

DIURNAL CHANGES IN PLANT GEOMETRY AND SUNLIT LEAF AREA IN COTTON PLANT

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Abstract

The diurnal changes in plant geometry due to leaf orientation behaviour of row-planted cotton plants (*Gossypium hirsutum* L. cv. 'DES 119') and its relationship to sunlit leaf area distribution at three different stages of development were studied in the field. Three-dimensional electromagnetic digitizing was used for plant geometrical structure measurement at three different periods of the day.

Cotton leaves displayed a diurnally diaheliotropic response (leaf movement perpendicular to the sun direction) with changes in their locations. Sunlit leaf area distribution varied according to stage of development. Light interception was greater in the morning and in the afternoon than at noon. Cotton plants would intercept less direct radiation in the morning and in the afternoon if they had not presented a diurnal change in canopy structure. According to plant geometry, cotton plant presented regular leaf dispersion at the LAI of 0.12 and 2.84, but it was clumped at the LAI of 1.09. The pattern of leaf arrangement was more regular in the morning and the afternoon than at noon. Leaf dispersion however changed primarily with sun direction and not with canopy structure. This reveals that small diurnal changes in leaf location do not significantly affect light interception.

Introduction

Cotton is an indeterminate plant which exhibits rapid development of leaf area index (LAI, total leaf area per planted area) during vegetative growth. In addition, cotton leaves have been reported to present heliotropic behaviour, i.e., leaf movement as response to the change of sun direction (Lang, 1973; Fukai and Loomis, 1976; Ehleringer and Hammond, 1987; Sassenrath-Cole, 1995, among others). These spatio-temporal changes of plant elements throughout the day and throughout the growing season influence the penetration of direct sunlight into the canopy. However, the effects of changes in plant structure on light interception in cotton had been studied in terms of changes in leaf angle orientation but not in term of changes in leaf

location during the day whereas light interception depends not only on leaf angles but also on the spatial distribution of leaves within the canopy.

The information about the relationship between diurnal changes in leaf orientation, in spatial leaf arrangement and sunlit (intercepting direct sunlight) leaf area during the day and during the growing season in cotton needs to measure the three-dimensional (3D) distribution of the leaves. Sinoquet and Rivet (1996) showed that an electromagnetic digitizing device could be used for measuring both spatial coordinates and orientation angles of plant elements in the field with good accuracy and insensitivity of masking. The objective of this study is therefore to characterize diurnal changes in plant geometrical structure by using an electromagnetic digitizing system, and to quantify sunlit leaf area distribution of cotton plant during the day and during the growing season.

Materials and Methods

Plant growth

The experiment was conducted in a field of Domaine de Lavalette, CIRAD-CA, Montpellier, in France. Cotton (*Gossypium hirsutum* L. cv. 'DES 119') seeds were planted on May 6, 1995 in north-eastern (NE) - south-western (SW) row direction on a plot of 3,375 m² of sandy loam soil. The spacing between rows was 0.80 m. Plants were thinned to one plant per 18 cm of row, that is a population density of 69,440 plants/ha, when plants had 4 unfolded mainstem leaves (20 days after emergence). Cultural practices are described by Thanisawanyangkura et al. (1996).

The average monthly temperature in May was 16°C. The weather was warmer in June (20°C) and July (25°C). Total rainfall was 48.5 mm during May-July 1995. There were some cloudy periods in the afternoon of measurement days at the LAI 0.12 and 1.09 stages but the sky was clear when the LAI was 2.84.

Measurement of plant geometry

Foliage digitizing was done with a 3D electromagnetic digitizer (Polhemus® 3 Space® FasTrak®, Polhemus Inc., VT, U.S.A.) and data acquisition software DiplAmini (Sinoquet and Rivet, 1996). Digitized positions on cotton plant were the nodes on main stem and branches, the insertion of the most recently fully expanded leaves of each plant with petiole orientation, and the proximal and distal tips of the mid rib with leaf blade orientation and mid rib direction (Figure 1).

At 4 days after thinning, four plants were visually selected as representative of the crop at the center of the plot. In this study, three growth stages were compared: the LAI 0.12, 1.09, and 2.84. Digitizing was conducted three times a day by assuming that the leaves did not change significantly their orientation during the two hour measurement period: in the morning (07h00-09h00 True Solar Time), at noon

(11h00-13h00), and in the afternoon (15h00-17h00). At the LAI 1.09 and LAI 2.84 stages, three of the same four plants were studied in order to reduce the digitizing duration and then to avoid significant leaf movements during the measurement periods. Non-destructive estimation of the leaf area of each leaf was performed by an allometric relationship set for each stage between the length of mid rib and leaf area (Thanisawanyangkura et al., 1996).

Models and calculations

1. Cosine of the angle of incidence

The cosine of the angle of incidence (angle between leaf normal and sun direction; β) is calculated as (Ross, 1981):

$$\cos \beta = \cos \alpha_n \sin h + \sin \alpha_n \cos h \cos (A_z - \phi_n)$$

where α_n is the inclination of leaf normal, ϕ_n is the azimuth of leaf normal, h is the solar elevation, and A_z is the solar azimuth.

