

Leaf movement in *Calathea lutea* (Marantaceae)

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Summary. *Calathea lutea* is a broad-leaved, secondary successional plant which shows complex leaf movements involving both elevation and folding of the leaf surface about the pulvinus. In the plants studied, mean leaf elevation increased from approximately 34 degrees in the early morning to 70 degrees at noon while the angle of leaf folding increased from 13 degrees to 50 degrees over the same time period. During the period from early morning to noon, these movements resulted in a significant decrease in the cosine of the angle of incidence, a measure of the direct solar radiation intercepted. The observed changes in elevational angle significantly reduce the cosine of angle of incidence while folding does not significantly reduce the fraction of direct solar radiation intercepted during the period of direct exposure of the leaf surface to the solar beam. Since elevational changes seem to account for the reduction in exposure to direct solar radiation, the role of folding remains unclear.

The orientation of photosynthetic surfaces with respect to the radiation environment has been shown to be an important factor in the regulation of the amount of photosynthetically active radiation (PAR) intercepted by plants and the maintenance of optimal leaf temperatures (Darwin 1881; Yin 1938; Dubetz 1969; Wien and Wallace 1973; Wainwright 1977; Schwartz and Koller 1978; Forseth and Ehleringer 1980; Ehleringer and Forseth 1980). In particular Fisher and Honda (1979a, b) have demonstrated that the spacial arrangement of leaves in *Terminalia* optimizes interception of direct solar radiation and Oikawa and Sacki (1977) and Oikawa (1977a, b) have described the importance of spacial organization in plant stands for effective interception of direct radiation. Numerous other examples of the importance of orientation of photosynthetic surfaces and the geometry of spacial organization for interception of solar radiation have been given in the reviews by Monsi, Uchijima, and Oikawa (1973) and Fisher (1974) and the book by Ross (1981).

Leaf movement as a heat avoidance mechanism usually has been described for desert annuals or leguminous agricultural plants under conditions of drought (Dubetz 1969; Ehleringer and Forseth 1980; Forseth and Ehleringer 1980; Shackel and Hall 1979; and Wainwright 1977). However,

even in generally rainy climates, heat and drought stress can occur during periods of maximum insolation (Tazaki et al. 1980). This is especially true in large tropical rain forest clearings where midday decreases in relative humidity can produce evaporative water losses an order of magnitude greater than those in the understory of the surrounding forest (Longman and Jenik 1974). Under these conditions, if air temperature is high, large leaves have particular difficulty in optimizing temperatures because convective heat losses are minimized as the result of unfavorable boundary conditions (Taylor and Sexton 1972) while transpirational heat losses are restricted by water stress.

The ability to control leaf temperature permits the photosynthetic reactions to occur close to their temperature optimum, avoids counterproductive increases in photorespiration, and decreases in transpirational water loss without requiring stomatal closure to the extent that carbon dioxide conductance is severely impaired (Ehleringer and Bjorkman 1978a, b; Ehleringer and Mooney 1978a, b; Ehleringer and Forseth 1980; Ehleringer 1980). Behavioral or structural adaptations which result in reduced heat absorption or increased convective loss should be of high selective value since neither involves alteration of water or carbon dioxide balance, the result of which might be a limitation of photosynthesis.

The purpose of this study was to characterize some of these behavioral and structural adaptations by observation of leaf movements of the broad-leaved, secondary successional plant *Calathea lutea* (Marantaceae) in rain forest clearings in Panama and Costa Rica. Since the orientation of leaf surfaces can be characterized completely by measurements of azimuth (compass direction), elevational angle, and the amount of folding or axial rotation of the surface about the midrib (Herbert 1983a), an accurate representation was developed of the orientation of these surfaces to direct solar radiation. This paper will present a description of these measurements and an analysis of the importance of different types of leaf surface orientation and movement to the regulation of light interception and temperature regulation.

