MODELING LIGHT INTERCEPTION AND PHOTOSYNTHESIS IN COTTON

S. Thanisawanyangkura
Department of Botany, Faculty of Science, Kasetsart University
Bangkok, Thailand
UA Bioclimatologie-PIAF, INRA
Clermont-Ferrand, France
H. Sinoquet and F. A. Daudet
UA Bioclimatologie-PIAF, INRA
Clermont-Ferrand, France
P. Kasemsap
Department of Agronomy, Faculty of Agriculture
Kasetsart University
Bangkok, Thailand

Abstract

Diurnal variations of light interception and photosynthesis in relation to canopy structure of cotton (*Gossypium hirsutum* L.) were studied. The three-dimensional (3D) electromagnetic digitizing system was used for measuring plant geometrical structure under field-growing condition. The 3D version of RIRI (Radiation Interception in Row Intercropping) model based on the turbid medium analogy was used to simulate light-interception distribution and net CO_2 assimilation rate of the canopy during 3 stages of development, i.e. at the leaf area index (LAI) of 0.7, 1.2 and 3.1. The net assimilation rates simulated by the model were compared with canopy photosynthesis measurement.

Due to their heliotropic behavior, cotton leaves tended to face the sun during the day, particularly at the stages of LAI 0.7 and 1.2. Diurnal changes of canopy structure resulted in greater light interception efficiency (LIE). The simulated LIEs increased as LAI increased. The simulated results of canopy photosynthesis showed that in the morning, net photosynthetic rates of morning and noon canopies were slightly different from those of afternoon canopy. The net photosynthetic rates of the 3 canopy structures (i.e. morning, noon, and afternoon canopies) increased and peaked at noon, then gradually decreased in the afternoon. With leaf movement in the afternoon, net photosynthetic rate of afternoon canopy was slightly greater than morning and noon canopy. Consequently, the model can be used to explain advantages of diurnal changes in canopy structure on light interception and photosynthesis of cotton canopy.

Introduction

Canopy structure is a major determinant of physical environment within the plant community. Variation of canopy structure results in change of light microclimate and affects physiological processes of the canopy. In cotton (*Gossypium hirsutum* L.), diurnal variations of canopy structure due to its heliotropic behavior have been reported (Fukai and Loomis, 1976 ; Sassenrath-Cole, 1995 ; Thanisawanyangkura et al., 1997ab ; among others). Because of leaf movement following the sun direction, cotton plant structure is favorable for light interception and this results in increased sunlit leaf area (Thanisawanyangkura et al., 1997a). However, very few information on the relationship between plant structure and canopy photosynthesis as affected by diurnal variations of light interception are available in cotton. Some models used for prediction of light interception and photosynthesis in plant canopy (e.g. Baker et al., 1983 ; Chen et al., 1994 ; Lloyd et al., 1995 ; Sands, 1995) have not taken realistic quantitative descriptions in three dimensions (3D) of canopy structure into account because these parameters with high spatial and temporal resolution are difficult to measure. The 3D electromagnetic digitizing system is a new technique for measurement of plant geometrical structure which provides the descriptions of leaf position and orientation with high accuracy (Sinoquet and Rivet, 1997 ; Thanisawanyangkura et al., 1997a). The model for simulation of light interception and photosynthesis taking these actual descriptions into account may be more realistic for cotton since the position and orientation of the leaves may change during the day. Moreover, this behavior may vary during the growing season (Thanisawanyangkura et al., 1997ab).

The objective of this study was to develop a model to characterize the effect of changes in canopy structure on diurnal variations of light interception and photosynthesis of a cotton canopy.

Materials and Methods

Field Experiment

The experiment was conducted at an experimental field of the Department of Agronomy, Faculty of Agriculture, Kasetsart University, Kamphaengsaen Campus, Nakhon Pathom, Thailand (14.02 °N, 99.97 °E). Cotton (*Gossypium hirsutum* L. cv. DES 119) seeds were planted on February 12, 1997 in North-South row direction on a 45-m² plot of fine silty soil. Spacing was 80 cm between rows and was 25 cm between plants (50,000 plants/ha). Crop was irrigated by sprinklers. Cultural practices were done similarly to recommendation in the region.

