Kasetsart J. (Nat. Sci.) 31 : 43 - 54 (1997)

Plant Geometrical Structure and Leaf Irradiance in Cotton : II. Measurement of Cotton Plant under Tropical Conditions

Sornprach Thanisawanyangkura[1], Hervé Sinoquet[2], and Poonpipope Kasemsap[3]

ABSTRACT

Leaf orientation behavior of cotton plants (*Gossypium hirsutum* L. cv. SSR 60) at two different stages of development were studied in the field under tropical conditions. Electromagnetic digitizing system was used for leaf angle and leaf position measurements at three different periods of two hours during the day.

Leaf azimuth distribution of SSR 60 cotton variety was not uniform. Cotton leaves tended to face the sun in the morning, but tended to lag at noon and in the afternoon. Most of cotton leaves inclined between 15°-45° during the day.

Cotton leaves showed a diaheliotropic movement throughout the day. They oriented more diaheliotropically at noon, but less in the morning and in the afternoon at both two stages of development. Because of actual leaf azimuth distribution, cotton plants could have 15-30 % of advantage in direct radiation interception compared to uniform leaf azimuth distribution. Without a diurnal leaf orientation, cotton plants would intercept less direct radiation in the morning and in the afternoon. The ecological significance of this leaf orientation behavior under tropical conditions is also discussed.

Key words : heliotropism, digitizing, plant geometrical structure.

INTRODUCTION

Diurnal change of leaf orientation in response to the change of sun direction occurs in a variety of plants including cotton (Ehleringer and Forseth, 1989). This solar tracking movement, so-called heliotropism, is classified in two types: diaheliotropism and paraheliotropism. Diaheliotropism is a movement in which the leaf lamina remains oriented perpendicular to the sun direction: this results in higher leaf irradiance. In contrast, paraheliotropism is a movement where leaves orient themselves parallel to the sun direct beams : this results in avoidance of high leaf irradiance, decrease in transpiration, and thus in heat loads, and reduction in photoinhibitory effects due to excessive direct radiation (Ehleringer and Forseth, 1989; Fu and Ehleringer, 1989, Isoda *et al.*, 1994; Kao *et al.*, 1994; Wang *et al.*, 1994, Yu and Berg, 1994).

Leaf orientation behavior in cotton has been quantitatively characterized for more than 20 years

[1] Department of Botany, Faculty of Science, Kasetsart University, Bangkok 10900. Thailand.
[2] UA Bioclimatologie - PIAF, I.N.R.A., Domaine de Crouelle, 63039 Clermont-Ferrand Cedex 02. France.
[3] Department of Agronomy, Faculty of Agriculture, Kasetsart University, Bangkok 10900. Thailand.

(Lang, 1973; Fukai and Loomis, 1976; Ehleringer and Hammond, 1987; Sassenrath-Cole, 1995, Thanisawanyangkura *et al.*, 1997a; Thanisawanyangkura *et al.*, 1997b, among others). Regarding the two most important species for agriculture, *Gossypium hirsutum* L. is reported to be diaheliotropic while *G. barbadense* L. is not heliotropic (Ehleringer and Hammond, 1987; Sassenrath-Cole, 1995). Thanisawanyangkura *et al.* (1997a) showed that leaf orientation behavior of *G. hirsutum* L. changed throughout the day and varied during growing season. Moreover, cotton leaves also moved in space and the moving distance increased with stage of development, in agreement with petiole and blade lengths. Because of heliotropism, cotton leaves could intercept more direct solar beam, particularly in the morning and in the afternoon, due to diurnal change in plant geometrical structure.

Although more than 50 % of cotton has been grown in tropical climate (F.A.O., 1995), however, there is no information of heliotropic behavior in cotton, particularly local varieties which adapt well under tropical environment where there is a great fluctuation of radiation flux due to cloudy condition during growing periods.

The objective of this study is to characterize diurnal changes in leaf orientation of local variety of cotton under tropical conditions by using an electromagnetic digitizing system (Thanisawanyangkura *et al.*, 1997a; 1997b). The information from this study will lead to further study on the relationship between diurnal changes in leaf orientation, in spatial leaf arrangement and light interception throughout growing season and allows us to understand more about the ecological significance of heliotropism in cotton under tropical conditions.

