SOLAR TRACKING AND PHOTOSYNTHESIS IN COTTON LEAVES

J.R. EHLERINGER and S.D. HAMMOND

Department of Biology, University of Utah, Salt Lake City, UT 84112 (U.S.A.)

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ABSTRACT

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Leaf solar tracking movements (ability of leaf to orient perpendicularly to the sun's direct rays) and photosynthetic responses to photon flux level were examined in three cultivars of Upland cotton (*Gossypium hirsutum*) and one cultivar of Pima cotton (*Gossypium barbadense*). Exposed canopy leaves of upland cotton exhibited strong solar tracking abilities diurnally, whereas leaves of Pima cotton remained in a fixed position throughout the day. Diurnal photosynthetic rates measured on an individual exposed leaf of Upland cotton (Delta Pine 62) that was allowed to solar track or fixed in a horizontal position did not differ except at the low irradiances occurring in the early morning and again in late afternoon. Upon further examination, it appeared that the photosynthetic dependence on photon flux was saturated by approximately 60% of midday irradiance levels and that these photosynthetic–irradiance relationships did not differ among the cotton cultivars examined. These data suggest that, in contrast to the responses observed in several native annual plant species, leaf solar tracking in cotton does not enhance photosynthetic rates of fully exposed sun-lit leaves.

INTRODUCTION

Diurnal leaf movements in response to changes in the sun's position have been quantified for a number of species (Lang, 1973; Shell et al., 1974; Fukai and Loomis, 1976; Shackel and Hall, 1979; Ehleringer and Forseth, 1980; Travis and Reed, 1983). As a result of these diaheliotropic movements, the photon flux incident on solar tracking leaves can be substantially higher than on leaves with fixed orientations (Begg and Torssell, 1974; Fukai and Loomis, 1976; Ehleringer and Forseth, 1980). At low leaf area indices (LAI), the increased light interception could result in higher leaf and canopy photosynthetic rates (Fukai and Loomis, 1976; Mooney and Ehleringer, 1978), but this would require the leaf photosynthetic capacity of the exposed leaves to be high enough to utilize the higher incident photon fluxes (Mooney and Ehleringer, 1978; Ehleringer and Forseth, 1980; Forseth and Ehleringer, 1983b).

Although leaf solar tracking is known to occur in cotton (Lang, 1973; Fukai and Loomis, 1976), cultivar variation has not been investigated and the significance of leaf solar tracking to primary productivity is unclear. Two factors bear on this point. First, reported photosynthetic rates for leaves of domes-

ticated cotton are similar to values from other C_3 plants (El-Sharkawy et al., 1965; McArthur et al., 1980), and therefore leaves may be saturated well before midday irradiances. Secondly, under agricultural conditions with a high canopy LAI and strong solar tracking capabilities, most of the incident solar radiation would be intercepted by the uppermost canopy leaves, resulting in low photon fluxes available for the lower canopy leaves. Fukai and Loomis (1976) modeled light interception by cotton canopies and calculated that leaf solar tracking could enhance total canopy productivity early in the growing season when LAI was 0.55, but that later in the growing season canopy productivity might actually be decreased relative to a fixed leaf canopy because of the uneven light distribution. Their modeling was based on limited estimates of photosynthetic light response curves for cotton.

In this paper, we have quantified leaf solar tracking ability, photosynthetic rate, and the shape of the photosynthesis–light response curve for several cotton cultivars in order to determine to what extent upper canopy leaves might be able to utilize the higher incident photon fluxes that result from solar tracking.

MATERIALS AND METHODS

The cotton cultivars studied included Upland cotton (*Gossypium hirsutum*) cv. Delta Pine 62, cv. Delta Pine 70, and cv. Stoneville 825, and Pima Cotton (*Gossypium barbadense*) cv. Pima S5. Field measurements of leaf solar tracking were made at the Cotton Research Farm of the University of Arizona in Phoenix, Arizona, where plants were being grown for breeding studies. For one set of gas exchange measurements, plants were grown from seed individually in 20-l pots with potting soil. These plants were grown outdoors in Salt Lake City during the summer and were adequately watered daily and fertilized weekly. These plants were used for measurements of the photosynthetic light response curves. For diurnal gas exchange measurements under natural conditions, a limited number of plants were grown in an open field at the University of Utah. These plants were irrigated to field capacity approximately once every 10 days and fertilized monthly. Detailed simultaneous measurements of solar tracking and photosynthesis were not made at a single location because of equipment and space limitations; baseline data clearly indicated that cotton plants in Salt Lake City followed the sun in a manner identical to that documented in Arizona.