Plant digitizing was done on April 1, 3 and 18, 1997 (i.e. at 48, 50 and 65 days after planting, DAP) when leaf area index (LAI) was 0.7, 1.2 and 3.1, respectively. Canopy photosynthesis was measured on April 3, 5 and 20, 1997 (i.e. at 50, 52 and 67 DAP). During measuring period, i.e. April 1-20, 1997, the average temperature was 27°C (36°C max. / 22°C min.). Total rainfall was 31 mm. There were some cloudy periods during the day of measurement. Mean sunshine duration was 9 hrs.

Description of the Model

Light microclimate is computed by using a 3D version of the model RIRI (Radiation Interception in Row Intercropping, Sinoquet and Bonhomme, 1992). The model is based on the turbid medium analogy and deals with direct and diffuse incident radiation and scattered radiation. The cotton canopy is abstracted by an array of 3D cells which may be either empty or contain leaf area (Figure 1). In this version of the model, the content of each cell is expressed as a series of individual leaves, of which the blade area and orientation are known. Beam interception within a cell is derived from a binomial law (Nilson, 1971), i.e. the gap fraction p_0 in a given 3D cell may be written:

$$p_0 = \prod_{i=1}^{N} \left(1 - \frac{S_i \cdot \cos \beta_i}{S_R \cdot \sin h} \right) \qquad (1)$$

where N is the number of leaves in the 3D cell, S_i is the blade area of leaf i, β_i is the angle between leaf normal and the beam direction, S_R is the reference area, i.e. the surface area of the 3D cell basis, and h is the beam elevation. Cos β_i depends on both the leaf orientation (inclination α_i and azimuth θ_i) and the beam direction (height h and azimuth ω) :

$$\cos \beta_i = \cos \alpha_i \cdot \sin h + \sin \alpha_i \cdot \cos h \cdot \cos (\theta_i - \omega) \qquad (2)$$

For each direction, a sample of beams are pushed in the vegetation from the top of the canopy. Beam extinction after crossing a series of K cells may be written :

$$P_0(K) = \prod_{k=1}^{K} \prod_{i=1}^{N_k} \left(1 - \frac{\Delta z_k}{\Delta z} \cdot \frac{S_{ik} \cdot \cos \beta_{ik}}{S_R \cdot \sin h} \right) \qquad (3)$$

where N_k is the number of leaves in cell k, Δz_k is the vertical thickness crossed by the beam in cell k, and Δz is the vertical thickness of the 3D cells. Geometrical computations are needed to derive the sequence of cells visited by a given beam and the thickness Δz_k in each cell k, this depends on beam direction and the point where the beam enters the canopy.

Beam interception in each visited cell contributes to radiation exchanges factors between radiation sources (incident radiation from the sky and scattered radiation from leaf and soil surfaces) and receivers (leaf and soil surfaces and the sky for reflected radiation). In case of direct radiation, the only sun direction is considered. In contrast, a set of 46 directions chosen to optimize radiation integration over the whole sky (den Dulk, 1989) are used to describe diffuse and scattered radiation components. For each 3D cell, the radiation balance including multiple scattering is solved using an approach similar to the radiosity method (Ozisik, 1981).

The probability that a leaf be sunlit in a given cell is derived from Eq. 3 applied to the sun direction. This value is compared to a random number sampled between 0 and 1, in order to stochastically decide whether the leaf is sunlit or shaded. If shaded, the leaf is assumed to receive only the fraction of diffuse and scattered radiation reaching the leaf area in the 3D cell. If sunlit, the leaf receives the same fraction of diffuse and scattered radiation plus the direct incident radiation, according to the sun beam incidence on the leaf, i.e. the angle β between leaf normal and sun direction. This way allows to stochastically derive foliage irradiance distribution at the leaf level.

