheliotropic movements will have dramatic effects upon canopy microclimate. In a planophile canopy, radiation absorption, and hence leaf temperature maxima, is concentrated in the upper few leaf layers. The vertical leaf angles achieved by water-stressed soybean crops (Meyer & Walker, 1981; Oosterhuis *et al.*, 1985) have the effect of displacing these maxima towards the ground surface (Baldocchi, Verma & Rosenberg, 1983). Since water stress significantly reduces photosythetic capacity and the ability of plants to use bright light for carbon dioxide uptake (Hsiao, 1973; Bradford & Hsiao, 1982; Forseth & Ehleringer, 1983(*a*)) the reduction in the amount of radiation intercepted by the canopy will have minimal impact on productivity. Also, due to these changes in leaf angle, radiation extinction coefficients will show marked diurnal variation, with a midday minimum and morning and afternoon maxima (Baldocchi *et al.*, 1983). Depending upon soil water status, paraheliotropic crops with high leaf area indices (LAI) such as soybean and cowpea (*Vigna unguiculata*) are thus able to modify radiation interception between that of a planophile canopy with high, constant extinction coefficients to that of an erectophile canopy with diurnal changes in extinction coefficients (Shackel & Hall, 1979; Baldocchi *et al.*, 1983).

There are four ways in which net plant performance benefits from paraheliotropic leaf movements under conditions of water stress. Reducing the amount of light incident upon the leaf greatly modifies the leaf energy balance through a reduction in the incident heat load. This has two beneficial effects: a lowered leaf temperature and a

consequent reduction in transpiration rate without necessarily any change in leaf conductance. Temperature changes can be substantial. Forseth & Teramura (1986) demonstrated that leaf temperatures of the weedy vine *Pueraria lobata* increased by 4 to 5 °C when leaves were prevented from cupping (Fig. 7.5). Such increases in leaf temperature will cause the transpiration rate to increase by 60–80%, solely because of the temperature-associated changes in the leaf to air water vapour gradient. A third benefit is that leaflet reorientation results in an increased water use efficiency of the leaves (photosynthesis/transpiration ratio). Under water-limited conditions when leaf conductances are already reduced, a reduction in cos(*i*) has a greater effect on lowering leaf temperature (and thus transpiration) than it does on reducing photosynthesis (Forseth & Ehleringer, 1983(*b*)). Lastly, a reduction in the amount of light absorbed by the leaf under water stress conditions reduces the likelihood of photo-inhibitory damage. Ludlow & Björkman (1984) have shown that if the reversible leaf movements are prevented in *Macroptilium atropurpureum*, a plant

Fig. 7.5. Photon irradiance (400–700 nm) and air temperatures adjacent to kudzu (*Pueraria lobata*) leaves near College Park, Maryland on 21 July and the corresponding leaf temperatures of naturally orientated and horizontally restrained leaves of kudzu (based on Forseth & Teramura, 1986).



which typically exhibits paraheliotropic leaf movements under conditions of water stress, there is a time-dependent reduction in photosynthetic activity caused by exposure to bright light.

Limitations associated with diurnal leaf movements

Diaheliotropic leaf movements maximise the interception of direct solar irradiation. This has consequences for canopy structure, light penetration within canopies, and on canopy size.

For most native desert annuals in North America, individuals are widely spaced and LAI values are generally between 1.0 and 1.5 (Adams, Strain & Adams, 1970; Beatley, 1969; Ehleringer & Mooney, 1983). Thus, for those species with either diaheliotropic or paraheliotropic leaf movements, effectively all leaves are fully exposed to sunlight. Canopy development is therefore constrained more by the period of adequate soil moisture than it is by light levels within the canopy leaves.