In most radiative transfer models, the distribution of leaf azimuth is assumed to be uniform. In order to test the effect of this assumption on $\cos \beta$, a value of cosine of incidence $(\cos \beta)^u$ with uniform leaf azimuth distribution was also calculated for each individual leaf (Sinoquet et al., 1993). For a population of N leaves, the average values of $\cos \beta$ and $(\cos \beta)^u$ called G -functions (see Ross, 1981) were computed by weighting individual $\cos \beta$ and $(\cos \beta)^u$ by leaf area S :

$$G = \sum_{i=1}^N S_i \cos \beta_i / \sum_{i=1}^N S_i$$

$$\text{and } G^u = \sum_{i=1}^N S_i (\cos \beta_i)^u / \sum_{i=1}^N S_i$$

2. Diurnal change of leaf blade location

Motion of the central point of leaf blade between two observation times was calculated in order to quantify the diurnal change in leaf blade location as follows:

$$D_{a-b} = \sqrt{(X_a - X_b)^2 + (Y_a - Y_b)^2 + (Z_a - Z_b)^2}$$

where D_{a-b} is the change in blade location between observation times a and b , (X_a, Y_a, Z_a) and (X_b, Y_b, Z_b) are the spatial coordinates of the central point of the leaf blade at observation times a and b , respectively.

3. Sunlit leaf area and light interception

Images of the plants with actual leaf orientation and leaf position were created from digitizing data with the 'smooth curve' function of Microsoft Excel® Version 5.0 (Microsoft Corp., U.S.A.) (Thanisawanyangkura et al., 1996). Sunlit leaf area S_p was estimated from pictures of the plants

viewed in the sun direction. Sunlit leaf area coloured by hand was measured with a Licor 3100 Leaf Area Meter® (Licor Inc., Lincoln, NE, U.S.A.). On the plant pictures, a reference area S_R (i.e., soil surface area occupied by a plant) was estimated as the smallest ellipse including the leaf area projected onto the soil surface. Plant pictures allowed us to derive light interception probability from sunlit leaf area estimated from digitizing (P_{Digit}):

$$P_{\text{Digit}} = S_p / (S_R \sin h)$$

In order to quantify the pattern of leaf arrangement within the reference area for describing plant geometry, P_{Digit} was compared to two interception models, i.e., Beer-Lambert's law (P_{Beer}) and binomial model (P_{Binom}):

$$P_{\text{Beer}} = 1 - \exp \left[- \sum_{i=1}^N \cos \beta_i \cdot S_i / (S_t \sin h) \right]$$

$$P_{\text{Binom}} = 1 - \prod_{i=1}^N \left[1 - \cos \beta_i \cdot S_i / (S_t \sin h) \right]$$

where N is the leaf number and S_i is the area of leaf i .

P_{Beer} estimates the probability of light interception for random leaf dispersion while P_{Binom} corresponds to a case of regular dispersion. In this binomial model, leaf dispersion is explicitly related to leaf size. This means a leaf does not shade itself. The ratio $P_{\text{Binom}} / P_{\text{Beer}}$ therefore indicates departure from randomness due to leaf size distribution while the ratio $P_{\text{Digit}} / P_{\text{Binom}}$ describes the pattern of leaf dispersion due to non-randomness of leaf locations.

4. Comparative effects of plant geometry variation and sun position variation

$\cos \beta$, sunlit leaf area, and leaf dispersion were calculated for each combination of plant geometry and sun direction (i.e., in the morning, at noon and in the afternoon). By cross comparison, the effects of change in plant geometrical structure and sun direction on the attributes of light interception could be distinguished.

Results

1. Diurnal leaf orientation

1.1 Leaf azimuth distribution

Cotton leaves changed significantly ($P < 0.01$) their azimuths during the day. Leaf azimuths tended to lead the sun position in the morning, but lagged at noon and in the afternoon during the early stage of development. The results showed that change in leaf azimuth from morning to noon was greater than the change from noon to afternoon, particularly at the LAI 0.12 and LAI 2.84 stages.

1.2 Leaf inclination distribution

The distribution of leaf inclinations changed significantly ($P < 0.01$) during the day. At more the advanced stages, cotton leaves tended to incline more erectly in the morning (average leaf inclination of 25° , 40° and 42° at LAI 0.12, LAI 1.09, and LAI 2.84 stages, respectively) and at noon (25° , 33° and 41° , respectively), whereas there was virtually no change in the afternoon (38° , 34° and 37° , respectively).

1.3 Distribution of cosine of incidence angle

Most cotton leaves had a $\cos \beta$ greater than 0.6 at each period of day for all three stages of development (Figs. 2 to 4). Cotton leaves displayed more diaheliotropic orientation at noon, but less in the morning and in the afternoon. However, the leaves showed non-significantly different orientation behaviour ($P > 0.05$) in the morning and in the afternoon (Table 1).

As $\cos \beta$ values result from the relative geometry of both the sun position and the leaf orientation, diurnal changes in $\cos \beta$ were clearly due to changes in canopy geometry and sun course. Supposing the sun direction changes without any change in canopy geometry, or the canopy structure changes without any change in sun direction, the cross analysis of $\cos \beta$ allows us to distinguish the change in $\cos \beta$ due to sun position or leaf orientation (Table 1). For the morning sun direction, the morning leaf orientation allowed the greatest values of $\cos \beta$ while the noon and afternoon leaf orientation would have led to a decrease in $\cos \beta$ of 15-20 % and 35-50 %, respectively. Therefore, if there was no leaf movement between the afternoon and the next morning, the orientation of cotton leaves would have been significantly less favorable to intercept direct sunlight.