Leaf photosynthesis A_i ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) is computed by using a simple rectangular hyperbola model :

$$A_i = \frac{\rho \cdot I_i \cdot A_{max}}{\rho \cdot I_i + A_{max}} \qquad (4)$$

where ρ is the quantum yield ($\mu mol\ CO_2\ \mu mol^{-1}$ of Photosynthetically Active Radiation, PAR), I_i is the leaf irradiance and A_{max} is the maximum rate of CO_2 assimilation at saturated light ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$). Canopy assimilation is merely derived by summing up leaf photosynthesis contributions. In this study, ρ and A_{max} were assumed to be independent of leaf position and time. The single-leaf photosynthetic parameters used for calculation were 0.06, 0.07 and 0.04 $\mu mol\ CO_2\ \mu mol^{-1}$ PAR for ρ and 38.3, 42.5 and 33.5 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ for A_{max} at the LAI stages of 0.7, 1.2 and 3.1, respectively.

Canopy Structure Measurement

At each LAI stage, five consecutive plants on the same row were selected as representatives of the crop. Plant digitizing was conducted three times a day with a 3D electromagnetic digitizer (Polhemus® 3 Space® FasTrak®, Polhemus Inc., VT, USA) and data acquisition software DiplAmi (Sinoquet and Rivet, 1997) assuming that the cotton leaves did not change significantly their orientation during the two-hour measuring period : in the morning (07:00-09:00 h, True Solar Time, TST), at noon (11:00-13:00 h), and in the afternoon (15:00-17:00 h). Digitized positions on cotton plant were described by Thanisawanyangkura et al. (1997b). Non-destructive estimation of the leaf area was performed by an allometric relationship between the length of midrib (L) and leaf blade area (S) measured by a Licor 3100 Leaf Area Meter (Licor Inc., Lincoln, NE, USA) :

$$\qquad \qquad _2 \qquad (r^2=0.92,\ n=225) \qquad (5)$$

Canopy Photosynthesis Measurement

Net photosynthetic CO_2 uptake rates by the same 5 digitized plants were measured simultaneously at 2 days after digitizing using an open circuit photosynthesis system (Daudet, 1987). The cotton plants were enclosed in a $0.8 \times 1.25 \times 1.0\text{-}m^3$ transparent chamber made of polyethylene plastic film (0.05 mm thickness). At the base of the chamber, the plastic film was folded outwards and clamped onto a metallic frame placed on top of a stable base 5-cm height above ground. The canopy chamber was also clamped onto the base of the plants excluding soil surface.

External air was blown into the chamber. Air entering and leaving the measurement chamber was determined for CO_2 and water vapor content using a Licor 6400 Portable Photosynthesis System (Licor Inc., Lincoln, NE, USA). Gas exchanges and water vapor data were recorded at 20-seconds interval during 07:00-09:00 h, 11:00-13:00 h and 15:00-17:00 h TST (i.e. during digitizing periods), and at 2-minutes interval during the remaining periods of the day. Air temperatures inside and outside the chamber determined by shaded thermocouples were logged into a CR21X data logger (Campbell Scientific Ltd., Logan, UT, USA) at 5-minutes interval. The data presented were averaged hourly. Canopy photosynthetic rates are presented on a soil surface basis.

Light Interception Efficiency
In order to quantify effect of canopy structural changes on radiation interception, Light Interception Efficiency (LIE), i.e. the mean leaf irradiance per unit incident irradiance, was calculated for each canopy structure of all the 3 stages of development. The LIE is also the ratio of projected sunlit leaf area (Planchais and Sinoquet, 1998).

Results

Diurnal Variations of Cosine of Incidence Angle
Cotton leaves tended to face the sun (cos β ≈ 0.8) during 09:00-13:00 h at the LAI 0.7 and 1.2 stage (Figure 2ab). This heliotropic behavior decreased as the canopy developed more leaves, i.e. at the LAI 3.1 stage (Figure 2c). Because cos β values may change due to changes in sun course without leaf movement, the model allows to simulate diurnal variations of cos β values in order to characterize how cotton canopy structures are favorable to intercept direct solar beam during the day.