Materials and methods

Field site. Studies were performed between 9 and 13 March, 1982 on Barro Colorado Island in Panama (9° 10'N latitude, 79° 10'W longitude). Some additional observations were made in late February and early March, 1981 in the

Corcovado National Park on the Osa Peninsula in Costa Rica (8°30'N latitude, 83°35'W longitude) and at the LaSelva Field Station in Costa Rica (10°26'N latitude, 84°0'W longitude) between 13 and 17 February, 1984. These additional observations were consistent with those made in Panama and increase confidence in the general applicability of our conclusions. All study sites were areas where successional vegetation had appeared following recent clearance for agriculture or construction. Although rainfall in the study areas is substantial (2,500–5,000 mm/year), only a very small amount occurs during the dry season from late December through April. For example, at Rincon, near Sirena, Costa Rica, only 249 mm of the 3,749 mm annual rainfall occurs from January through March and at LaSelva only 470 mm of the 3,649 mm annual rainfall occurs during the months of February through April (Holdridge, Grenke, Hatheway, Liang, and Tosi 1971). At Rincon, this results in a progressive increase in the soil moisture deficit from 0 to 127 mm of water over the course of the dry season. On Barro Colorado Island, only 300 mm of the annual average rainfall of 2,718 mm occurs during the month of March (Croft 1978). In all three study areas, direct insolation of the experimental plants ceased in the early afternoon (1300–1500 h) because of shading from neighboring forest stands.

Measurement and description of leaf surface orientation. The orientation of a leaf surface was described by measurement of three parameters. The elevational angle of the midrib above the horizontal, β ; the azimuthal angle or compass direction η_0 into which the leaf midrib points; and the axial rotation angle τ , (Herbert 1983a). The axial rotation angle τ is a particularly good measure of leaf folding since it is independent of other measures of vertical surface orientation such as elevational angle and is descriptive of rotational movement about the pulvinar axis. Elevation and azimuth were measured directly with inclinometer and compass and axial rotation angles were calculated from inclinometer and compass measurements by methods described previously by Herbert (1983a).

One measure of the orientation of leaf surfaces with respect to the direct solar beam is given by the angle of incidence, θ , the angle between a vector from the leaf surface to the sun and a vector normal to the leaf surface. The cosine of angle of incidence represents the fraction of the maximum possible direct solar radiation which is intercepted by the leaf surface and is given by (Herbert 1983a);

$$\cos \theta = (\cos \beta \cos \zeta + \cos \alpha \sin \beta \sin \zeta) \cos \tau - \sin \alpha \sin \zeta \sin \tau \quad (1)$$

where ζ is the zenith angle of the sun and $\alpha = \eta_0 - \eta_s$, where η_s is the azimuth or compass direction into which the solar beam points. The zenith angle and azimuth of the sun were obtained from a FORTRAN program based upon equations given by List (1951). Additionally, a measure of the orientation of the leaf midrib towards the sun is given by the angle ϕ between a vector from the leaf surface to the sun and a vector parallel to the leaf midrib and pointing from the pulvinus towards the leaf tip. The cosine of this angle is shown in the appendix to this paper to be given by the expression;

$$\cos \phi = \sin \beta \cos \zeta - \cos \alpha \cos \beta \sin \zeta \quad (2)$$

Data analysis and statistics. Data was pooled into one hour time intervals centered on the hour. Thus, data points desig-

nated as 1200 h include data from 1130 thru 1229 h. Measured and derived quantities based on angular variables such as leaf elevational angle, axial rotation angle, and cosine of angle of incidence were calculated as true vectorial averages of circular variables (Batschelet 1981). Confidence limits on these averages were calculated using the methods given by Stephens (1962). Stephens presents an exact and an approximate method for calculation of nomographs from which confidence limits on the mean of circular variables can be obtained. For ease in computation, a FORTRAN computer program was written which uses the approximate method of Stephens to calculate confidence limits. These approximate methods were tested against the exact methods of Stephens for values of the probability P that the true mean lies outside the confidence limits between 0.01 and 0.99 and were found to be at least as good estimates of the confidence limits as given by Stephens for values of $P = 0.90, 0.95, \text{ and } 0.99$.