The results also showed that if leaf azimuth distribution was uniform, the $\cos \beta$ values (i.e., G-function G^u) of the leaves would have been smaller than $\cos \beta$ obtained for the actual azimuth distribution, particularly in the morning and in the afternoon. Comparing to the uniform distribution, the distribution of actual leaf azimuth gave about 16 % of advantage to cotton plant in $\cos \beta$ in the morning and in the afternoon, but only 4 % at noon at the LAI 0.12 stage. This advantage of diurnal changes in leaf azimuth is less than 10 % during the day when the LAI was 1.09. However, when the mutual shading became more important (LAI 2.84), changes in leaf azimuth showed higher advantage in $\cos \beta$ than the previous stage.

14. Diurnal change of leaf blade location

The location of leaf central point varied significantly ($P < 0.01$) during the day depending on the period of the day and stage of plant development. Change in location between morning and noon of leaf blade was 2.4 cm at LAI 0.12 stage, which differed significantly ($P < 0.01$) from that at LAI 1.09 stage (4.7 cm) and LAI 2.84 stage (5.0 cm). Afternoon motion of each stage showed small difference as that of morning: 2.7, 3.2 and 4.1 cm, respectively.

2. Sunlit leaf area and probability of light interception.

2.1 Sunlit leaf area

The soil surface area occupied by a plant (S_R) increased with LAI (from 322 cm^2 at LAI 0.12, to $1,976 \text{ cm}^2$ at LAI 1.09 and $3,858 \text{ cm}^2$ at LAI 2.84) whereas the ratio of S_R to the leaf area of a plant decreased (from 1.74 at LAI 0.12 to 1.25 at LAI 1.09 and 0.98 at LAI 2.84). This means that the efficiency of space occupation by the leaves of a plant decreased with the stage of development.

The diurnal fraction of sunlit leaf area varied significantly ($P < 0.01$) according to the stage of development. Sunlit leaf area decreased from LAI 0.12 to LAI 1.09 stage but increased from LAI 1.09 to LAI 2.84 stage. The results showed that sunlit leaf area increased from morning to noon, and decreased from noon to afternoon (Table 2). However, sunlit leaf area in the morning did not differ significantly ($P > 0.05$) from that in the afternoon at all three stages.

In this study, sunlit leaf area responded to the combination of sun direction and plant geometry in a similar way to $\cos \beta$ (Table 2). For the morning and afternoon sun directions, the morning and afternoon plant geometry allowed the largest fraction of sunlit area, respectively. Adopting an afternoon leaf distribution for the morning sun direction or a morning plant structure for the afternoon sun would have reduced the fraction of sunlit area by 30-43 %. Similar to $\cos \beta$, the fraction of sunlit area for the noon sun direction was much less influenced by changes in plant geometry.

2.2 Probability of light interception

The probability of light interception computed from digitizing data (P_{Digit}) within the reference area S_R was greater in the morning and in the afternoon than at noon, at all three stages of development. The same behaviour was found with light interception probabilities calculated by Beer-Lambert's model (P_{Beer}) and binomial model (P_{Binom}) (Fig. 5).

The light interception probability was also affected by diurnal changes in plant geometry (Fig. 5). Plant structure in the morning allowed more light interception in the morning than plant structure at noon and in the afternoon, at all three stages of development. The probability of light interception in the afternoon sun direction was the highest for the afternoon plant geometry while plant structure at noon showed only little advantage for light interception at noon.

2.3 Diurnal changes in leaf arrangement of plant

There was no significant difference ($P > 0.05$) between P_{Beer} and P_{Binom} , meaning that finite leaf size did not have a significant effect on leaf dispersion. In contrast, the

difference between the actual light interception (i.e., P_{Digit} estimated from digitizing) and the models (either the Beer-Lambert's model or the binomial model) was significant ($P < 0.05$). Dispersion of cotton leaves expressed by the ratio $P_{\text{Digit}}/P_{\text{Binom}}$ varied significantly ($P < 0.01$) during the day and during plant development (Table 3). Cotton leaves presented a diurnally regular dispersion ($P_{\text{Digit}}/P_{\text{Binom}} > 1.0$) (particularly at the LAI 0.12 and 2.84 stages). Conversely, the leaf dispersion tended to be random ($P_{\text{Digit}}/P_{\text{Binom}} \approx 1.0$) in the morning and in the afternoon but clumped ($P_{\text{Digit}}/P_{\text{Binom}} < 1.0$) at noon at the LAI 1.09 stage.

Discussion

Leaf orientation in cotton

Leaf orientation may be quantified by leaf angle distributions (Lang, 1973; Fukai and Loomis, 1976) or by the incidence angle β (Ehleringer and Hammond, 1987). In our study, leaf azimuth and inclination distributions were not obviously related to the sun position. Only leaf azimuths at the LAI 2.84 stage clearly followed the sun course. The lack of a clear relationship in our study may be due to the relationship between leaf inclination and leaf azimuth as reported by Lang (1973).