The results show that if the leaves had remained at their morning positions, this morning canopy structure would have been less favorable to intercept direct radiation (i.e. decreasing cos β values) at noon by 12, 21 and 6% and in the afternoon by 26, 49 and 26% at the LAI stages of 0.7, 1.2 and 3.1, respectively (Figure 2). Noon canopy showed its advantages to intercept more direct radiation (i.e. increasing cos β values) than morning canopy in the afternoon by 5, 21 and 12% and than afternoon canopy in the morning by 26, 14 and 13% at the stages of LAI 0.7, 1.2 and 3.1, respectively. If there was no leaf movement between the afternoon and the next morning, the afternoon canopy would have been less favorable to receive solar direct beam in the morning by 35, 32 and 19% at the stages of LAI 0.7, 1.2 and 3.1, respectively.

Effect of Canopy Structural Changes on Light Interception
The simulated LIEs increased as LAI increased (Figure 3). In the morning, morning canopy presented greater LIEs than noon canopy by 2, 7 and 0.4% and than afternoon canopy by 13, 13 and 3% at the LAI stages of 0.7, 1.2 and 3.1,

respectively. Afternoon canopy had the lowest LIEs in the morning for all the 3 LAI stages. At noon, the LIEs of morning and noon canopies decreased while afternoon canopy started to increase. The LIEs at noon of noon canopy were greater than morning canopy by 11, 6 and 1% at the LAI stages of 0.7, 1.2 and 3.1, respectively. However, differences of LIEs at noon between the noon and afternoon canopies were small (less than 2%) for all the 3 stages of development. The LIEs of afternoon canopy increased in the afternoon while those of morning and noon canopies gradually decreased. The LIEs of morning and noon canopies increased again after 15:00 h when solar elevation became low. With leaf movement in the afternoon, the afternoon canopy showed greater LIEs than morning canopy by 17, 17 and 2% and than the noon canopy by 13, 7 and 1% at the LAI stages of 0.7, 1.2 and 3.1, respectively (Figure 3).

Effect of Canopy Structural Changes on Canopy Photosynthesis
Comparisons between measured and simulated canopy photosynthesis are shown in Figure 4. The model gave satisfactory results in predicting canopy photosynthesis, although there were some differences from the measurements.

Simulation of canopy photosynthesis showed that in the morning, there would have been very slight differences of canopy photosynthesis between morning and noon canopy structures (Figure 4). Morning and noon canopies had slightly greater net CO_2 assimilation rates than afternoon canopy in the morning, particularly at the LAI 0.7 and 1.2 stages (by 6% and 3% at the LAI 0.7 and 1.2 stages, respectively). Canopy photosynthesis increased as solar elevation increased and peaked between 12:00-13:00 h for all the 3 canopy structures. Noon canopy appeared to have a slight advantage in enhancing photosynthetic rates by 2-5% at noon. In the afternoon, net photosynthetic rates of the canopy gradually decreased. The afternoon canopy showed higher net CO_2 uptake rates than the morning canopy by 7% and 4 % and than the noon canopy by 4% and 1% at the LAI 0.7 and 1.2 stages, respectively (Figures 4ab). At the LAI stage of 3.1, the photosynthetic rates of the afternoon canopy were slightly lower than the morning and noon canopy by 4% and 3%, respectively (Figure 4c).

Discussion

Variations of Light Interception and Photosynthesis
The patterns of diurnal heliotropic behavior of DES 119 cotton variety under tropical condition were similar to those under Mediterranean condition as reported by Thanisawanyangkura et al. (1997 ab). With leaf movement, cotton canopy presented higher cos β values (i.e. the leaves are oriented more facing towards the sun) than non-changed canopy structures (Figure 2). By heliotropism, the cotton canopy had a greater sunlit leaf area than non-heliotropic canopy (Thanisawanyangkura et al., 1997a). Increasing

simulated LIEs were found as LAI increased (Figure 3). This means that the cotton canopy captured more incoming radiation with increasing leaf area which progressively filled the gaps in the canopy. Morning and afternoon canopy structures exhibited higher LIEs in the morning and in the afternoon, respectively (Figure 3). This showed that leaf blades captured efficiently incoming radiation at low solar elevation. However, the simulated LIEs were relatively low at noon for all the 3 canopy structures. Thanisawanyangkura et al. (1997a) showed that the fraction of sunlit leaf area at noon was much less influenced by changes in canopy structure and noon canopy structure showed only little advantage for light interception at noon. Thus, the results supported that the cotton leaf dispersion tended to be more regular in the morning and in the afternoon but more clumped at noon and the cotton plants might not necessarily attempt to maximize light interception throughout the day (Thanisawanyangkura et al., 1997a).