MATERIALS AND METHODS

Field Growing Condition

Cotton plants (*Gossypium hirsutum* L. cv. Sri Sumrong 60 (SSR 60) : local recommended Thai variety) were sown on May 29, 1996, at the National Corn and Sorghum Research Center (Suwan Farm; latitude 14.7° N, longitude 101.2° E), Nakhon Ratchasima, Thailand, in North-Eastern (NE) - South-Western (SW) row direction. Row spacing was 1.25 m and between plant spacing was 0.40 m after thinning at 28 days after emergence (DAE). Cultural practices (fertilization, herbicide application, hand weeding, and insecticide application) were done similarly to experimental practices in the research station. The crop was irrigated by sprinkler.

During the growing period, the weather was warm and rainy with some strong wind during afternoon. For the measurement days (42 DAE and 58 DAE) when the leaf area index (LAI, total leaf area per planted area) was 0.9 and 1.8, there were some cloudy periods during the day (Figure 1).

Leaf Orientation Measurement

Leaf position and leaf orientation angles were measured by using an electromagnetic digitizer (Polhemus® 3Space®, Fastrak®, Colchester, VT, U.S.A.) and acquisition software DiplAmi Version 2.0 written by P. Rivet (INRA, Clermont-Ferrand, France) (Sinoquet and Rivet, 1997). Two consecutive plants on the same row of cotton were digitized three times a days: in the morning (07h00-09h00 True Solar Time), at noon (11h00-13h00), and in the afternoon (15h00-17h00). Digitized positions on cotton plant (i.e. nodes on main stem and branches, and proximal and distal tips of the midrib) were described by Thanisawanyangkura *et al.* (1997b).

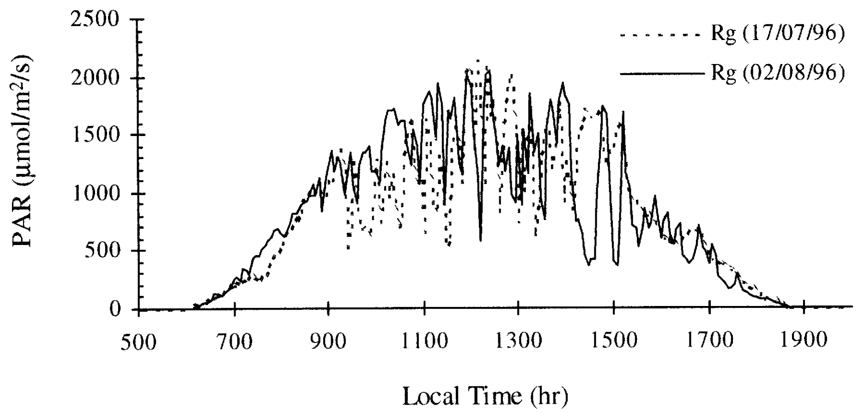

Figure 1 Global incident radiation (Rg) of two measurement days : July 17, 1996 (Day of Year, DOY=199) and August 2, 1996 (DOY=215), at National Corn and Sorghum Research Center, Nakhon Ratchasima, Thailand.

Leaf Area Measurement

Leaf area was estimated from an allometric relationship between midrib length (L, cm) and leaf area (S, cm^2) measured by a LiCor 3100® Leaf Area Meter (LiCor Inc., Lincoln, NE, U.S.A.) :

$S = 0.732\ L^2 \quad (n = 329, R = 0.937^{**})$

Data Analysis

Angular determination is defined as shown in Thanisawanyangkura *et al.* (1997a). Calculation for leaf orientation and cosine of the angle of incidence (angle between leaf normal and sun direction, β) was described by Thanisawanyangkura *et al.* (1997a). The cos β indicates how the leaf faces the sun, thus it may be used as an indicator for heliotropic behavior (Ehleringer and Forseth, 1989) : a value of cos β close to 1.0 indicates a leaf with a strong diaheliotropic behavior. In contrast, the leaf with a cos β close to 0 shows strong paraheliotropic behavior. 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 β, a value of cosine of incidence $(\cos\beta)^u$ with uniform leaf azimuth distribution was also calculated for each individual leaf and then for the whole plant foliage (Thanisawanyangkura *et al.*, 1997a).

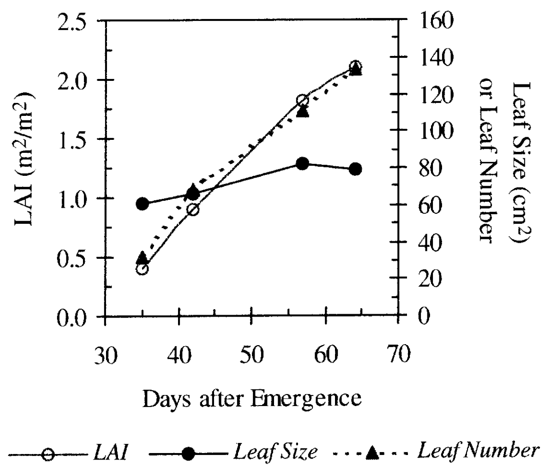

Figure 2 Development of leaf area index (LAI), leaf size, and leaf number of SSR 60 cotton variety under tropical condition.