Gas exchange measurements on plotted plants were made in the laboratory (elevation of the University of Utah is 1515 m) on recently matured, attached leaves using an open gas exchange system as described previously by Ehleringer (1983). The photosynthetic dependence on irradiance was measured by first exposing the leaves to an irradiance of 2.0 mmol photons $m^{-2} s^{-1}$ (400–700 nm), a leaf temperature of 30°C, an ambient CO_2 concentrations of $330 \mu l l^{-1} CO_2$ 21% O_2, and a leaf-air vapor pressure deficit (vpd) of 1.0 kPa. After equilibrium had been obtained, the irradiance was reduced in steps by placing neutral density filters above the cuvette. Gas exchange parameters were calculated as

described by von Caemmerer and Farquhar (1981). Sample size was three to four leaves from different plants for each cultivar. Data presented are means ± 1 SE unless otherwise noted.

For diurnal measurements under ambient field conditions, photosynthesis was measured using an open gas exchange system and well-ventilated cuvette described by Mooney et al. (1971). In these measurements, a single leaf was enclosed within a cuvette and allowed to orient diurnally or restrained in a horizontal position using nylon line.

Leaf angles and leaf azimuths were measured with an inclinometer and a compass, respectively, in order to calculate the cosine of the angle of incidence using methodology previously described by Forseth and Ehleringer (1980). Solar tracking movements may be quantified by calculating the cosine of the angle of incidence ($\cos(i)$) between the normal to the leaf lamina and the direct solar beam; this varies between 0 and 1 depending on the relative geometrical positions of the leaf lamina and the sun. $\cos(i)$ is calculated as

$$\cos(i) = \cos(\alpha_1)\sin(\alpha_s) + \sin(\alpha_1)\cos(\alpha_s)\cos(\beta_s - \beta_1)$$

where α_1 is the angle above the horizon of the leaf lamina and α_s is the angle from the horizontal of the sun and β_1 and β_s are the azimuthal positions of the leaf and sun, respectively (Gates, 1962). A $\cos(i)$ value close to 1.0 through the day indicates a leaf with a strong diaheliotropic ability. If leaves remained at a fixed leaf angle and had a random leaf azimuth distribution, then the average $\cos(i)$ should vary sinusoidally through the day as the sun passes across the sky. For leaf azimuths south is $0°$, east is $-90°$, west is $+90°$, and north is $-180°$ and $+180°$.

Initial evidence for leaf solar tracking was investigated by measuring the azimuth on leaves both at the top and the bottom of canopies in Arizona; the canopies were in an early flowering stage. The azimuth measurements were made approximately one hour after sunrise and again in the afternoon approximately one hour before sunset on several hundred leaves. Estimates of diurnal leaf solar tracking were collected by measuring the $\cos(i)$. Sample sizes for the diurnal observations on different cotton cultivars were ten randomly chosen sun-lit leaves from the top of the canopy. The standard error on these estimates was ± 0.02.

RESULTS AND DISCUSSION

Early in the morning, leaves at the top of the canopy of Upland cotton (*G. hirsutum*) were all facing an easterly direction and late in the afternoon they had moved to face a westerly direction (Figs. 1 and 2). The directional changes in leaf position showed little dispersion and almost all leaf azimuths were within $30°$ of the sun's azimuth. However, relative to the sun's azimuthal position, leaves in the morning and again in the late afternoon appeared to be at somewhat more southerly azimuths. That is, in terms of diurnal leaf movements, leaf azimuthal changes were not as great as those of the sun. As a
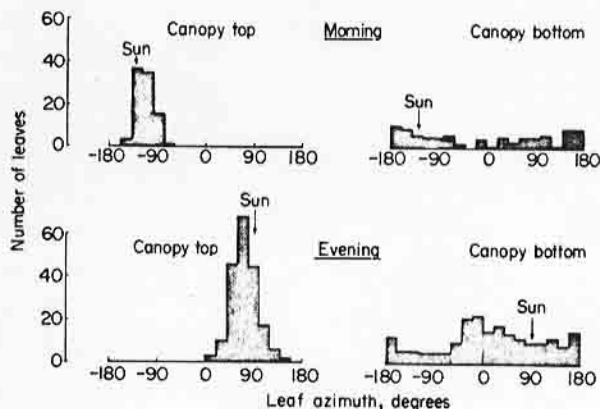
Fig. 1. Frequency histograms of leaf azimuths for leaves of *Gossypium hirsutum* cv. Stoneville 825 from the top and bottom of a closed canopy in the early morning and again in the late afternoon. Arrow indicates position of the sun. Data are from Phoenix, AZ.