Regarding canopy photosynthesis, the model allowed investigations of the effects of canopy structural changes on canopy photosynthesis. It should be noted that although there were relatively large differences of the cos β values and the LIEs between the 3 canopy structures during each period of the day, the canopy photosynthetic rates were relatively close. There were slight differences of canopy photosynthesis in the morning between the 3 canopy structures. However, diurnal changes in canopy structure were slightly more advantageous at noon and in the afternoon, particularly at early stages of development (Figure 4ab). Comparing with morning and noon canopies, afternoon canopy showed slightly lower canopy photosynthesis in the afternoon at the LAI stage of 3.1 (Figure 4c). Fukai and Loomis (1976) showed that with leaf movement from noon to afternoon, the photosynthetic rates of upper layer of cotton canopy were greater than non-changed canopy but lower photosynthetic rates occurred at the middle and low layers in the afternoon. This might be the reason why the canopy photosynthetic rate was greater with the morning and noon canopy structures than with the afternoon canopy structure (Figure 4c) as Fukai and Loomis (1976) found. It should also be emphasized that although the effects of diurnal changes in canopy structure on instantaneous canopy photosynthetic rates were generally not large, the cumulative effect over a growing season could be significant.

The Modeling Approach

In GOSSYM model (Baker et al., 1983), canopy light interception and photosynthesis are calculated from the classical Beer-Lambert's law without taking realistically geometrical descriptions of the canopy structure and leaf photosynthetic parameters into account (Jallas, 1991). In addition, potential canopy photosynthetic rates are calculated from the relationships between leaf nitrogen content and photosynthetic rates and water- and nutrient-deficit effects on photosynthesis (Reddy et al., 1997).

The 3D RIRI model offers some improvements in comparison with classical light models based on the turbid medium analogy. First, the classical Beer-Lambert's law has been replaced by a binomial law (Eq. 1). This allows one to explicitly take into account the effect of leaf size on light interception. The binomial law specifies that a planar leaf is unable to shade itself, this contributes to increase the regular leaf dispersion within a cell (Fukai and Loomis, 1976). Moreover, the model is fed with the foliage digitizing data. It is therefore able to take into account not only a mean leaf size but also the distribution of leaf size and leaf orientation within the 3D cells. Second, differences in cell content allow one to take into account spatial variations of canopy structure. This may be regarded as a means to deal with leaf dispersion at the canopy scale. Ultimately, this way combining the abstraction of the canopy as an array of 3D cells and the leaf distribution within cells is very close to other modeling approaches dealing with ray-tracing techniques where leaf location, size and orientation are explicitly taken into account (e.g. Dauzat, 1993). The only difference is that the exact location of the leaf inside a cell is not taken into account in the present model, since leaf location in the cells is assumed to be random.

Irradiance is computed at the individual leaf level by using a stochastic approach. This allows one to simulate leaf irradiance distributions, especially to distinguish sunlit and shaded leaves. As leaf photosynthesis is a non linear function of leaf irradiance, this is useful for canopy photosynthesis computation.

Conclusion

Diurnal changes in cotton canopy structure due to heliotropic behavior resulted in greater light interception efficiency than non-changed canopy structure. Daily net photosynthetic rates of the 3 canopy structures (i.e. morning, noon, and afternoon canopy structure) were slightly different during the day. The model allows to investigate the effects of different canopy structures on light interception and photosynthesis of cotton canopy. For further study, variations of the leaf photosynthetic parameters relating to leaf age and position in the canopy may be taken into account in the model. Spatial distribution of light interception and photosynthesis should be further studied in order to explain variations of boll development and fiber quality in the cotton canopy.