RESULTS

1. Leaf Area Development of Cotton Plant

Leaf area of SSR 60 cotton plants developed well under growing conditions (Figure 2). Leaf area development showed a closer relationship to number of leaves (R^2=0.99) than leaf size (R^2=0.92). The LAI reached 0.4 at 34 DAE and 0.9 at 42 DAE when there were 32 and 68 leaves on a plant, respectively. Then, plants developed indeterminate numbers of vegetative and reproductive branches with numerous leaves. The LAI attained 2.1 at 64 DAE. At this time, plants had 133 leaves.

2. Leaf Orientation Distribution

2.1 Leaf azimuth distribution

The distribution of leaf azimuth changed significantly (P<0.01) during the day. Leaf azimuths tended to face the sun position in the morning, but tended to lag at noon and in the afternoon, particularly during the early stage of development (Figure 3). When plant developed more leaves, leaf azimuths tended to still face the sun position in the morning, but lagged in the afternoon (Figure 4).

2.2 Leaf inclination distribution

Cotton leaves changed their inclinations significantly (P<0.01) during the day. At the LAI 0.9 stage, most of cotton leaves inclined between 15°-45° during the day (Figure 5). However, about 20 % of total leaf area tended to stand erectly (>60) in the morning, but less than 10 % at noon and in the afternoon. At the more advanced stages, most of cotton leaves (about 60 % of total leaf area) still kept their inclination of 15°-45° during the day (Figure 6). It could be also noted that cotton plants were likely to maintain their leaf areas in the same class of 15° interval of inclination during the day at the LAI 1.8 stage.

2.3 Reconstruction of plant image showing diurnal leaf orientation

In order to visualize the diurnal change of leaf orientation of cotton plant, the digitizing informations were used and plant images (Figure 7) made by the << smooth curve >> function of Microsoft Excel® Version 5.0 (Microsoft Corp., U.S.A.) were created from the digitizing information on actual leaf orientation and leaf position. Figure 7 illustrated that cotton leaves oriented and changed

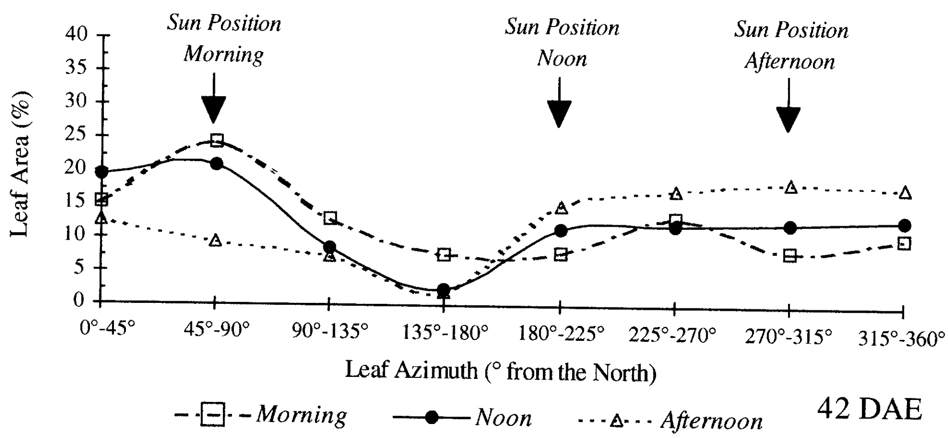

Figure 3 Leaf azimuth distribution of SSR 60 cotton variety at 3 times of day at LAI 0.9 stage (42 DAE).

their location in space during the day, i.e. from morning to noon, from noon to afternoon, and from afternoon to next morning, for both stages of development (LAI=0.9 and 1.8) due to varying positions of the sun. This method can also allow for further analysis of light interception by cotton canopy with image analysis.