Table 1 shows that values of $\cos \beta$ are greater at noon than in the morning or the afternoon. This does not mean that leaf heliotropism is greater at noon: as a matter of fact, any kind of planophile canopy would show similar diurnal patterns of $\cos \beta$, even if leaves do not move during the day. Therefore, Table 1 gives some evidence that there are changes in leaf angles to allow the leaves to better face the sun during the day.

Our results reveal that the $\cos \beta$ values of the noon sun direction were the greatest values but they were much less influenced by the leaf orientation at all three stages of development. This suggests that planophile canopy like cotton is less sensitive to intercept direct solar beam than erectophile one at noon when the direction of incident radiation is high (Sinoquet and Andrieu, 1993).

It was also noted that heliotropic behaviour tended to decrease as LAI increase (Thanisawanyangkura et al., 1996). This varying response might relate to leaf age and plant maturity (Lang and Begg, 1979; Ehleringer and Forseth, 1989). Firstly, leaf movement is related to petiole mechanics, then motion of older leaves is likely to decrease due to petiole lignification. Secondly, heliotropic behaviour is reported to be driven by blue light signals (Ehleringer and Forseth, 1989; Firn, 1994) or intra-leaf irradiance gradients (Fisher and Fisher, 1983). This suggests that leaf movement is likely to decrease as mutual shading increases with plant development.

Leaf motion

Light interception in heliotropic canopies has only been considered from a leaf orientation point of view. However,

leaf angles cannot change without change in leaf blade location. Although leaf blades moved during the day, this did not much influence leaf dispersion (Table 3): for a given sun direction, any kind of plant geometry as at morning, noon or afternoon, leads to similar leaf dispersion. This is especially the case at LAI of 1.09 and 2.84 stages. This would mean that leaf motion during the day does not allow leaves to better exploit or avoid direct sunlight, by tracking light or shade microsites.

Plant geometry and light interception

Plant geometry of cotton varies between the stages of development. Cotton plant presented relatively more regular leaf dispersion in the morning and in the afternoon, and more clumped at noon (Table 2). Leaf dispersion was regular at the LAI 0.12 and 2.84 stages while clumped at the intermediate growth stage. As changes in leaf dispersion are not related to small leaf displacements, this results from the spatial leaf distribution at the plant level, i.e., plant architecture. Without change in canopy structure, leaf dispersion may change with solar elevation (Nilson, 1971; Prévot, 1985; Andrieu and Sinoquet, 1993). In the case of cotton, data on diurnal changes in leaf dispersion is rare. Sassenrath-Cole (1995) used light measurements to infer patterns of leaf dispersion at two stages of plant development. In case of mature *G. hirsutum*, leaf dispersion was regular at both early morning and noon. However, leaf dispersion was quantified by a Markov model (Nilson, 1971) in the morning and a binomial model (Fukai and Loomis, 1976) at noon: this prevents a comparison of the degree of regularity at the two times of day. Our results showed that most changes in leaf dispersion were related more to changes in sun direction than to changes in plant geometry. This pattern is clearly observed at LAI 1.09 and LAI 2.84 stages while differences in leaf dispersion at LAI 0.12 stage are smaller and not clearly related to changes in sun direction nor plant structure.

Ecological significance of heliotropism

Most authors (e.g., Fukai and Loomis, 1976; Ehleringer and Forseth, 1989; Gutschik, 1991) pointed out that diurnal change in leaf orientation is beneficial for photosynthesis when solar altitude is low but this behaviour does not improve photosynthesis since leaves with a high $\cos \beta$ are light-saturated while this increases risks of water, temperature and light stress. Our results suggest that cotton plants do not necessarily attempt to maximize light interception throughout the day. Even if leaf inclination distribution changes during the day, overall the foliage remains planophile. In other words, cotton plants would be unable to change leaf inclination by a large amount. Consequently, values of $\cos \beta$ at noon (i.e., at high solar elevation) must be high whatever the leaf azimuth distribution. Most work on cotton leaf orientation (Lang, 1973; Fukai and Loomis, 1976; and some of ours) shows that leaf azimuth distribution follows the sun course. The correlation between leaf and sun azimuth at noon could have been misinterpreted: if plants tend to face the sun in

the morning and afternoon by adjusting leaf azimuths, they cannot make an abrupt shift from east-facing to west-facing and have to gradually move. South-facing of leaves at noon could just be an intermediate azimuth angle between those of morning and afternoon. This assumption is corroborated by the weak influence of leaf azimuth on $\cos \beta$ for planophile canopies at high sun elevation. Moreover, spatial distribution of leaves within the plant leads to more clumpiness (or less regularity) at noon (Table 3). This could be a way to decrease light interception at noon when leaves keep planophile throughout the day. Plant architecture could then be designed in a way which compensates for the drawback of a planophile foliage. Another interpretation could be that new leaves locate themselves in light gaps found for the low sun directions.

Conclusion

Light interception depends on the spatial distribution of leaves within the plant. In this study, diurnal changes in plant geometry due to heliotropism of *G. hirsutum* in terms of incidence angle of direct sun light on the leaves was observed, in agreement with all previous works (Lang, 1973; Fukai and Loomis, 1976; Ehleringer and Hammond, 1987; Sassenrath-Cole, 1995). However, diurnal patterns of leaf dispersion showed that cotton foliage is more regular in the morning and in the afternoon than at noon. Location of new leaves within the plant could then be arranged to exploit light gaps found for the low sun altitudes. In order to complete this work at a canopy level, interactions between plants will be considered in a further study. This would allow us to identify how leaf dispersion is influenced by intra-plant and inter-plant leaf locations.