consequence, upper canopy leaves were in advance of the sun's azimuthal position in the morning and behind it in the afternoon; this phase difference has been noted previously by Lang (1973). A greater proportion of the photon flux received by lower canopy leaves was diffuse radiation and thus these leaves showed no directional change in leaf azimuth throughout the day (Figs. 1 and 2). In the late afternoon lower canopy leaves did appear to be more southerly oriented than uniform in distribution. This may be the result of direct solar radiation penetrating into the canopies in the spaces between canopy rows. Previous observations have also showed variations in leaf solar tracking
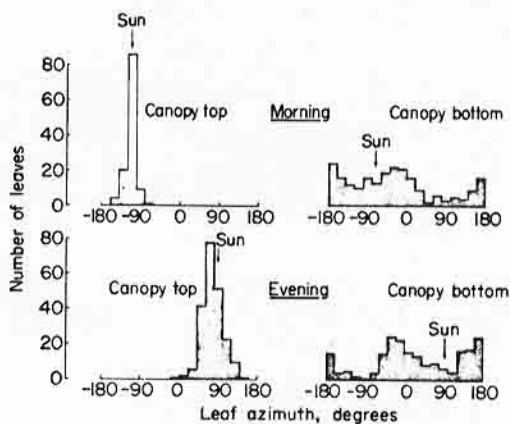

Fig. 2. Frequency histograms of leaf azimuths for leaves of *Gossypium hirsutum* cv. Delta Pine 62 from the top and bottom of a closed canopy in the early morning and again in the late afternoon. Arrow indicates position of the sun. Data are from Phoenix, AZ.

depending on canopy position, presumably reflecting the intensity of the incident direct solar beam (Lang, 1973; Shell and Lang, 1975).

No diurnal leaf solar tracking movements, however, were observed in leaves of Pima cotton (*G. barbadense*). As shown in Fig. 3, the distributions of leaf azimuths for outer canopy as well as lower canopy leaves early in the morning were nearly uniform. There was no clustering of leaf azimuths at the sun's azimuthal position, although there was some excess in southerly azimuths and a deficiency in east/west azimuths. A similar distribution of leaf azimuths was again seen in late afternoon.

When the cosine of the angle of incidence ($\cos(i)$) for upper, sun-lit canopy leaves was measured through the day, there were additional differences between Upland and Pima cotton cultivars (Fig. 4). Leaves of Upland cotton moved and closely followed the sun throughout the day and, utilizing both leaf angle and leaf azimuth changes, maintained a $\cos(i)$ value close to 1.0 (i.e., leaf blade was nearly perpendicular to the sun's direct rays). In constrast, $\cos(i)$ for leaves of Pima cotton varied from 0.1 to 0.2 early and late in the day and up to 0.97 at midday. These changes resulted from the relative movement of the sun through the sky. Leaf solar tracking was also measured in planting of an experimental Upland-Pima cotton hybrid (*G. hirsutum* × *barbadense*). Leaf movements were observed in the hybrid (Fig. 3). $\cos(i)$ for leaves of this hybrid was intermediate between those of the two parents.