2.4 Distribution of cosine of the angle of incidence

At the LAI 0.9 stage, cotton leaves tended to orient diaheliotropically at noon, but less in the morning and in the afternoon (Table 1 and Figure 8). The leaves showed non-significantly different orientation behavior in the morning and in the

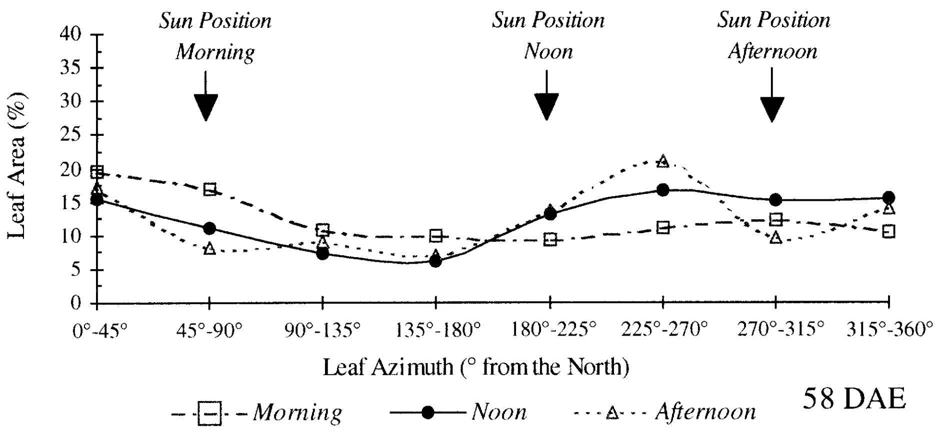

Figure 4 Leaf azimuth distribution of SSR 60 cotton variety at 3 times of day at LAI 1.8 stage (58 DAE).

Table 1 The cosine of the angle of incidence of the sun on the cotton leaves computed from the actual leaf azimuth distribution, Cos b, and from a uniform azimuth distribution, $(\text{Cos b})^u$, and the enhanced light interception due to non-uniform leaf azimuth distribution at 3 times of day of the LAI 0.9 and 1.8 stages.

	Morning	Noon	Afternoon
LAI 0.9			
Cos b	0.582^b	0.755^a	0.594^b
$(\text{Cos b})^u$	0.302^c	0.774^a	0.295^c
Advantage by Leaf Orientation	+ 28.0 %	- 1.9 %	+ 29.9 %
LAI 1.8			
Cos b	0.537^b	0.808^a	0.524^b
$(\text{Cos b})^u$	0.383^c	0.816^a	0.341^c
Advantage by Leaf Orientation	+ 15.4 %	- 0.8 %	+ 18.3 %

The cos b and $(\text{cos b})^u$ values of each stage of development followed by the same letter are not significantly different (P>0.05), tested by Student-Newman-Keuls Method.

afternoon (P>0.05). This pattern of diurnal heliotropic behavior still remained with more diaheliotropism at noon at the LAI 1.8 stage (Table 1 and Figure 9).

Table 1 showed that if the cotton leaves were uniformly distributed in azimuth, $(\cos \beta)^u$ would have been smaller than $\cos \beta$ obtained from the actual leaf azimuth distribution, particularly in the morning and in the afternoon. In comparison with a uniform distribution, the actual azimuth distribution allowed the cotton plant to increase about 28 % at the LAI 0.9 stage and 15 % at the LAI 1.8 stage in $\cos \beta$ in the morning and about 30 % at the LAI 0.9 stage and 18 % at the LAI 1.8 stage in the afternoon, but there was no advantage by leaf orientation at noon.

As $\cos \beta$ values result from the relative geometry of both the sun position and the leaf

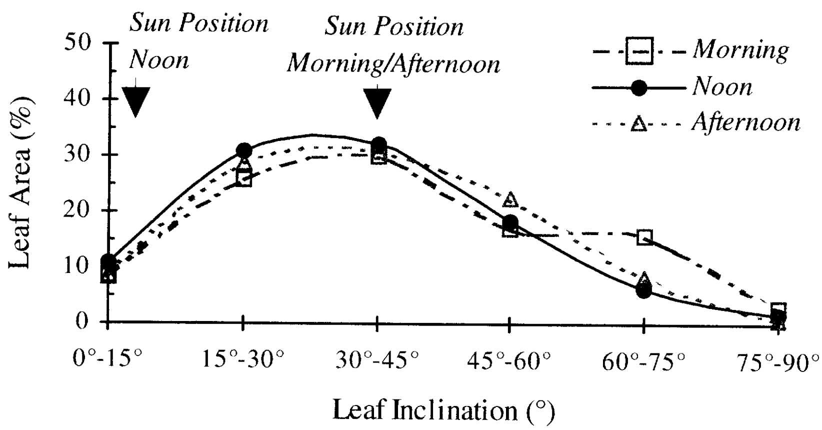

Figure 5 Leaf inclination distribution of SSR 60 cotton variety at 3 times of day at LAI 0.9 stage (42 DAE).