Concerning to a methodological point of view, 3D digitizing provides us with an accurate description of the plant geometry in terms of leaf location and leaf orientation. Using these measurements with rough image synthesis and image analysis gave us an improved method for studying relationships between plant geometry and light interception.

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References

Andrieu B. and H. Sinoquet. 1993. Evaluation of structure description requirements for predicting gap fraction of vegetation canopies. *Agric. For. Meteorol.* 65: 207-227.

Ehleringer, J. R. and I. N. Forseth. 1989. Diurnal leaf movements and productivity in canopies. In: G. Russell, B.

Marshall and P. G. Jarvis (Editors). *Plant canopies: their growth, form and function*. Cambridge University Press. Great Britain. pp. 129-142.

Ehleringer, J. R. and S. D. Hammond. 1987. Solar tracking and photosynthesis in cotton leaves. *Agric. For. Meteorol.* 39: 25-35.

Firn, R. D. 1994. Phototropism. In: R. E. Kendrick and G. H. M. Kronenberg (Editors). *Photomorphogenesis in plants*. Kluwer Academic Publishers. Netherlands. pp. 659-681.

Fisher, F. J. F. and P. M. Fisher. 1983. Photosynthetic patterning: a mechanism for sun tracking. *Can. J. Bot.* 61: 2632-2640.

Fukai, S. and R. S. Loomis. 1976. Leaf display and light environments in row-planted cotton communities. *Agric. Meteorol.* 17: 353-379.

Gutschick, V. P. 1991. Joining leaf photosynthesis models and canopy photon-transport models. In: R. B. Myneni and J. Ross (Editors). *Photon-vegetation interactions: applications in optical remote sensing and plant ecology*. Springer-Verlag. Berlin. pp. 516-535.

Lang, A. R. G. 1973. Leaf orientation of a cotton plant. *Agric. Meteorol.* 11: 37-51.

Lang, A. R. G. and J. E. Begg. 1979. Movements of *Helianthus annuus* leaves and heads. *J. App. Ecol.* 16: 299-305.

Nilson, T. 1971. A theoretical analysis of the frequency of gaps in plant stands. *Agric. Meteorol.* 8: 25-38.

Prévot, L. 1985. Modélisation des échanges radiatifs au sein des couverts végétaux, application à la télédétection, validation sur un couvert de maïs. Thèse d'université. Paris VI. 178 p.

Ross, J. 1981. The radiation regime and architecture of plant stands. W. Junk Pub. The Hague. 391 p.

Sassenrath-Cole, G. F. 1995. Dependence of canopy light distribution on leaf and canopy structure for two cotton (*Gossypium*) species. *Agric. For. Meteorol.* 77: 55-72.

Sinoquet, H. and B. Andrieu. 1993. The geometrical structure of plant canopies: characterization and direct measurement methods. In: C. Varlet-Grancher, R. Bonhomme and H. Sinoquet (Editors). *Crop structure and light microclimate: characterization and applications*. INRA Editions. Paris. pp. 131-158.

Sinoquet, H., C. Varlet-Grancher, and R. Bonhomme. 1993. Modelling radiative transfer within homogeneous canopies: basic concepts. In: C. Varlet-Grancher, R. Bonhomme and

H. Sinoquet (Editors). Crop structure and light microclimate: characterization and applications. INRA Editions. Paris. pp. 207-228.

Sinoquet, H. and P. Rivet. 1996. Measurement and visualisation of the architecture of an adult tree based on a three-dimensional digitizing device. Trees. In press.

Thanisawanyangkura, S., H. Sinoquet, P. Rivet, M. Cretenet, and E. Jallas. 1996. Leaf orientation and sunlit leaf area distribution in cotton. Agric. For. Meteorol. In press.

Table 1 The cosine of the angle of incidence of the sun on the cotton leaves, $\cos \beta$, calculated for the leaf angles measured at three times of day and for three positions of the sun. Results are given for the three development stages when LAI was 0.12, 1.09 and 2.84. The results for the leaf angle appropriate to the sun's position are highlighted by printing in bold italics.

Leaf Orientation	Sun Position		
	Morning	Noon	Afternoon
LAI 0.12			
Morning	0.697 ^b	0.866 ^a	0.380 ^d
Noon	0.578 ^c	0.862 ^a	0.507 ^c
Afternoon	0.339 ^d	0.731 ^b	0.682 ^b
LAI 1.09			
Morning	0.597 ^{c,d}	0.712 ^b	0.441 ^{e,f}
Noon	0.507 ^{d,e}	0.813 ^a	0.515 ^{d,e}
Afternoon	0.394 ^f	0.772 ^{a,b}	0.613 ^c
LAI 2.84			
Morning	0.645 ^a	0.648 ^a	0.401 ^d
Noon	0.522 ^c	0.685 ^{a,b}	0.487 ^c
Afternoon	0.406 ^d	0.724 ^b	0.616 ^a

The $\cos \beta$ values of each stage of development followed by the same letter are not significantly different ($P>0.05$), tested by Student-Newman-Keuls method.

