

Diurnal Movements of Cotton Leaves Expressed as Thermodynamic Work and Entropy Changes

Solar induced leaf movement and wilting are differentiated by their relative entropy and relative work differences.

INTRODUCTION

SOME IMPORTANT agricultural crops show heliotropic leaf movements. In these species the proclivity of leaves to orient either perpendicularly (diaphotonastically) or parallel (paraphotonastically) or in some combination of these positions with respect to the sun is controlled by the leaf turgor and

of the sun at high elevation. In this latter instance, the leaf need only be turgid at sunrise, then roll slightly and wait for the solar trajectory to maximize the intercepted sunlight. This behavior is particularly noticeable for cotton. Schutt *et al.* (1985) have detailed leaf trajectories using three angles. The pitch angle, or the angle between the leaf normal and the vertical direction in a global coordinate

ABSTRACT: *Three angles were measured per leaf to establish the solar induced trajectories for cotton leaves comprising both irrigated and unirrigated cotton canopies. These data and values for the solar coordinates were subsequently used to calculate changes in the angle γ between the normal to each leaf and the sun. Values of γ , pitch, and roll averaged over quadrants set up according to the points of the compass, were shown to differentiate leaf movements with respect to solar quadrant. Plots of pitch and roll provided a graphical means of ascertaining the energy expended in leaf movement. Values of γ determined from pitch, roll, and yaw angles were applied to the calculation of the relative thermodynamic work and entropy. Both work and entropy, when compared with the graphically estimated relative energy required to generate continuous leaf movements, showed identical numerical ordering by quadrant. These results indicate that, if γ or a quantity related to γ can be found from radiometric measurements (specifically bidirectional reflectance surfaces), in select instances it is possible to show the temperature dependence of multitemporal data.*

the availability of water. For a well-watered canopy, this orientational response may take two forms. In one case the petiole of a given leaf may be positioned such that solar tracking by the leaves is required for the leaf to minimize the angle between its normal and the solar direction when the sun is close to its zenith, while in the second the petiole is positioned on the plant at an azimuth close to that

system, replaces the more conventional elevation angle. The azimuthal position, termed yaw, was followed by projecting the midrib of a leaf onto the horizontal plane. The third angle, referred to as the roll angle, is rotation about the midrib. Because turgid leaves in general cannot assume a horizontal position, which would be optimum for high solar elevations, they instead twist all along the petiole,

thus rolling about the midrib to maximize their reception of sunlight.

This paper applies the three-angle representation to leaf trajectory mapping and to the calculation of the phase angle γ between the individual leaf normals and the solar direction. Using γ , the thermodynamic work and entropy functions are evaluated and used to distinguish between the behaviors of water-stressed and well watered cotton canopies.

MODEL

Numerous relatively sophisticated approaches to the measurement of leaf angle distributions have been worked out and tested under conditions where the dynamics of diurnal leaf movement have not taken precedence. These techniques, reviewed by Smith and Berry (1979), Smith and Ranson (1979), and Kimes and Kirchner (1983a), include the direct measurement by optical diffraction and point quadrant analysis and indirect measurements by photographic and photocell to obtain gap frequencies. To describe leaf dynamics studies, however, the protractor-compass approach described by Ranson *et al.* (1981) is the most feasible for repeated measurements at frequent intervals. Kimes and Kirchner (1983b) have applied this approach to an investigation of the diurnal leaf behavior of both cotton and soybeans canopies.

Figure 1 shows the angles used to describe the position of a leaf, which has been idealized as free from foliar irregularities. Quadrants were set up according to the directions of the compass counting clockwise from north (the negative x -axis) to facilitate the detailing of diurnal movements on an aggregate rather than an individual basis. The leaf depicted in Figure 1 is shown with a negative pitch, ϕ , or the angle the normal (n) to the plane of the leaf makes with the positive z -axis. The sign of the pitch has been chosen to correspond with the elevation angle, ϕ_e , also shown in Figure 1. Thus, a clockwise rotation of the normal corresponds to a negative angular displacement in ϕ . Correspondingly, a positive elevation or pitch is derived from a counterclockwise rotation of the normal with respect to the z -axis. The yaw of the leaf, ψ , is the projection of the midrib on to the x - y plane, and is measured with respect to the negative x -axis (North). This angle accounts for lateral leaf movement with respect to the petiole. The third angle, θ referred to as the roll angle, quantifies the ability of a leaf to rotate about its midrib. It is shown in Figure 1 as a rotation about the y -axis of a local coordinate system positioned along the midrib.