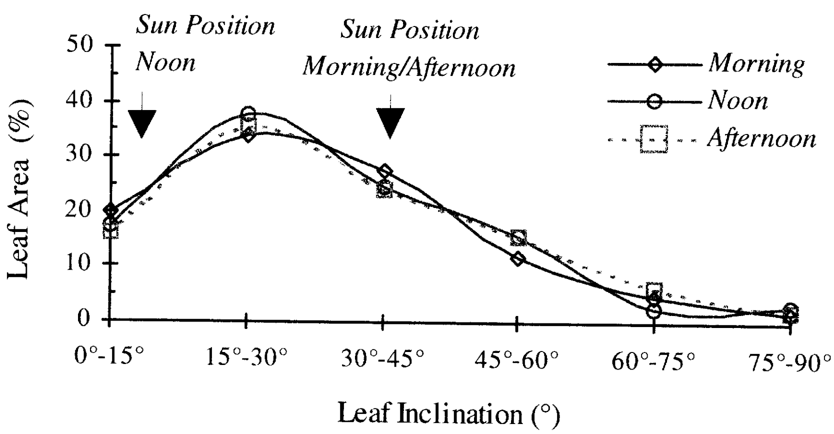

Figure 6 Leaf inclination distribution of SSR 60 cotton variety at 3 times of day at LAI 1.8 stage (58 DAE).

orientation, diurnal changes in cos β may be due to changes in canopy geometry and sun course. Assuming a situation with a change in the sun direction without any change in canopy geometry during the day, or change in canopy structure without any change in sun direction, allows us to distinguish the change in cos β due to sun position or leaf orientation (Table 2).

For the morning sun position, the morning leaf orientation allowed the greatest values of cos β (0.582 and 0.537 at the LAI 0.9 and 1.8, respectively) while the noon and afternoon leaf orientation would have led to a decrease in cos β of 3.5-8.5 % (from cos β = 0.582 to 0.547 at the LAI 0.9 stage and from cos β = 0.537 to 0.452 at the LAI 1.8 stage) and 8.4-16.1 % (from cos β = 0.582 to 0.421 at the LAI 0.9 stage and from cos β = 0.537 to 0.453 at the LAI 1.8 stage), respectively (Table 2). This means that, if there was no leaf movement from the afternoon to the next morning, the orientation of cotton leaves would have been significantly less favorable to intercept solar direct beam.

The afternoon sun position showed a symmetrical behavior with the greatest values of cos β for the afternoon leaf orientation : at the LAI 0.9 stage, the reduction in cos β due to the morning and noon leaf orientation would have been 15.5 % and 12.4 %, respectively, whereas this reduction in cos β was not significantly different (P>0.05) at stage of LAI 1.8 (Table 2). Otherwise, the greatest values of cos β were for the noon sun direction, but they were not significantly influenced by the leaf orientation (P>0.05).

DISCUSSION

SSR 60 cotton leaves exhibit varying heliotropic response during the day, eventhough there were some cloudy periods during the growing season. The leaves oriented diaheliotropically during the day, particularly at noon (Table 1).

Table 2 The cosine of the angle of incidence of the sun on the cotton leaves, Cos b, calculated for the leaf angles measured at 3 times of day and for 3 positions of the sun. Results are given for the 2 development stages when LAI was 0.9 and 1.8. The results for the leaf angle appropriate to the sun's position are highlighted by printing in bold numbers.

Leaf orientation	Sun position		
	Morning	Noon	Afternoon
LAI 0.9			
Morning	**0.582** ^{b}	0.699 ^{a}	0.439 ^{c}
Noon	0.547 ^{b}	**0.755** ^{a}	0.470 ^{c}
Afternoon	0.421 ^{c}	0.735 ^{a}	**0.594** ^{b}
LAI 1.8			
Morning	**0.537** ^{bc}	0.800 ^{a}	0.468 ^{cd}
Noon	0.452 ^{d}	**0.808** ^{a}	0.555 ^{b}
Afternoon	0.453 ^{d}	0.786 ^{a}	**0.524** ^{bc}

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

Heliotropism is generally defined as changes in leaf orientation to track or avoid direct sunlight, it may be quantified by leaf angle distributions (Lang, 1973; Fukai and Loomis, 1976) or by the incidence angle β (Ehleringer and Hammond, 1987; Fu and Ehleringer, 1989; Sassenrath-Cole, 1995). Thanisawanyangkura *et al.* (1997a) had shown that characterization of heliotropic behavior by using both the leaf angle distributions and the cos β values can explain more about this solar tracking movement, particularly, we can distinguish the effects of diurnal changes in leaf orientation and sun position on light interception due to the diurnal changes of cotton plant geometrical structure.