In order to evaluate the functional significance of leaf elevation and axial rotation, the observed mean values of the cosine of angle of incidence were compared with values which were obtained by setting the axial rotation angles at zero or the elevational angles at their minimum early morning values. Mean values of the angle of incidence were compared by use of the Watson-Williams test for differences in the means of circular variables (Batschelet 1981).

Instrumentation and experimental techniques. Leaf temperatures were measured using Omega 870 and Bailey BAT-12 digital thermocouple thermometers employing probes of bead diameter less than 0.23 mm. For some measurements, temperatures were measured by briefly touching the probe to the leaf surface opposite to that receiving direct solar radiation. For other measurements, the thermocouple was secured in contact with the leaf surface with surgical thread to permit continuous recordings.

Results

Observation of the movement of leaf surfaces of *Calathea lutea* showed large changes in both elevational angle and axial rotation angle and generally insignificant changes in leaf azimuth. On Barro Colorado Island, Panama, during early March, the average elevational angle for three adjacent plants (plants A, B, C) was observed to reach a minimum of near 30 degrees in the early morning between about 5.5 and 6.5 h before solar noon. The average elevational angle rapidly increased to about 70 degrees at or slightly before solar noon and then decreased to an evening minimum of about 30 degrees about 4.5 h after solar noon (Fig. 1). Near noon, a few leaves were observed to have elevational angles as large as 108 degrees, indicating that the surfaces were oriented with the white, abaxial surface pointing upwards. (At the two sites in Costa Rica, the exposure of the abaxial surface to the direct solar beam was particularly noticeable.) During the early evening, elevational angles again increased as the leaves moved into a vertical orientation characteristic of the "sleeping" position.

During the night and the nearly morning hours, leaves were observed to be unfolded with axial rotation angles of zero (Fig. 1). Beginning about 6.5 h before solar noon, the leaves folded rapidly, with the average axial rotation angle for leaf surfaces reaching a maximum of about 50

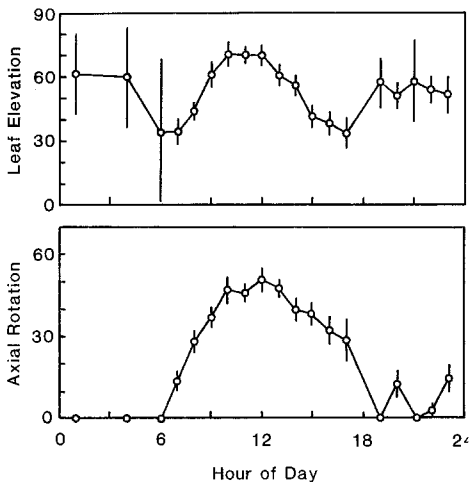


Fig. 1. Average elevational and axial rotation angles for 38 leaf surfaces of plants A, B, and C. Error brackets represent 95% confidence limits on the mean. The number of leaf surfaces N measured for each hourly period ranges from 8 to 202 with a minimum of $n=66$ between 0700 and 1600 h

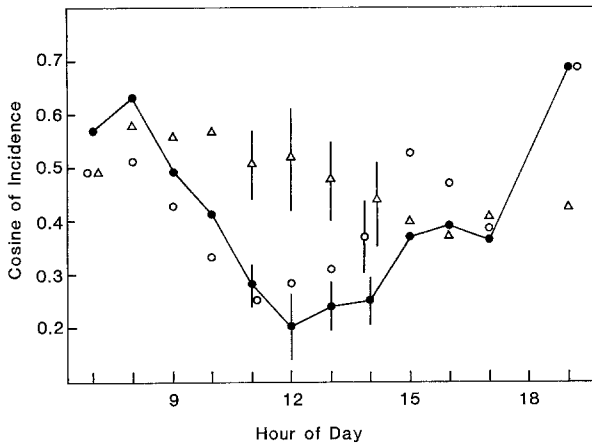


Fig. 2. Average cosine of angle of incidence for 8 leaf surfaces of plant A (filled circles). Open circles represent values of the cosine calculated for $\tau=0$, and measured values of β and triangles for values of the cosine calculated for measured values of τ and morning minimum values of β . Error brackets representing 95% confidence limits are shown only for those values for which there are significant differences between the values represented by filled and open symbols. N varies from 8 to 64 with a minimum of $n=24$ between 0700 and 1600 h

degrees near noon. After noon, the leaves unfolded with a time course which was somewhat slower than that of the afternoon decrease in elevational angles.