Elsewhere it has been shown (Schutt *et al.*, 1985) that the angle γ between the leaf normal and the solar direction can be represented as

$$\cos \gamma = A \sin \phi_s \cos \psi_s + B \sin \phi_s \sin \psi_s + C \cos \phi_s \quad (1)$$

where ϕ_s and ψ_s represent the polar and azimuthal trajectory coordinates of the sun, with

$$\begin{aligned} A &= \sin \phi \cos \psi \cos \theta - \cos \phi \sin \theta \\ B &= \sin \phi \sin \psi \\ C &= \sin \phi \cos \psi \sin \theta + \cos \phi \cos \theta \end{aligned}$$

where ϕ , ψ , and θ represent the pitch, yaw, and roll, respectively.

To approximate the energy expended by the foliar structure of a plant to fill with water and subsequently transpire, we introduce the notion of work. The fundamental assumption involved in this task was the proportionality between the leaf orientation force and the cosine of the angle γ between the normal to the leaf and the sun: i.e.,

$$dW = d(FL \cos \gamma) \cong FL d \cos \gamma \quad (3)$$

where W is the work, and F and L are the fluid dynamic force and the trajectory followed by the orienting leaf, respectively. By multiplying and dividing Equation 3 by the area of the leaf A , there results

$$dW = PV d(\cos \gamma)$$

with $P = F/A$ and $V = LA$, where the pressure P is the hydrostatic pressure within the leaf and V is the volume of the leaf. Integrating Equation 3 gives

$$\Delta W \cong PV(\cos \gamma - \cos \gamma_1) \quad (4)$$

with γ_1 being the initial value of γ , chosen to make $\Delta W = 0$ when $t = 0$.

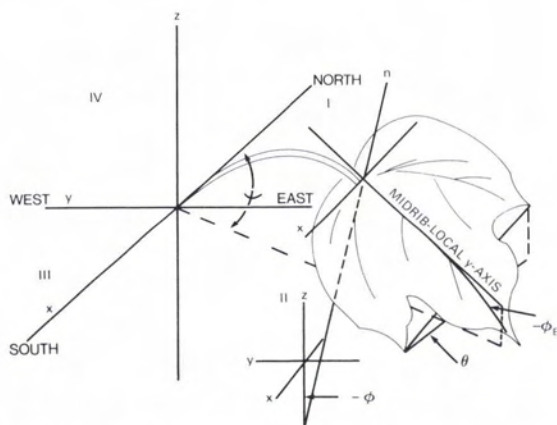


FIG. 1. Schematic of leaf geometry. The negative elevation of the leaf shown as $-\phi_e$ is shown as the pitch, ϕ , of the leaf intersecting the z -axis of the translated global coordinate system used to establish quadrants relative to the points of the compass. The azimuth, ψ , is shown as the angle between North and the projection of the midrib (local y -axis) onto the x - y plane of the global coordinate system. The roll, θ , is shown on the leaf as a rotation about the local y -axis and, in an enlarged view, as the relative rotation of the secondary apices of the leaf.

An experimental justification for this trial function was shown by the work of Beggs (1980), who carried out a series of experiments during which both $\cos \gamma$ and relative leaf water content were measured as a function of time of day. These data were collected on Townsville stylo (*Stylosanthes humilis* H.B.K.) under two sets of circumstances. The first set was collected on water cultured plants, and plants cultivated in a greenhouse, while the second set was collected from field grown plants. The authors took the liberty of correlating these results and found the coefficients of determination relating $\cos \gamma$ to relative leaf water content (RLWC) were about 0.92 and 0.85, respectively. The second set of data was collected on potted plants in dry soil and field plants entering the drying season. Correlating these sets of data, the resulting coefficients of determination found by the authors were about 0.94 and 0.80, respectively. These results showed rather clearly that $\cos \gamma$ can be used to estimate water contents from about 65 percent to about 90 percent (Rowland, 1983).

Because γ was dependent on both time and canopy temperature, with the canopy temperature being time dependent as well, a single quantity capable of weighting these variables to show the temperature dependence of γ is desirable. Such a quantity is entropy. The relative entropy change per leaf, ΔS_N , was calculated using (Rushbrooke, 1949)

$$\Delta S_N = K \frac{\partial(T(t) \ln PF_N)}{\partial T(t)} \quad (4)$$

with

$$PF_N = \sum_{ij} \frac{N_{ij}}{N} \exp \left\{ \frac{(\cos \gamma_{ij}(t) - \cos \gamma_1(t))}{KT(t)} \right\}, \quad (5)$$

where $T(t)$ is the canopy temperature. The summation is over all leaves i and all observation times j , N_{ij} , and N the total number of leaves. K is a scale factor which was set equal to one. Equation 5 has been divided by N to make the relative entropy independent of sample size.