In our study, leaf azimuth and inclination distributions are not obviously related to sun position (Figures 3 to 5). These results agreed with Thanisawanyangkura *et al.* (1997a) which had been studied on DES 119 (an american cotton variety) under Mediterranean conditions. One could notice that foliage inclination of SSR 60 variety was mostly planophile (i.e. with leaf inclinations between 0° and 30°), especially at noon when solar elevation is high under tropical conditions (Figures 5 and 6). Table 2 shows that the values of cos β are greater at noon than in the morning and in the afternoon, even if cotton leaves do not move during the day. Although any kind of non-solar tracking planophile canopy would show similar diurnal patterns of cos β, it is evident that diurnal changes in leaf angles allows the cotton leaves to better face the sun during the day.

Solar tracking movement had been reported to decrease as the plant develops (Lang and Begg, 1979; Ehleringer and Forseth, 1989; Thanisawanyangkura *et al.*, 1997a). This might relate to leaf age and plant maturity (Lang and Begg, 1979; Ehleringer and Forseth, 1989; Saitoh, 1996). Because leaf movement is reported to be related to petiole mechanics (Satter and Galston, 1981; Fisher and Fisher, 1983; Fu and Ehleringer, 1989), motion of older leaves might be likely to decrease according to petiole lignification. In addition, heliotropism 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 heliotropism is likely to decrease as mutual shading increases with plant development. However, this pattern of response was not observed in our study.

With regard to the ecological significance of diaheliotropism, 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. However, for high sun elevations, this behavior does not improve photosynthesis since leaves with a high cos β are light-saturated and 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 angle 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 β 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 : they 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 supported by the weak influence of leaf azimuth on cos b for planophile canopies at high sun elevation.