To evaluate the impact of leaf solar tracking on photosynthetic rates, the diurnal gas exchange of a sun-lit, solar-tracking leaf of Upland cotton cultivar Delta Pine 62 was measured under clear skies in Salt Lake City. Photon flux (400–700 nm) on a horizontal surface varied sinusoidally through the day, peaking at 1.96 mmol photons $m^{-2} s^{-1}$ (Fig. 5). The photon flux on a horizontal surface exceeded 1.2 mmol $m^{-2} s^{-1}$ between 1000 and 1730 h. On the following
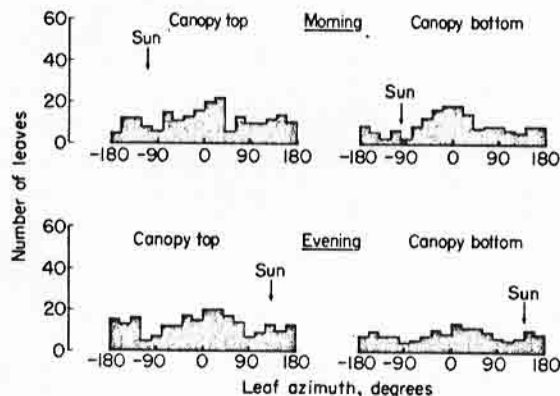

Fig. 3. Frequency histogram of leaf azimuths for leaves of *Gossypium barbadense* cv. Pima S5 from the top of the canopy early in the morning. Arrow indicates position of the sun. Data are from Phoenix, AZ.
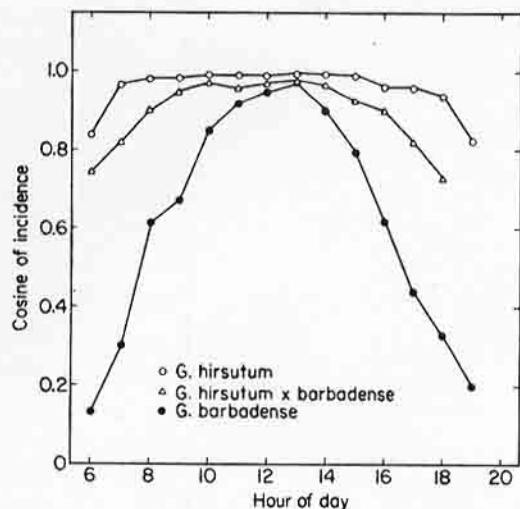
Fig. 4. The diurnal course of the cosine of the angle of incidence for leaves of *Gossypium hirsutum* cv. Stoneville 825, *G. barbadense* cv. Pima S5, and *G. hirsutum × barbadense*. Data are from Phoenix, AZ.

day, which was climatically similar (peak photon flux of 1.98 mmol photons $m^{-2} s^{-1}$), the same leaf was restrained into a horizontal position with nylon wires and the diurnal course of gas exchange again measured. There were no differences in the observed maximum photosynthetic rates whether the leaf
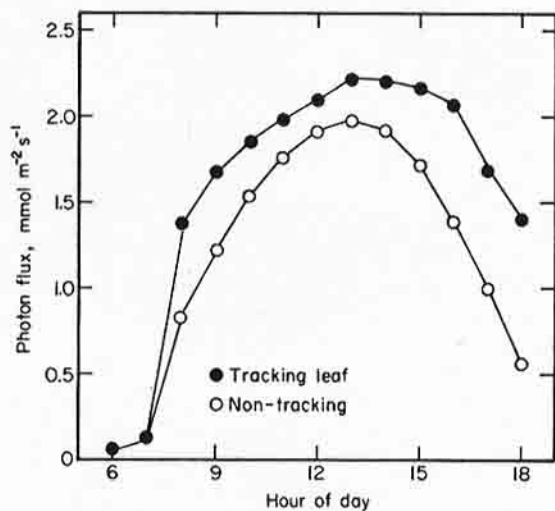