EXPERIMENT

Leaf angle measurements were taken on a wilting canopy and on a well-watered canopy using the three angle approach (Figure 1) for cotton grown in Phoenix, Arizona. The mean row spacing, plant height, and plant separation were nominally 100, 30, and 20 cm, respectively. Prior to commencing the experiment, each of the 48 leaves measured was tagged so its respective diurnal response could be followed on an individual basis.

Angle and radiometric temperature measurements were taken four times—0600, 0800, 0900, and 1115 (MST)—on 27 June 1982. Each measuring session was less than thirty minutes. Three angles were measured for each leaf. Both series of angles

were taken by means of a protractor constructed with a housing containing a movable vectored indicator weighted to maintain a vertical position. Pitch was taken along the midrib while roll was measured orthogonal to the midrib. Yaw was measured from the midrib to north (Figure 1) by means of a compass. Furthermore, all leaves had received total exposure to the solar beam for the duration of the experiment. The precision of the angular measurements has been discussed by Kimes *et al.* (1983b) and Schutt *et al.* (1985). Canopy temperatures for the entropy calculations were acquired by means of a radiometric thermometer.

RESULTS AND DISCUSSION

Figure 2 summarizes the movements of the leaves by quadrant in terms of their pitch and roll for the well-watered canopy. The direction of increasing time is indicated by the arrows. The yawing or azimuthal motion was not plotted because each leaf is constrained by the azimuth of its petiole and, consequently, shows relatively little displacement when compared with the pitching and rolling motions. Each quadrant plot comprising Figure 2 has been divided into an adaxial and abaxial movement because the same average pitch occurred for both a positive and negative roll creating adaxial and abaxial exposures, respectively. Notice that the maximum occurred in each quadrant when the second set of observations was taken. At 0800, the response of the leaves to the ample supply of water was most in evidence. This effect is extreme for quadrant III where elevations in excess of 90° were measured. Thereafter, the pitching motion eased as the orientation process for each assembly of leaves was activated as the rolling motion was initiated. The shaded portions in Figure 2 represent the net motion of the leaves and, hence, the net thermodynamic work performed by the leaves because it is proportional to the integral over the coordinates of the leaves. The shaded portions of each plot, in units of square radians, are in the order of decreasing magnitude 0.163, 0.063, 0.058, and 0.015 for quadrants IV, I, II, and III, respectively.

Error bars have been omitted from Figure 2 to avoid clutter. To provide a feel for the natural variability in leaf movement on a quadrant resolved basis, a tabulation of standard deviations in the pitch and roll angles has been provided in Table 1. From this listing it can be seen that standard deviations are in several instances larger than the mean values for the pitch and roll (Figure 2), and that in most instances the standard deviations apply to the roll in one direction only. Otherwise, an adaxial exposure would become an abaxial exposure and visa versa. From Table 1 it is apparent that rolling is the most active response. In all instances the roll angles ended up below 10°. With respect to the pitch, it