Table 2 The sunlit leaf area of cotton as a percentage of total leaf area calculated for the plant structures measured at three times of day and three positions of the sun. Results are given for the three development stages when LAI was 0.12, 1.09 and 2.84. The results for the plant structure appropriate to the sun's position are highlighted by printing in bold italics.

Plant Structure	Sun Position		
	Morning	Noon	Afternoon
LAI 0.12			
Morning	60.8 ^{s,t,u}	81.1 ^w	33.9 ^{c,d,e,f,g,h,i}
Noon	54.9 ^{p,q,r,s}	73.3 ^v	42.5 ^{h,i,j,k,l,m,n}
Afternoon	34.6 ^{c,d,e,f,g,h,i,j}	63.6 ^{t,u}	55.7 ^{q,r,s,t}
LAI 1.09			
Morning	36.8 ^{d,e,f,g,h,i,j,k}	37.1 ^{d,e,f,g,h,i,j,k,l}	25.5 ^{a,b,c}
Noon	30.7 ^{b,c,d,e,f}	42.2 ^{g,h,i,j,k,l,m,n}	32.9 ^{c,d,e,f,g,h}
Afternoon	24.1 ^{a,b}	42.3 ^{h,i,j,k,l,m,n}	37.9 ^{d,e,f,g,h,i,j,k,l}
LAI 2.84			
Morning	46.4 ^{k,l,m,n,o,p,q}	43.9 ^{i,j,k,l,m,n,o}	33.5 ^{c,d,e,f,g,h}
Noon	39.2 ^{e,f,g,h,i,j,k,l,m}	48.0 ^{m,n,o,p,q}	39.5 ^{f,g,h,i,j,k,l,m}
Afternoon	32.9 ^{c,d,e,f,g,h}	50.6 ^{n,o,p,q,r,s}	49.6 ^{n,o,p,q,r}

The values of sunlit leaf area percentage followed by the same letter are not significantly different ($P>0.05$), tested by all pairwise multiple comparison method.

Table 3 The ratio of the measured probability of light interception, P_{Digit} , to the probability of light interception for a binomial distribution of leaves at three times of day and three positions of the sun. The results are presented for three stages of development of the cotton plants when LAI was 0.12, 1.09 and 2.84. The results for the plant structure appropriate to the sun's position are highlighted by printing in bold italics.

Plant Structure	Sun Position		
	Morning	Noon	Afternoon
LAI 0.12			
Morning	1.26 ^c	1.33 ^a	1.24 ^{b,c}
Noon	1.30 ^a	1.22 ^{b,d}	1.20 ^d
Afternoon	1.20 ^d	1.24 ^{b,c}	1.26 ^c
LAI 1.09			
Morning	0.97 ^a	0.79 ^b	0.93 ^a
Noon	0.96 ^a	0.81 ^b	0.96 ^a
Afternoon	0.93 ^a	0.82 ^b	0.96 ^a
LAI 2.84			
Morning	1.29 ^b	1.06 ^c	1.29 ^b
Noon	1.26 ^b	1.11 ^c	1.30 ^{a,b}
Afternoon	1.30 ^{a,b}	1.10 ^c	1.38 ^a

The P_{Digit} / P_{Binom} values of each stage of development followed by the same letter are not significantly different ($P>0.05$).

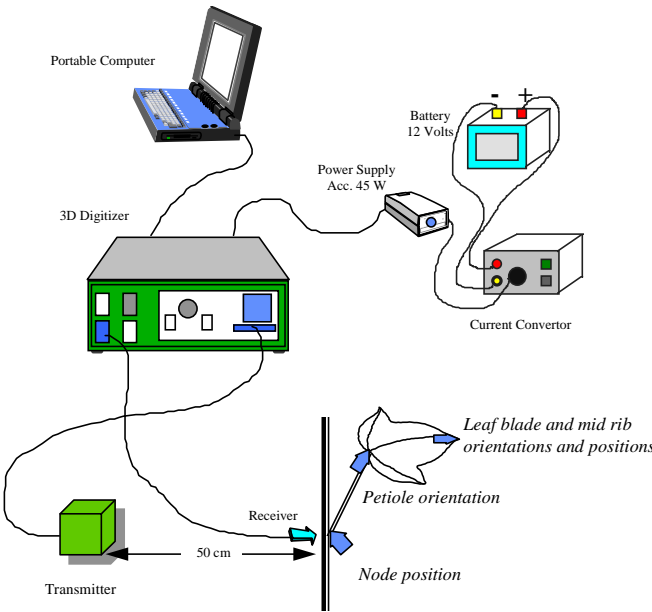
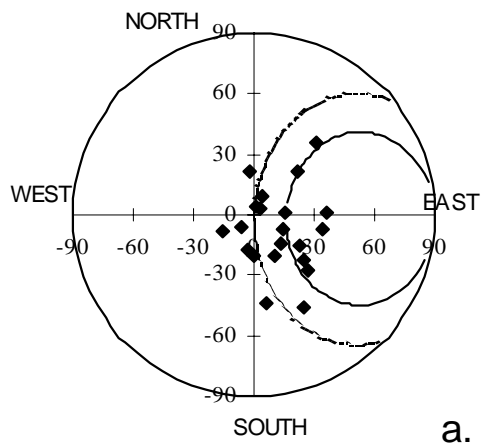
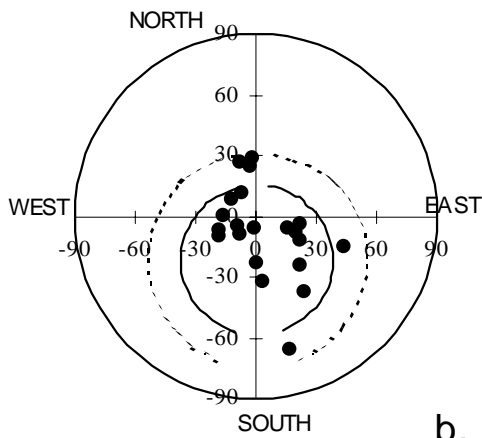