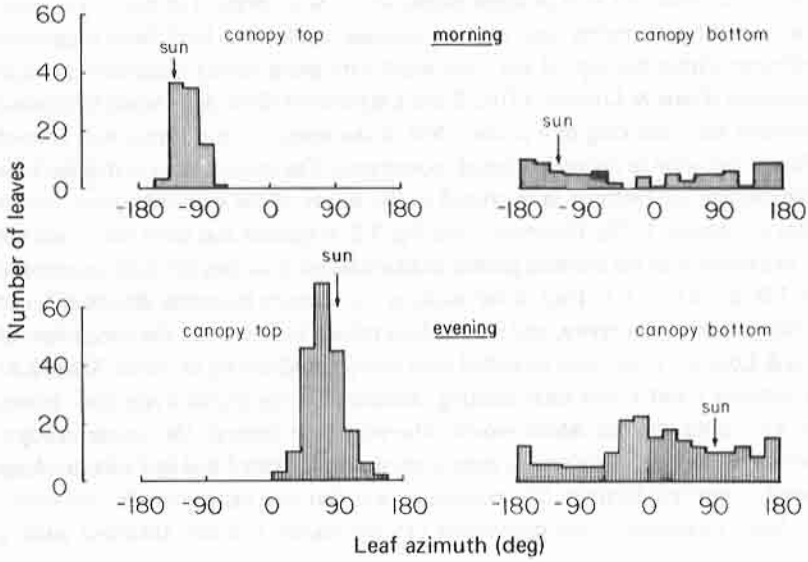
By contrast, in intensive agriculture sufficient water is available to the plants for a longer period of time and so they support a larger leaf area. In row-planted cotton, the upper canopy leaves are fully illuminated and exhibit strong diaheliotropic movements (Lang, 1973; Ehleringer & Hammond, 1987). As shown in Fig. 7.6, almost all the upper canopy leaves in a stand with an LAI of approximately 4 were oriented to within 60° of the sun's azimuth both early in the morning and again late in the afternoon. In contrast, the leaves in the lower canopy did not exhibit any pronounced tendency to orientate towards the sun. In the early morning the distribution of these leaves is uniform with respect to azimuth. By the end of the day there was an indication that a significant fraction was orientated to the south, probably reflecting the higher light levels on the southern side of these crops, which were planted in east–west rows. Data on light penetration into cotton canopies, indicate a high light extinction coefficient within the top 30 cm associated with these strong diaheliotropic leaf movements (Fukai & Loomis, 1976). Since a significant direct solar beam is required to achieve solar tracking movements, few of the inner canopy leaves will receive sufficient radiation to maintain diurnal movements. The consequence is that the bulk of the canopy productivity is restricted to the leaves of the extreme upper canopy (Fukai & Loomis, 1976). However, from Fig. 7.2, it appears that these leaves are not able to capitalise on the elevated photon irradiances, because they are light saturated at only 1.0 mmol m^{-2} s^{-1}. Thus, solar tracking movements in cotton do not enhance overall canopy productivity, and may indeed reduce it. Such was the conclusion of Fukai & Loomis (1976), who modelled total canopy productivity in cotton. When LAI was between 1 and 2, leaf solar tracking enhanced canopy productivity since leaves were absorbing photons which would otherwise pass through the sparse canopy. However, when LAI was above 4, simulation results indicated that leaf solar tracking reduced canopy productivity. The conclusion was that total canopy production would have been increased if the uppermost canopy leaves had not absorbed such a

significant fraction of the incident light, but instead had allowed for greater light penetration into the canopy.

Begg & Jarvis (1968) investigated photosynthetic characteristics and canopy productivity in Townsville stylo (*Stylosanthes humilis*), a plant with diaheliotropic movements under well-watered conditions and paraheliotropic movements under droughted conditions. Their observation was that while less than 10% of the total LAI was located in the top 10 cm, this layer absorbed 80–86% of the sunlight under well-watered conditions. Their photosynthetic canopy models predicted that the maximum canopy productivity would be attained with a 20 cm canopy, and that productivity should be lower in taller canopies.