As a result of the movement of the leaf surfaces during the daylight hours, the average cosine of angle of incidence dropped from early morning values of about 0.6 to 0.7 to a midday minimum which rarely exceeded 0.25. An example of this striking drop in the cosine is shown in Fig. 2 for one plant (plant A) studied in Panama. This plant maintained a low value for the average cosine of incidence from approximately noon to about 1500 h, at which time the plant began to become shaded by adjacent trees and the cosine increased. These temporal changes in the cosine of angle of incidence are the result of the morning increase and afternoon decrease in the angle of incidence, θ (Fig. 3). Simultaneously with the morning increase in the angle of

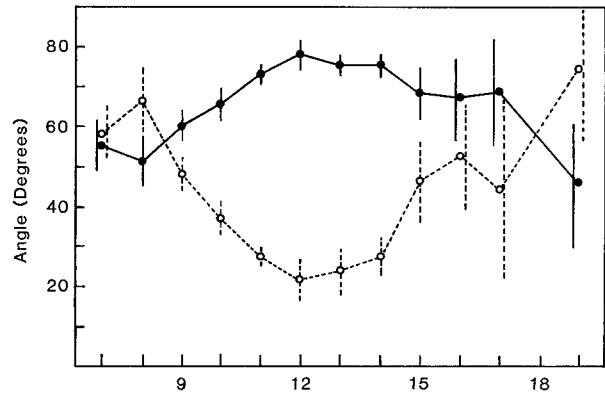


Fig. 3. Average angle of incidence θ (filled circles) and midrib angle ϕ (open circles) for the 8 leaf surfaces of plant A as in Figure 2. Error brackets represent 95% confidence limits

incidence, there was a sharp decrease in the angle between the midrib and the solar beam. This angle reached a minimum approximately at noon just as the angle of incidence reached a maximum and did not change significantly until 1500 h when shading began.

In order to assess the relative importance of leaf elevation and folding in the midday reduction of the average cosine of angle of incidence, the cosine was calculated under three sets of conditions. First, the average cosine of angle of incidence was calculated using measured values for leaf elevation, rotation, and azimuth. Then, values for the average cosine of angle of incidence were recalculated under the assumption that either axial rotation was fixed at zero or elevational angle of each leaf was fixed at minimum morning values. Confidence limits at the 95% level were obtained for each value of the cosine of angle of incidence through calculation of the error brackets on the angle of incidence using circular statistics. As shown in Fig. 2, during the early to mid-afternoon, a significant difference appeared between values of the cosine of angle of incidence calculated using measured values for the axial rotation angle and values of the cosine calculated by setting axial rotation angles to zero. For each plant studied, the period of time during which there were significant differences between these values for the cosine coincided with the onset on shading of the leaves by adjacent vegetation. Comparison of values of the cosine of angle of incidence calculated using measured and minimum morning values of elevational angles shows significant differences over a longer period of time extending from mid-morning through mid-afternoon, an interval extending just up to the onset of shading.

The results of the effects of leaf elevation and folding upon the average angle of incidence for plants A, B, and C in Panama and plants C and D at LaSelva, Costa Rica are summarized in Table 1. These results were obtained by comparison of values of angle of incidence averaged over one hour periods of time centered on one hour intervals relative to solar noon. Examination of this table shows that elevational changes have a significant effect upon the angle of incidence from two hours before solar noon to one hour after solar noon, at which time shading of plant A begins. However, changes in axial rotation angle have a significant effect upon the angle of incidence only during the period of progressive shading of plants A, B, and C (from one hour to three hours after solar noon).