Fig. 5. The diurnal course of photon flux (400–700 nm) on a solar tracking *Gossypium hirsutum* cv. Delta Pine 62 and the same leaf restrained in a horizontal position on the following day. Data are from Salt Lake City, UT.
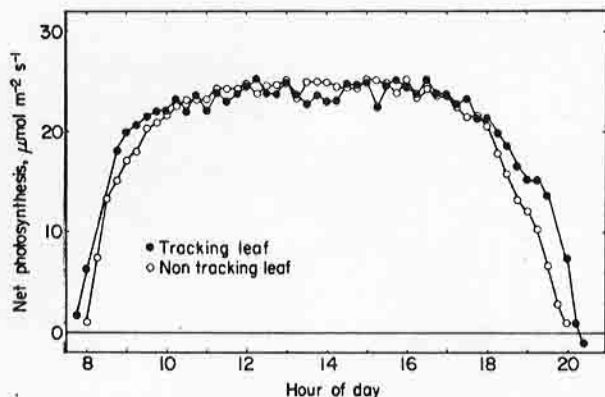
Fig. 6. The diurnal course of net photosynthesis under ambient conditions for a solar tracking *Gossypium hirsutum* cv. Delta Pine 62 leaf (measured on August 7) and the same leaf restrained in a horizontal position (measured on August 8). Skies were clear and air temperature and humidity patterns were very similar on both days. Data are from Salt Lake City, UT.

was allowed to track the sun or was restrained in a horizontal position (Fig. 6), even though there were differences in the incident solar radiation levels as calculated from the angle of incidence of the direct-beam component. Photosynthetic rates of both the solar tracking and restrained leaf remained effectively constant at 22 to 24 μmol CO_2 m^{-2} s^{-1} between 1000 and 1800 h. It was only when the sun was at an elevation angle lower than approximately 40° that the photosynthetic rate of the solar tracking leaf exceeded that of the non-tracking leaf. Since the solar declination was approximately $+15°$ at this time of the year (early August), the sun was high in the sky throughout most of the day. The high solar elevation would result in a high cos(i) for all leaves with low leaf angles, and this may have minimized any potential advantage of leaf solar tracking. Certainly if the solar declination had been 0° (as in late March and again in late September), then the hours over which the photosynthetic rate of the solar tracking leaf would be expected to exceed those of a horizontal, nontracking leaf would have been greatly expanded.

Due to the high velocity fans within the cuvette, there was little difference between leaf and air temperatures (measured with fine-wire thermocouples) either when the leaf was unrestrained or when it was restrained in a horizontal position. Consequently, we were not able to determine the extent to which leaf temperatures and transpiration rates under more natural wind speed conditions would have been higher under increased photon fluxes in the solar tracking leaf.

The diurnal photosynthetic observations suggested that cotton leaves were light saturated at moderate photon fluxes. In order to determine photon fluxes where leaves become light saturated, photosynthetic rates were measured on several cultivars of Upland cotton and on one of Pima cotton. Although these plants had been grown in pots outdoors, photosynthesis in all cultivars was

TABLE I

Photosynthetic characteristics of cotton cultivars pot-grown in Salt Lake City in full vegetative growth

Cotton cultivar	A_{max} (μmol CO_2 m^{-2}s^{-1})	g (mol m^{-2}s^{-1})	c_i (μl l^{-1})	I_{sat} (mmol photons m^{-2}s^{-1})
Gossypium hirsutum				
Delta Pine 62	24.6	0.520	249	1.25
Delta Pine 70	24.6	0.467	246	1.18
Stoneville 825	21.9	0.487	255	1.29
Gossypium barbadense				
Pima S5	27.2	0.468	231	1.27
LSD 0.05	NS*	NS	NS	NS

* NS = Differences among all cultivars were not significant ($P > 0.05$).
A_{max} is the maximum photosynthetic rate measured under ambient conditions (330 μl l^{-1} CO_2, leaf temperatures of 30°C and vpd of 1.0 kPa, g is the leaf conductance to water vapor measured at A_{max}, c_i is the intercellular CO_2 concentration of A_{max}, and I_{sat} is the incident photon flux at which photosynthetic rates were 95% of A_{max}.