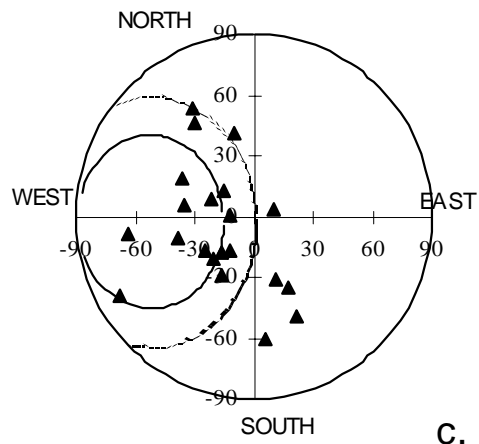
Figure 1 Schematic representation of digitizer installation for plant geometry measurement in the field.



a.

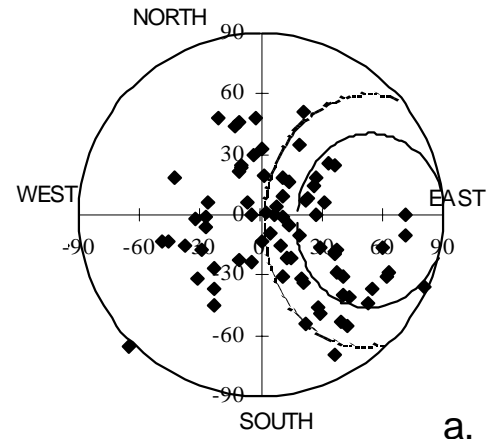


b.

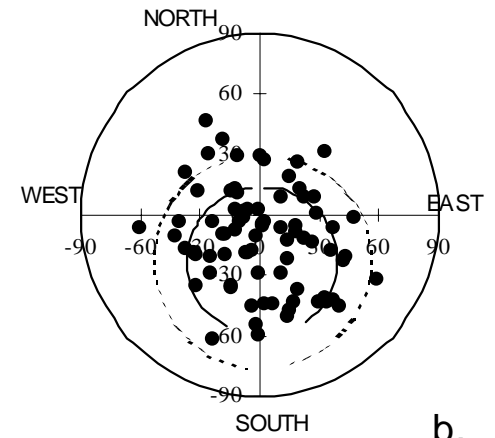


c.

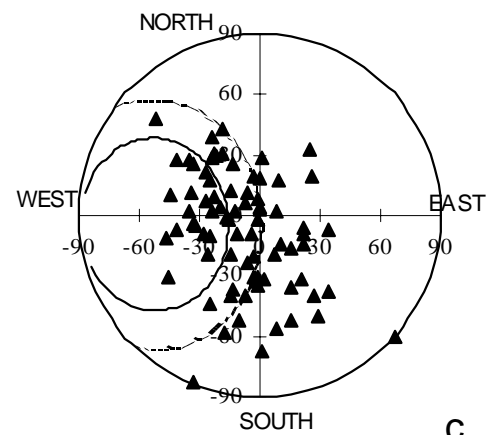
Figure 2 Distribution of cotton leaf orientation and lines of cosine of incidence angle, $\cos \beta$, of 0.6 (----) and 0.8 (—) as a function of leaf orientation (a) in the morning, (b) at noon, and (c) in the afternoon at LAI of 0.12 stage. Each point represents the orientation of one leaf described by its inclination angle and azimuth angle.



a.

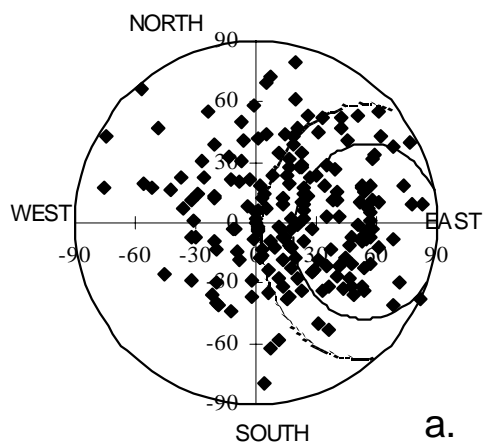


b.