Table 1. Significant differences between averages of the angle of incidence θ for plants A–D during one hour periods relative to solar noon. A positive sign indicates a difference significant at the 95% confidence level for comparison between: (I) the average angle computed for measured β , τ and that computed for measured β , $\tau=0$ or (II) comparison between the average angle computed for measured β , τ and that computed for measured τ and minimum morning values of β . The period of progressive shading of these plants is represented by the hour periods marked as (*)

Hours relative to solar noon	Number of surfaces	Significant differences between actual values for cosine and:	
		Model I ($\tau=0$)	Model II (minimum β)
-4	184	-	-
-3	102	-	-
-2	194	-	+
-1	168	-	+
0	60	-	+
+1*	184	+	+
+2*	146	+	+
+3*	148	+	+
+4	108	-	-

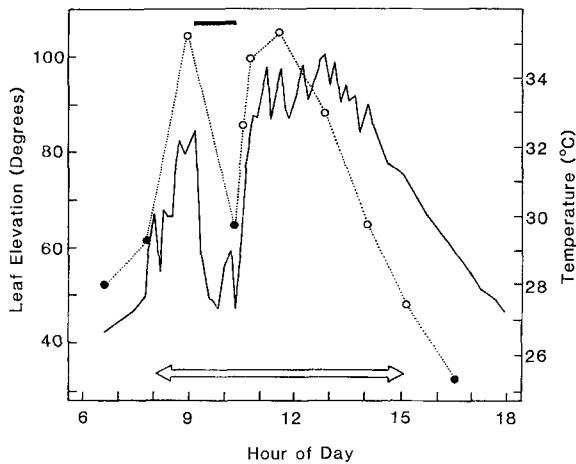


Fig. 4. Leaf elevation (circles) and temperature (solid line) for one leaf of plant A. Solid circles represent points for which the average cosine of angle of incidence for the two halves of this leaf is equal to or exceeds 0.5. The filled horizontal bar indicates the time period during which a water spray was applied and the open horizontal bar indicates the period during which the leaf was unshaded

Individual plants were subjected to a fine cool water spray in an attempt to assess the effect of reduced temperature upon leaf orientation under conditions of full exposure to the direct solar beam. Figure 4 shows an example of the results obtained from such an experiment in which continuous recordings of leaf temperature were made on individual leaves by attaching a thermocouple in contact with the abaxial leaf surface. In this experiment, onset of the water spray resulted in a sudden decrease in leaf temperature of about 5° C, reduction in leaf elevation of over 40°, unfolding of the leaf surface to an orientation with approximately zero axial rotation angle, and an increase in the cosine of angle of incidence from 0.27 to 0.76. After cessation of the water spray, elevational and axial rotation angles and the cosine of angle of incidence all returned to values

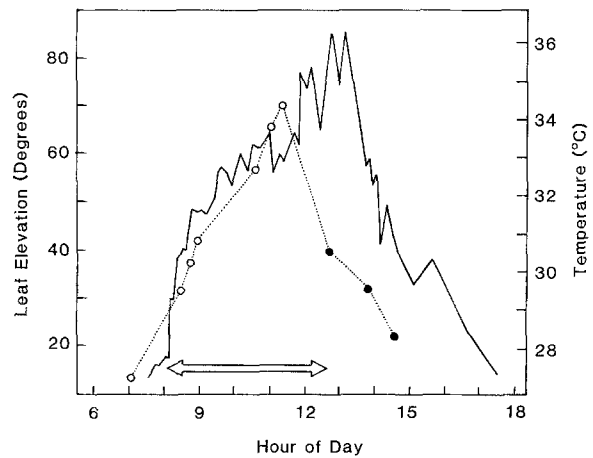


Fig. 5. Leaf elevation (circles) and temperature (solid line) for one leaf of plant B. Solid circles represent points for which the average cosine of angle of incidence for the two halves of this leaf is equal to or exceeds 0.5. The open horizontal bar indicates the period during which the leaf was unshaded

that were not significantly different from those measured on the same leaf at the same time on the previous or the next day. The results of this type of experiment on a total of 30 leaf surfaces all indicate that the onset of the water spray results in a decrease in elevational and axial rotation angles and an increase in the cosine of the angle of incidence and that soon after the water spray is stopped all parameters return to the values predicted in the absence of spray.