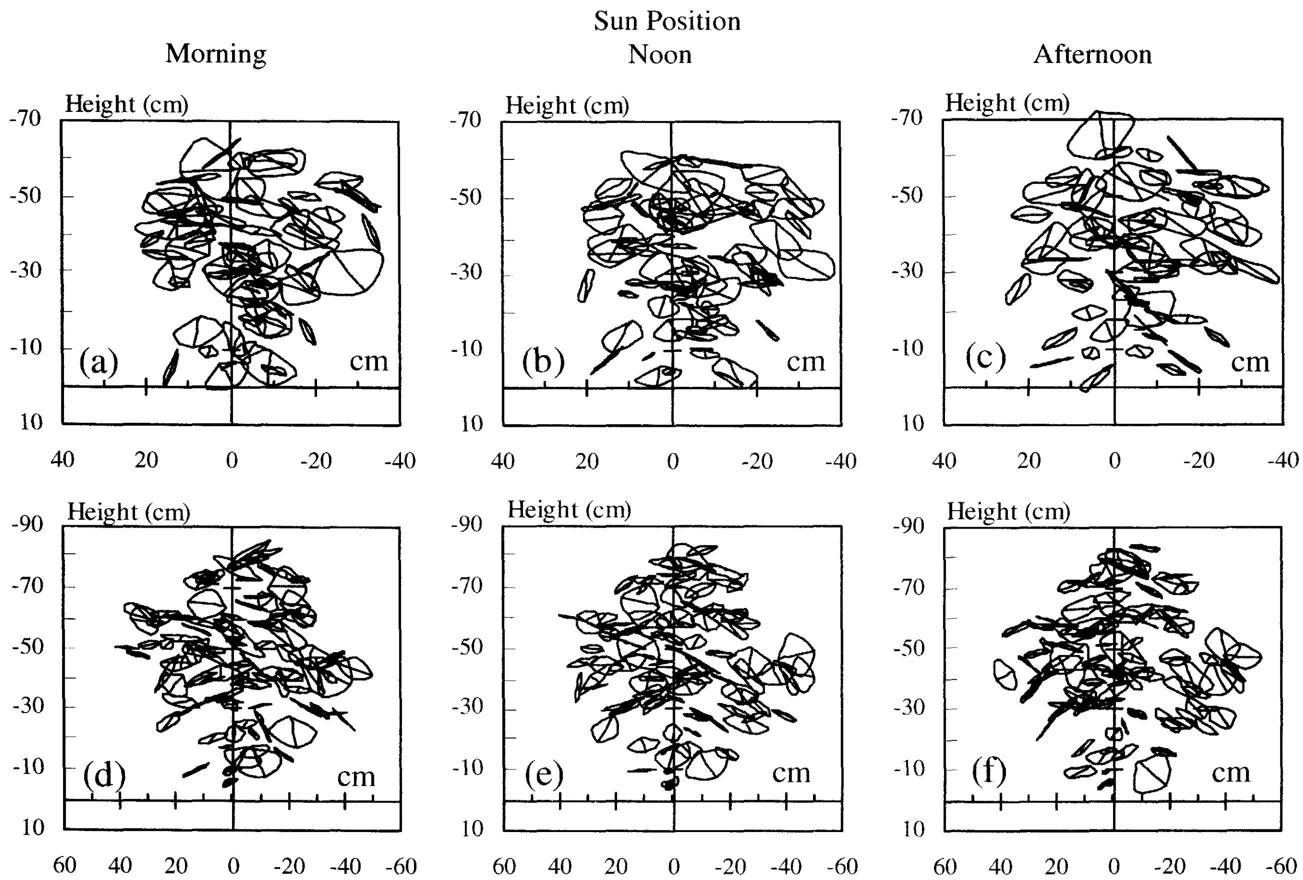

Figure 7 Reconstruction of leaf area orientation of a SSR 60 cotton plant viewed from the East (90 from the North) during the day from digitizing data at the LAI 0.9 stage (a, b, c) and the LAI 1.8 stage (d, e, f) , at 3 times of day (morning, noon, and afternoon) : height was shown in negative value (cm) from cotyledonary node.

Thanisawanyangkura *et al.* (1997a) showed that spatial distribution of cotton leaves within the plant leads to more clumpiness (or less regularity) at noon. 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 by genetic improvement for better adaptability under high radiation load condition like in the tropic.

CONCLUSION

Diurnal leaf orientation is an adaptive behavior of cotton (*Gossypium hirsutum* L.) which is beneficial to cotton plant for better direct sunlight interception in the morning and in the afternoon. Although there were some short cloudy periods during the day, cotton leaves still exhibited a diaheliotropic movement.

Heliotropic behavior can be quantitatively characterized under field condition by using

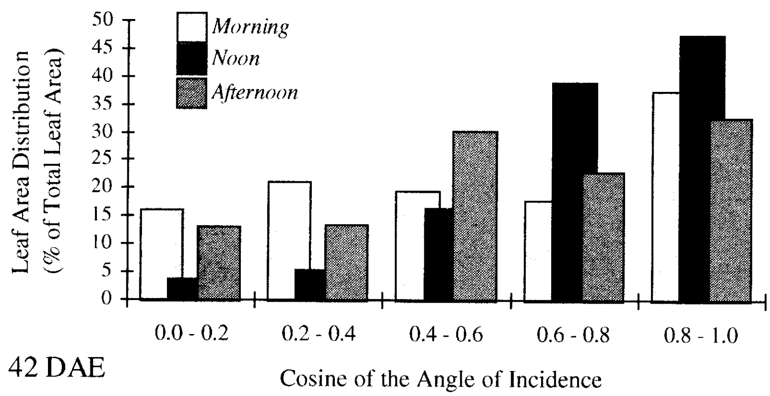

Figure 8 Cosine of the angle of incidence (cos b) distribution of SSR 60 cotton variety at 3 times of day at LAI 0.9 stage (42 DAE).

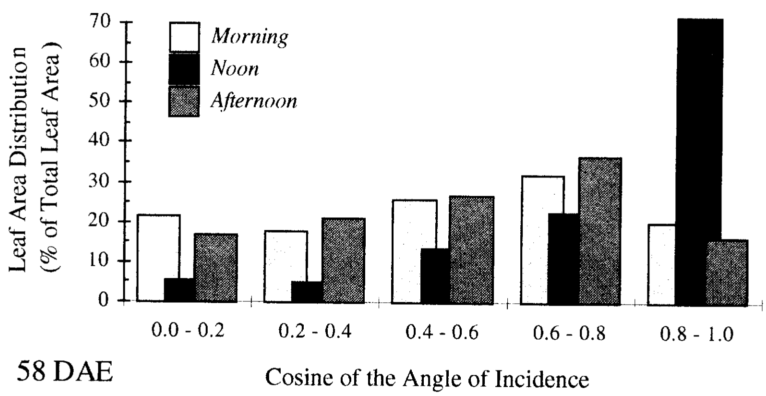

Figure 9 Cosine of the angle of incidence (cos b) distribution of SSR 60 cotton variety at 3 times of day at LAI 1.8 stage (58 DAE).