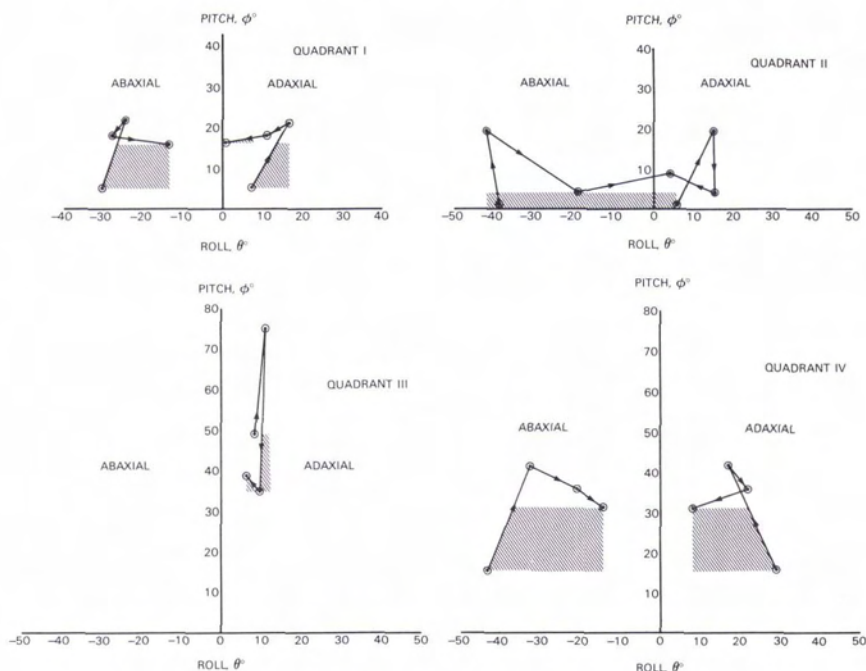


FIG. 2. Plots of the changes in the average pitch and roll of the leaves as a function of time with the net movement and hence the net work performed by the sun on the leaves shown as shaded regions. (a) Results for quadrant I, showing that both adaxial and abaxial exposures occurred with an intermediate amount of net orientational response. (b) Results for quadrant II, showing only the occurrence of adaxial exposures when the experiment was terminated. The net orientational response was close to that of quadrant I. (c) Results for quadrant III, showing only adaxial exposures and the minimum orientational response. (d) Results for quadrant IV, showing exposure of both surfaces and the maximum orientational response. Note that in each instance the minimum pitch (maximum elevation) was the incipient response prior to the onset of heliotropism.

can be seen that, although the leaves showed a definite mean trajectory (Figure 1), their standard deviations remained large compared to those for the roll but with a noticeable downward trend.

Figure 3 shows the relative work plotted against time by quadrant for the well watered canopy and as a composite average for the unwatered canopy. The curve showing the maximum performed work

TABLE I. TABULATION OF STANDARD DEVIATIONS FOR PITCH AND ROLL DATA BY QUADRANT

Quadrant	Time, MST	Pitch, Deg.	Roll, Deg.	
			Adaxial	Abaxial
I	6:30	29.0	16.0	14.9
	8:20	24.8	19.0	17.5
	9:30	20.4	13.4	11.8
	11:20	20.6	0.00	4.8
II	6:30	38.1	26.8	23.0
	8:20	34.3	19.1	12.9
	9:30	30.5	22.3	15.0
III	11:20	23.5	9.6	2.1
	6:30	33.9	33.9	—
	8:20	30.0	29.9	—
	9:30	25.1	25.1	—
IV	11:20	26.2	2.2	—
	6:30	32.4	25.4	14.7
	8:20	32.1	20.5	16.4
	9:30	25.0	17.0	9.0
	11:20	24.7	5.3	7.1

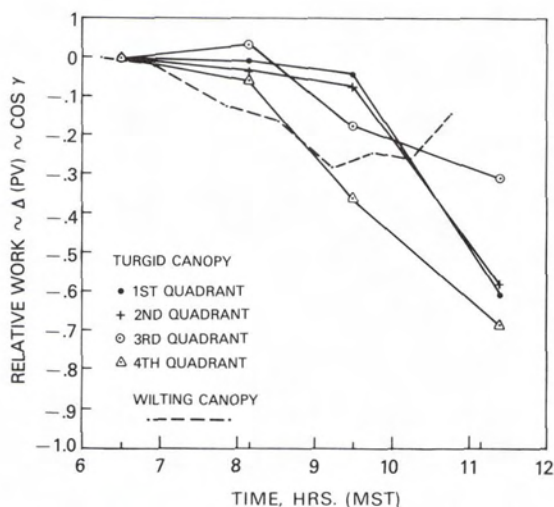


FIG. 3. Relations between relative work and time for a turgid and wilting canopy. Leaves present in quadrant IV of the canopy showed maximum movement or the minimum for $\Delta(PV)$ (greatest interaction with sunlight). The ordering of the responses by quadrant follows the shaded areas in Figure 2. The wilting canopy responded only moderately to the solar movement until about 0930, at which time the leaves commenced to lose turgidity.

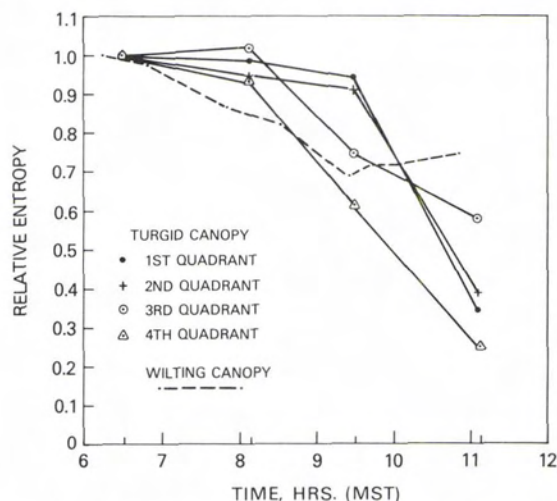


FIG. 4. Relations between entropy changes and time for a turgid and a wilting canopy. Leaves present in quadrant IV of the canopy showed the maximum decrease in entropy. The ordering of response follows those in Figure 3. The effect of temperature was to increase the curvatures relative to those of Figure 3.