Although changes in leaf orientation seem to be correlated to the onset and cessation of the water spray, and the rapid temperature changes associated with the spray, a striking feature observed in each experiment was that the normal decrease in elevational angles in the early afternoon precedes a drop in temperature by approximately 2–4 h. The results of an experiment in which no water spray was applied to the plant confirms that elevational angles drop sharply near noon and precede a decrease in temperature for all plants, not just those subjected to experimental cooling (Fig. 5).

Discussion

Leaves of *Calathea lutea* show a pronounced increase in both elevational angle and folding as the solar zenith angle increases during the morning and a corresponding decrease in the inclination of surface elements during the afternoon. During a period of 3 to 4 h around solar noon, both elevational angles and folding are at their maximum values. However, if the leaf surfaces were either folded or elevated at this time of high solar elevation, the interception of direct solar radiation could be reduced to very low values without having simultaneous change in both parameters. Previously, Herbert (1983a) has shown that axial rotation or folding permits any leaf surface to reduce the interception of direct solar radiation to zero, independent of leaf or solar elevation or azimuth. Additionally, that study demonstrated that the effect of folding upon reduction of interception of the direct solar beam was greatest at low leaf elevations and high solar elevations. Furthermore, Ledent (1976, 1978) has shown that helicoid twisting of leaves and undulation of leaf surfaces has the greatest effect upon reduction of inter-

ception of direct solar radiation when the leaf elevation is small and the sun is nearly overhead.

Therefore, since the leaves of *Calathea lutea* show nearly simultaneous increases in leaf elevation and folding, it is unlikely that leaf folding contributes significantly to a reduction in the interception of the solar beam around noon. This hypothesis is supported by the results presented in Table 1. These data show that the only significant differences between interception of the solar beam by normal, folding leaves and hypothetical leaves which elevate normally but do not fold occur after solar noon and during a period of progressive shading of the leaf surfaces by surrounding plant structures. These results are similar to those found for leaves of *Erythrina herbacea* (Herbert 1984). For those plants, similar calculations indicated that there was no evidence of a significant effect of axial rotation of the leaf surface upon interception of the direct solar beam during any part of the day for which leaves were exposed to the direct solar beam.

Additionally, inspection of the results presented in Fig. 3 shows that, while the angle of incidence increased significantly near noon, the angle between the midrib and a vector from the leaf to the sun decreased very rapidly in the morning. Since this angle was relatively small near noon, one would expect that changes in axial rotation angle would only slightly affect the cosine of angle of incidence.

What, then, is the value of axial rotation or folding of leaf surfaces? Some reduction in water loss might be expected as the result of increased relative humidity caused by the proximity of the two upper surfaces of the leaf. However, measurements on leaves of *Calathea lutea* at La Selva show that while the stomate density was 305 ± 48 stomata/mm² on the abaxial surface on a sample of 6 leaves, there were only 19 ± 11 stomata/mm² on the adaxial surface. Additionally, other plants, such as *Erythrina*, which show axial rotation of widely spaced leaflets (Herbert 1984), intercept direct solar radiation in a way which is nearly identical to that described in this paper for the folding leaves of *Calathea lutea*.

One possible clue to the significance of axial rotation may be the fact that axial rotation seems to have the greatest effect upon the interception of the direct solar beam during periods of progressive shading of the leaves. This observation suggests that the control of axial rotation or folding may serve as one mechanism to regulate the amount of direct illumination reaching lower layers of leaves and to maximize the amount of direct and diffuse illumination intercepted by these lower layers. This concept is supported by observations of Wien and Wallace (1973) on the orientation of the leaflets of soybeans to a radiation source. These authors suggest that both elevational changes and axial rotation redistribute radiation among the leaves, resulting in higher net photosynthesis than could be achieved without daily leaf movement. However, in that study, the effects of either elevation or axial rotation alone were not quantified and the authors were unable to describe individually the separate contributions of the two types of leaf movement to the interception of direct solar radiation.