saturated at 1.2–1.3 mmol photons m^{-2}s^{-1} (Table I). Figure 7 shows the shape of this response curve for cv. Delta Pine 62; similar responses were found in all other cotton varieties measured. For all cultivars there were no statistical differences in the point of light saturation (Student's *t*-test comparison). Maximum rates of photosynthesis measured diurnally under field conditions were
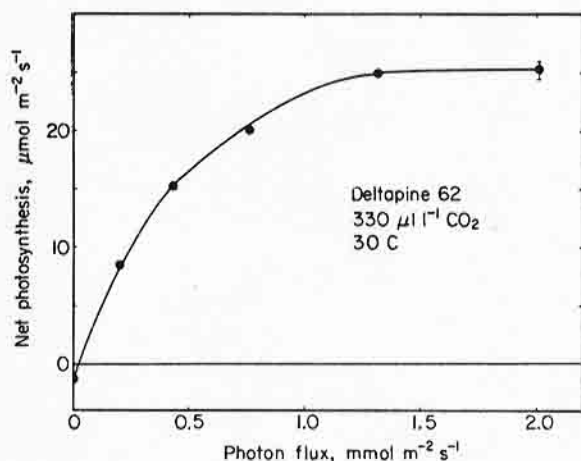

Fig. 7. The dependence of net photosynthesis on incident photon flux (400–700 nm) by leaves of *Gossypium hirsutum* cv. Delta Pine 62. Measurement conditions were an ambient CO_2 concentration of 330 μl l^{-1}, leaf temperature of 30°C, and vpd of 1.0 kPa. Vertical line indicates ± 1 SE. For a summary of curves for all cultivars see Table I.

nearly identical to those observed for individual potted plants, and these values were similar to maximum values reported by McArthur et al. (1980). The saturating irradiance level of 1.2 mmol photons $m^{-2} s^{-1}$ is only 60% of the daily maximum photon flux during the summer months. Yet solar tracking leaves will likely have incident irradiances near 2.0 mmol photons $m^{-2} s^{-1}$ (Fig. 5). This indicates that upper canopy leaves in Upland cotton were absorbing a far greater fraction of incident photon flux than they were capable of utilizing for CO_2 fixation. Two consequences are that outer canopy leaves of solar tracking plants should operate at lower water use efficiencies (mol CO_2 fixed per mol H_2O transpired) and that inner canopy leaves should receive less than optimum photon fluxes.

Lower water use efficiency should necessarily result when higher incident solar radiation loads increase leaf temperatures (and thus increase transpiration), but do not increase photosynthetic rate. This is expected in cotton, but was not experimentally tested. In contrast, a number of other solar tracking crop plants (e.g., alfalfa, cowpea, bean) avoid potential decreases in water use efficiency at high irradiances via paraheliotropic leaf movements (Begg and Torssell, 1974; Shackel and Hall, 1979; Ehleringer and Forseth, 1980; Travis and Reed, 1983). Even though these crop plants may have maximum photosynthetic rates similar to those observed in cotton, their leaves move to avoid the sun's direct rays at high radiation loads (paraheliotropism). The result is that enhancements in water use efficiencies of outer canopy leaves are expected and that inner canopy leaves are thus exposed to higher incident photon fluxes. In contrast, for those native Sonoran Desert annuals which exhibit solar tracking, LAI is low (usually < 1) and leaf photosynthetic rates are not light-saturated at midday irradiances (Forseth and Ehleringer, 1980, 1983a; Werk et al., 1983). As a consequence, canopy photosynthetic rates are maximized with leaf solar tracking movements under all but extreme water stress conditions (Forseth and Ehleringer, 1983b).

From their modeling studies with cotton, Fukai and Loomis (1976) concluded that solar tracking would reduce total canopy photosynthesis in a closed canopy relative to a fixed leaf orientation. This is because the outer canopy leaves were receiving photon fluxes in excess of those required for light saturation. While the measurement of total canopy photosynthesis was not possible in our study (the necessary equipment was not available), it appears from our measurements that canopy leaves were indeed receiving greater photon fluxes than necessary to saturate photosynthesis. Thus, leaf solar tracking in cotton was not enhancing photosynthetic rates of the fully exposed sun-lit leaves, and thus may be indirectly reducing total canopy photosynthesis at certain times of the season by not allowing greater light penetration to leaves within the canopy.

While leaf solar tracking may not be advantageous to the productivity of cotton grown under intensively managed agricultural conditions, it may not necessarily have been disadvantageous in natural communities. As a perennial wild plant, solar tracking by cotton leaves would restrict the light environment

of understory annual competitors in the disturbed habitats in which they are native (Fryxell, 1978). This would also tend to concentrate photosynthate production near the highest meristems, favoring height growth instead of lateral, spreading growth and over time contribute to achieving dominance within the community.

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