electromagnetic digitizing system. This method of 3D plant geometrical structure measurement provides us an accurate description of the plant geometry in terms of leaf location and leaf orientation. The data set allows us to create pictures of the plants measured in the field, from which information on light interception can be further derived. Therefore, using these measurements with rough image synthesis and image analysis permits us an improved method for studying the relationships between plant geometry and light interception.

ACKNOWLEDGEMENTS

This research was supported in part by grant from the European Economic Community (EEC) : STD III Project - DG XII N° TS3 - CT 94-0288, the Development-Oriented Research on Agrarian Systems (DORAS) Project, and the Kasetsart University Research and Development Institute (KURDI), Kasetsart University, Thailand. The authors would like to thank the National Corn and Sorghum Research Center, Nakhon Ratchasima, and the staffs for generous cooperation and their helps. We gratefully acknowledge the valuable assistance of all the staffs of DORAS Project, Thailand, and the National Institute of Agricultural Research (INRA) Bioclimatologie-PIAF, Centre de Clermont-Ferrand, France.

LITERATURE CITED

Ehleringer, J.R. and I.N. Forseth. 1989. Diurnal leaf movements and productivity in canopies, pp. 129-142. *In* G. Russell, B. Marshall and P.G. Jarvis. (eds.). Plant canopies : their growth, form and function. Cambrige University Press. Great Britain.

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

F.A.O. 1995. 1995 F.A.O. Production Year Book. Rome. Italy. p. 116-117.

Firn, R.D. 1994. Phototropism, pp.659-681.*In* R.E. Kendrick and G.H.M. Kronenberg (eds.). Photomorphogenesis in plants. 2nd Ed. Kluwer Academic Publishers. Netherlands.

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

Fu, Q.A. and J.R. Ehleringer. 1989. Heliotropic leaf movements in common beans controlled by air temperature Plant Physiol. 91 : 1162-1167.

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. pp.516-535. *In* R.B. Myneni and J. Ross (eds.). Photon-vegetation interactions : applications in optical remote sensing and plant ecology. Springer-Verlag, Berlin.

Isoda, A., T. Yoshimura, T. Ishikawa, H. Nojima, and Y. Takasaki. 1994. Effects of leaf movement on radiation interception in field grown leguminous crops. III. Relation to leaf temperature and transpiration among soybean cultivars. Jpn.J.Crop Sci. 63 : 657-663.

Kao, W-Y., J.P. Comstock, and J.R.Ehleringer. 1994. Variation in leaf movements among common bean cultivars. Crop Sci. 34 : 1273-1278.

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.

Saito, K. 1996. Relationship between leaf movements of trifoliate compound leaf and environmental factors in soybean canopy, p.

173. *In* Abstracts of 2nd International Crop Science Congress. New Delhi, India.

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.

Satter, R.L. and A.W. Galston. 1981. Mechanisms of control of leaf movements. Ann. Rev. Plant Physiol. 32 : 83-110.

Sinoquet, H. and P. Rivet. 1997. Measurement and visualisation of the architecture of an adult tree based on a three-dimensional digitizing device. Trees. 11 : 265-270.

Thanisawanyangkura, S., H. Sinoquet, P. Rivet, M. Cretenet, and E. Jallas. 1997a. Leaf orientation and sunlit leaf area distribution in cotton. Agric. For. Meteorol. 86 : 1-15.

Thanisawanyangkura, S., H. Sinoquet, M. Cretenet, and E. Jallas. 1997b. Diurnal changes in plant geometry and sunlit leaf area in cotton plant, pp. 1390-1396. *In* Proceedings of 1997 Beltwide Cotton Conferences. National Cotton Council of America, Memphis, Tenessee.

Wang, P., A. Isoda, G. Wei, T. Yoshimura and T. Ishikawa. 1994. Growth and adaptation of soybean cultivars under water stress conditions. II. Effects of leaf movement on radiation interception. Jpn.J.Crop Sci. 63 : 699-705.

Yu, F. and V.S. Berg. 1994. Control of paraheliotropism in two Phaseolus species. Plant Physiol. 106 : 1567-1573.