Leaf orientation in *Calathea* results in at least two important physiological effects: regulation of the amount of photosynthetically active radiation (PAR) reaching each surface and regulation of temperature and water loss. Experimental reduction of the leaf temperature and increase in relative humidity as a result of application of a fine water

spray effects rapid changes in both axial rotation and elevational angles and an increase in the cosine of angle of incidence. The movement of leaves under these conditions occurs simultaneously with onset and cessation of the spray. However, the results presented in Figs. 4 and 5 also indicate changes in leaf orientation which precede temperature changes when the leaf cools in response to the decrease in solar flux in the afternoon. These differences in timing between leaf movement in response to application of a water spray and movement resulting from natural cooling suggest that the movement of leaves to a more vertical orientation near midday may be a response to changes in leaf water potential and solar flux rather than temperature. Additionally, an important effect of the observed axial rotation and elevation of leaves might be optimization of total plant PAR interception and leaf temperature in addition to the reduction of water loss by the plant.

The relative importance of leaf movement to the optimization of net photosynthetic rate is an important factor in the development of a clear understanding of the cost-benefit relationships of the interception of solar radiation, temperature regulation, water loss, and the mechanical energy required to effect movement. Future studies will concentrate particularly on a more complete theoretical and experimental description of the distribution of solar radiation resulting from leaf movement and on the energetic costs of that movement.

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Appendix

From the matrix formulation of coordinate transformations given previously (Herbert 1983a), the unit vector **P**, pointing outward along a leaf midrib, is given by;

$$\mathbf{P} = \cos\beta \cos\eta_0 \mathbf{x} + \cos\beta \sin\eta_0 \mathbf{y} + \sin\beta \mathbf{z}. \quad (\text{A1})$$

The unit vector **S**, pointing from the leaf to the sun, is given by (Herbert 1983b);

$$\mathbf{S} = -\sin\zeta \cos\eta_s \mathbf{x} - \sin\zeta \sin\eta_s \mathbf{y} + \cos\zeta \mathbf{z}. \quad (\text{A2})$$

Since both vectors are normalized, the cosine of the angle ϕ between these vectors is given by the inner product of **P** and **S**;

$$\cos\phi = \mathbf{P} \cdot \mathbf{S} = \cos\zeta \sin\beta - \sin\zeta \cos\beta (\cos\eta_s \cos\eta_0 + \sin\eta_s \sin\eta_0). \quad (\text{A3})$$

Using the definition, $\alpha = \eta_0 - \eta_s$, and trigonometric identities, this equation becomes identical to that presented in equation 2.

References

- Batschelet E (1981) Circular statistics in biology. Academic Press, London
- Croat TB (1978) Flora of Barro Colorado Island. Stanford University Press, Stanford, California
- Darwin CR (1881) The power of movement in plants. Appleton, New York
- Dubetz S (1969) An unusual photonastism induced by drought in *Phaseolus vulgaris*. Can J Bot 47:1640-1641
- Ehleringer JR, Bjorkman O (1978a) Pubescence and leaf spectral characteristics in a desert shrub, *Encelia faarinoso*. Oecologia (Berlin) 36:151-162