occurred for quadrant IV, while the remaining curves followed the sequence I, II, and III. This result is in keeping with the sequence of areas determined (Figure 2). Notice that the unwatered canopy responded to the solar movement until about 0915 MST, at which time wilting commenced. This latter occurrence is indicated by an upturn in the curve. A similar behavior can be seen in Figure 4, where the entropy has been plotted against time. The shapes of these curves are similar to those for the work function, but possess a somewhat greater curvature because the entropy function is the average value of $\cos\gamma/T$. In other words, the effect of temperature was to accentuate the solar radiation induced response of the leaves. Because γ can in principle be found from radiometric information (Schutt *et al.*, 1984), the entropy function introduced above serves as a basis for formulating thermal and radiometric information into a description of vegetative behavior.

SUMMARY AND RECOMMENDATIONS

By resolving leaf movements with respect to an orthogonal coordinate system, pitching and rolling motions were shown to be primarily responsible for the heliotropic behavior of cotton leaves. Using these angles to calculate the angle between the leaf normals on an individual basis and the solar direction, a single quantity amenable to radiometric determination could then be used to represent the trajectory of leaves with respect to the sun. Using the evolution in γ or the trajectory, the relative work

and entropy were calculated and shown to represent the behavior of the leaves in keeping with the graphical evaluation represented by the shaded areas in Figure 2.

Introducing the concept of entropy from a physical viewpoint provides a means for incorporating temperature with radiometric data by means of Equations 3, 4, and 5. It is relevant, therefore, that similar experiments be carried out from which an identifying characteristic of the vegetation can be determined radiometrically under varying thermal conditions to establish a behavioral representation in terms of thermodynamic quantities. By so doing, statistical results such as regression coefficients can take on physical meaning and become more than a comparison of coefficient of determination.

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BOOK REVIEW

An Introduction to Solar Radiation, by Muhammad Iqbal. Academic Press Canada, Don Mills, Ontario, 1983. xviii and 390 pp., tables, figures, references, notes, appendices, subject index. \$32.00.

THIS VOLUME provides both a literature review and basic text on solar radiation, derived from scientific, meteorological, and engineering sources. Beginning with Earth-sun astronomical relationships, the author traces solar radiation through the atmosphere under both cloudless and cloudy sky conditions to the Earth surface. At the surface, issues of surface albedo and configuration are discussed, including radiation incident on tilted planes such as those used in solar collectors. The volume concludes with a discussion of solar radiation measurement and instrumentation.

Each chapter presents basic physical and geometrical principles in a concise and readable fashion. Equations are explained well, and most chapters include a section on relevant nomenclature and symbols for variables used. In addition, the presentation is strengthened by historical notes on the development of laws and methodologies employed, by suggestions for further reading, and by bibliographic references. Because there is no consolidated list of references for the whole volume, lack of an author index is unfortunate. Sample calculations are helpful, but there are no formal problems presented. Thus, instructors using the book must develop their own problem sets for student use. Typographical errors are not distracting, although they do occur.

An Introduction to Solar Radiation will be particularly useful for local assessment of solar radiation

for use in energy analysis, design of thermal and photovoltaic devices, architectural engineering applications, and environmental studies requiring knowledge of solar energy receipts. The effects of the atmosphere on solar radiation and the estimation of monthly, daily, and hourly diffuse radiation are well-developed in the text. Because the ASHRAE approach for clear-sky diffuse irradiance does not incorporate ground albedo or aerosol-generated diffuse radiation as well as that generated by water vapor content, Iqbal compares ASHRAE with three alternative estimation procedures, suggesting that one of the models is more accurate, particularly with regard to winter conditions. For those working in photogrammetry and remote sensing, discussion of reflectivity of the Earth surface is abbreviated, limiting application of the book beyond general principles in this area.

The book is well-designed with exceptionally clear and understandable graphics and tables. For those working in solar energy development, the book will provide a valuable review, update, and elaboration of basic solar radiation principles. For remote sensing students, the book provides useful background developed in an accessible and comprehensible manner.

—C. Gregory Knight
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