In contrast to diaheliotropic movements, paraheliotropic leaf movements are not expected to limit canopy size. Instead, paraheliotropism under well-watered conditions provides a mechanism whereby outer canopy leaves can regulate the extent of light penetration into lower canopy levels. Travis & Reed (1983) explored the consequences of solar tracking on light penetration into alfalfa canopies. Photosynthetic rates in alfalfa are light saturated at 1 mmol m^{-2} s^{-1} (Fig. 7.2). In alfalfa, cos(i) increases with depth into the canopy. Thus, the outermost leaves have a low cos(i), allowing a greater light penetration into the canopy. Since the lower canopy leaves have a cos(i) near 1.0 a greater fraction of the leaves in the canopy are able to operate at maximal photosynthetic rates. In contrast to the Townsville stylo

Fig. 7.6. The distributions of leaf azimuths of a solar-tracking cotton (*Gossypium hirsutum* cv. Delta Pine 62) measured at the top and bottom of a canopy in the early morning and again in the late afternoon. Based on Ehleringer & Hammond (1987).



canopy, alfalfa canopies exhibit maximum productivity at a canopy height of 65 cm (Stanhill, 1962).

Ecological patterns

Leaf solar tracking movements only influence plant performance when the ratio of direct to diffuse components of the solar radiation is high since only in these conditions will leaf movements be able to regulate or affect the incident light levels. This implies that diaheliotropism and paraheliotropism should be restricted to environments receiving high daily total photon irradiances or environments in which a significant fraction of the day is clear, i.e., they would not be expected to occur in habitats with a high incidence of overcast days or in understorey habitats.

Diaheliotropic leaf movements should have their greatest benefit in arid lands and in habitats with strong monsoon activity because in these situations the canopy LAI is low due to soil moisture limitations or short growing seasons.

This is in fact the pattern that has emerged. By far the overwhelming majority of species reported as having diaheliotropic leaf movements are in desert environments with short, unpredictable growing seasons, or in weedy, disturbed habitats (Yin, 1938; Schwartz & Koller, 1978; Ehleringer & Forseth, 1980).

Paraheliotropic leaf movements can be expected in any environment with a high direct irradiance and where either diurnal or seasonal environmentally-induced stress may occur. It is uncertain whether high temperature, photosynthetic photoinhibition, high rates of transpiration, or soil-induced water stress is more important for its occurrence. Single, or in combination they may all have played a role in the evolution of paraheliotropism. So far, reports of its occurrence range from 33 leguminous species in the seasonally-dry tropical environment of the Philippine Islands (Gates, 1916) to temperate tree species (McMillen & McClendon, 1979), subtropical legumes (Herbert, 1984), temperate lianas (Forseth & Teramura, 1986), leguminous crops (Dubetz, 1969; Wien & Wallace, 1973; Shackel & Hall, 1979; Meyer & Walker, 1981), semi-arid pasture legumes (Sheriff & Ludlow, 1985) and finally to arid land trees and annuals (Wainwright, 1977; Ehleringer & Forseth, 1980). These examples span a range of values of LAI from less than 1 to more than 5. This indicates that these leaf movements are not necessarily detrimental to productivity and may actually enhance productivity on a canopy basis.

Paraheliotropic movements are particularly evident during midday periods when the sun is high in the sky. Under these conditions, leaf angle changes affect cos(i) to a greater extent than do changes in leaf azimuth. In fact, most reports show random distributions of leaf azimuth during midday periods in paraheliotropic species (McMillen & McClendon, 1979; Travis & Reed, 1983; Oosterhuis *et al.*, 1985; Forseth & Teramura, 1986). Several lines of evidence, including (1) the requirement only for angle changes for midday effects, and (2) the widespread occurrence of paraheliotropism in many habitats as well as in situations of both high and low canopy

development, suggest that this type of movement may have evolved first. Paraheliotropism is widespread in compound-leaved species, especially in the Fabaceae (Gates, 1916; McMillen & McClendon, 1979; Herbert & Larsen, 1985). Compound leaves may represent a preadaptation for rapid changes of leaf angle at midday. This feature may explain the dramatic increase in the number of canopy species with compound leaves as you move along an environmental gradient from wet, evergreen tropical forests to seasonally dry, deciduous tropical forests (Givnish, 1978). Further evolutionary and biogeographical musings regarding leaf solar tracking must, however, await a more complete survey of habitats.

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