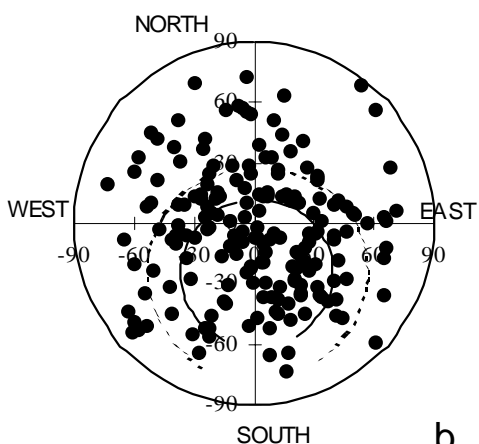


c.

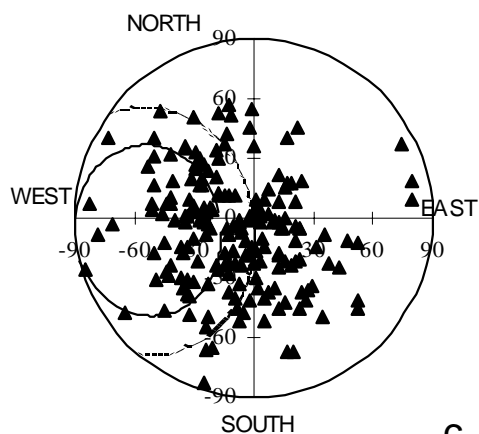
Figure 3 Distribution of cotton leaf orientation and lines of cosine of incidence angle, $\cos \beta$, of 0.6 (----) and 0.8 (—) as a function of leaf orientation (a) in the morning, (b) at noon, and (c) in the afternoon at LAI of 1.09 stage. Each point represents the orientation of one leaf described by its inclination angle and azimuth angle.



a.



b.



c.

Figure 4 Distribution of cotton leaf orientation and lines of cosine of incidence angle, $\cos \theta$, of 0.6 (---) and 0.8 (—) as a function of leaf orientation (a) in the morning, (b) at noon, and (c) in the afternoon at LAI of 2.84 stage. Each point represents the orientation of one leaf described by its inclination angle and azimuth angle.

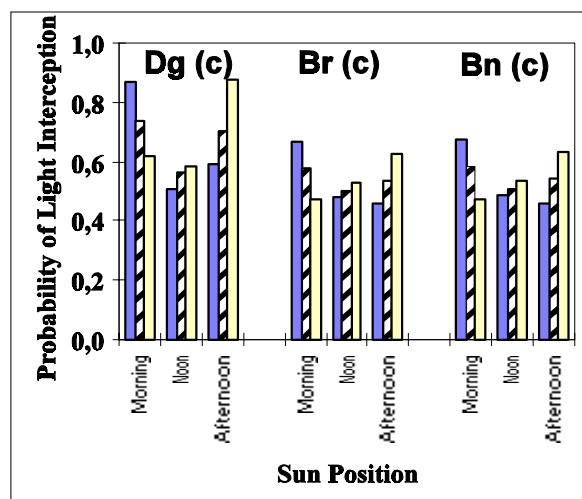
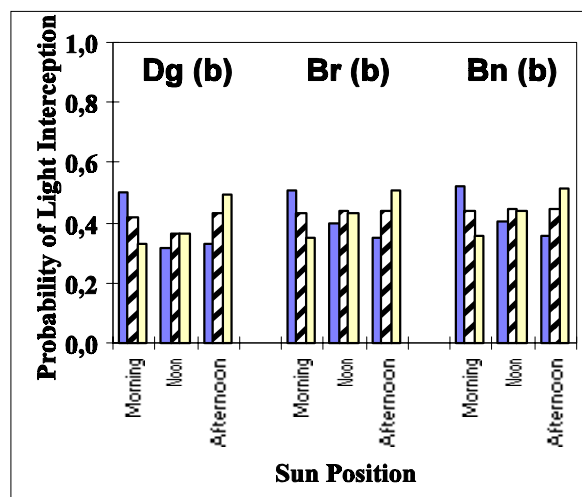
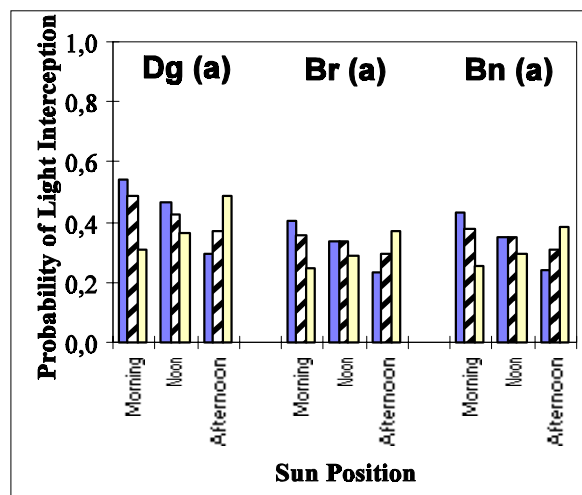


Figure 5 Probability of light interception of cotton plant as a function of sun position and diurnal changes in plant geometrical structure: **Dg** Measured, **Br** by Beer-Lambert's law, and **Bn** by binomial law, at the 3 stages of development; (a) LAI of 0.12, (b) LAI of 1.09, and (c) LAI of 2.84, with plant structure of ■ Morning ▨ Noon ■ Afternoon.