- Ehleringer JR, Bjorkman O (1978b) A comparison of photosynthetic characteristics of *Encelia* species possessing glabrous and pubescent leaves. *Plant Physiol* 62:185–195
- Ehleringer JR, Forseth IN (1980) Solar tracking by plants. *Science* 210:1094–1098
- Ehleringer JR, Mooney HA (1978) Leaf hairs: effects on physiological activity and adaptive value to a desert shrub. *Oecologia* 37:183–200
- Fisher JB (1984) Tree architecture relationships between structure and function. In: White RA, Dickison WC (eds), *Contemporary problems in plant anatomy*. Academic Press, Orlando Florida, pp 541–589
- Fisher JB, Honda H (1979) Branch geometry and effective leaf area: A study of *Terminalia*-branching pattern. 1. Theoretical Trees. *Am J Bot* 66:633–644
- Fisher JB, Honda H (1979) Branch geometry and effective leaf area: A study of *Terminalia*-branching pattern. 2. Survey of real trees. *Am J Bot* 66:645–655
- Forseth IN, Ehleringer JR (1980) Solar tracking response to drought in a desert annual. *Oecologia (Berlin)* 44:159–163
- Forseth IN, Ehleringer JR (1982) Ecophysiology of two solar tracking desert winter annuals. *Oecologia (Berlin)* 54:41–40
- Herbert TJ (1983a) The influence of axial rotation upon interception of solar radiation by plant leaves. *J Theoret Biol* 105:603–618
- Herbert TJ (1983b) On the relationship between interception of direct solar radiation by cactus bodies and plant leaves. *J Theoret Biol* 105:619–629
- Herbert TJ (1984) Axial rotation of *Erythrina herbacea* leaflets. *Am J Bot* 71:76–79
- Holdridge LR, Grenke WC, Hatheway WH, Liang T, Tosi Jr JA (1971) *Forest environments in tropical life zones*. Pergamon Press, Oxford pp 50–54
- Honda H, Fisher JB (1978) Tree branch angle: maximizing effective leaf area. *Science* 199:888–889
- Ledent JF (1976) Beam light interception by twisted leaf surfaces. *Agric Meteorol* 17:271–280
- Ledent JF (1978) Beam light interception by leaves with undulating edges – A simulation of maize leaf sections. *Agric Meteorol* 19:399–410
- List RJ (1963) *Smithsonian meteorological tables*, 6th ed. Smithsonian Institution, Washington DC pp 495–497
- Longman KA, Jenik J (1974) *Tropical forest and its environment*. Longman, London
- Monsi M, Uchijima Z, Oikawa T (1973) Structure of foliage canopies and photosynthesis. *Annual Review of Ecology and Systematics* 4:301–327
- Oikawa T (1977) Light regime in relation to plant population geometry. II. Light penetration in a square-planted population. *Bot Mag (Tokyo)* 90:11–22
- Oikawa T (1977) Light regime in relation to plant population geometry. III. Ecological implications of a square-planted population from the viewpoint of utilization efficiency of solar energy. *Bot Mag (Tokyo)* 90:301–311
- Oikawa T, Saeki T (1977) Light regime in relation to plant population geometry. I. A Monte Carlo simulation of light microclimates within a random distribution foliage. *Bot Mag (Tokyo)* 90:1–10
- Ross J (1981) *The radiation regime and architecture of plant stands*. Dr. W. Junk Publishers, The Hague
- Schwartz A, Koller D (1978) Phototropic response to vectorial light in leaves of *Lavatera cretica* L. *Plant Physiol* 61:924–928
- Shackel KA, Hall AE (1979) Reversible leaflet movements in relation to drought adaptation of cowpeas, *Vigna unguiculata* (L.) Walp. *Aust J Plant Physiol* 6:265–276
- Stephens MA (1962) Exact and approximate tests for directions I. *Biometrika* 49:463–477
- Taylor SE, Sexton OJ (1972) Some implications of leaf tearing in *Musaceae*. *Ecology* 53:143–149
- Tazaki T, Isihara K, Usijima T (1980) Influence of water stress on the photosynthesis and productivity of plants in humid areas. In: NC Turner and PJ Kramer (eds), *Adaptation of plants to water and high temperature stress*. Wiley and Sons, New York, pp 309–322
- Wainwright GM (1977) Sun-tracking and related leaf movements in a desert lupine (*Lupinus arizonicus*). *Am J Bot* 64:1032–1041
- Wien HC, Wallace DH (1973) Light-induced leaflet orientation in *Phaseolus vulgaris* L. *Crop Sci* 13:721–724
- Yin HC (1938) Diaphototropic movement of the leaves of *Malva neglecta*. *Am J Bot* 25:1–6

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