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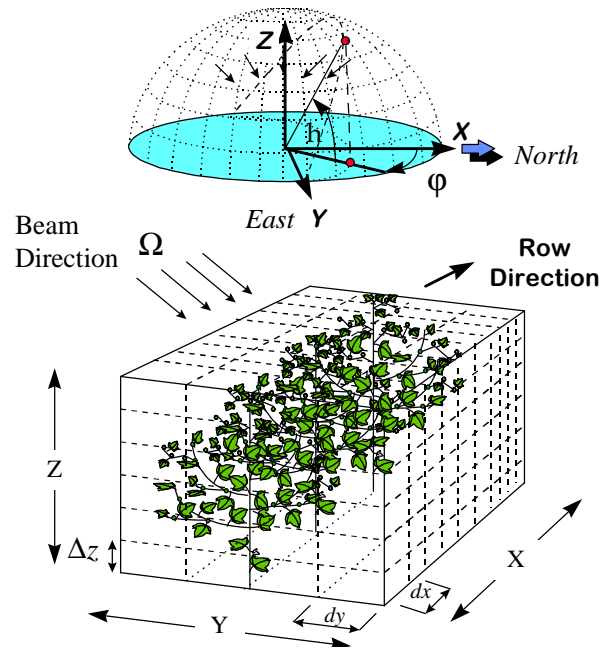
Figure 1. Row-planted cotton canopy in 3D cells of *dx* width, *dy* length and *Dz* vertical thickness on X, Y and Z axis, respectively. In the 3D RIRI model, sky is divided into 46 sectors for radiation integration over the whole sky with solar beam direction W (h, j) : h is the solar elevation and j is the solar azimuth.
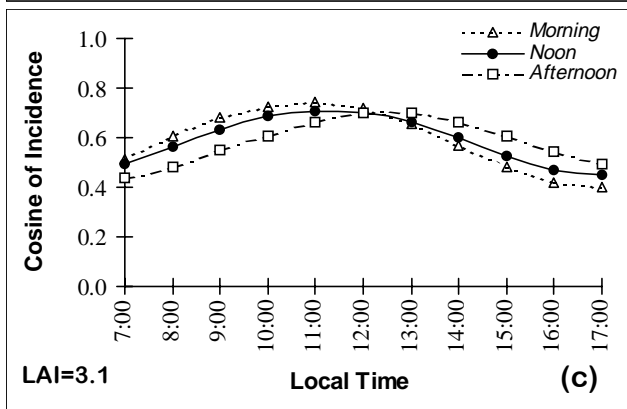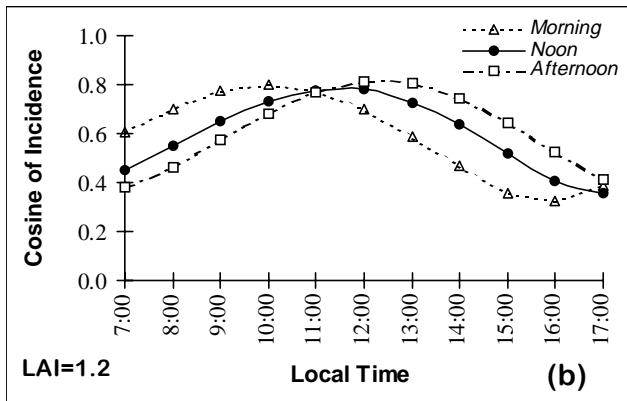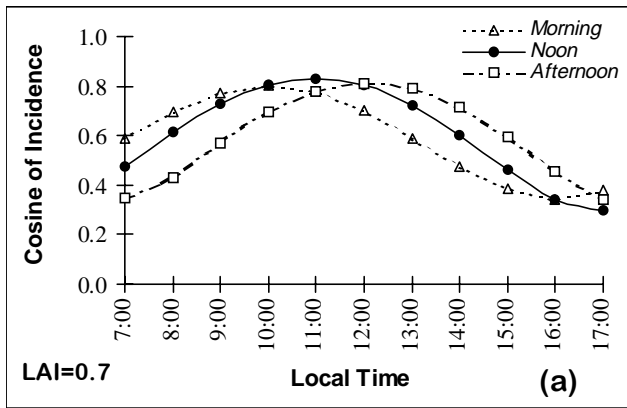
Figure 2. Diurnal variations of cosine of the incidence angle (cos β) for 3 different canopy structures : morning, noon and afternoon, at 3 stages of development of cotton : (a) LAI=0.7, (b) LAI=1.2, and (c) LAI=3.1.
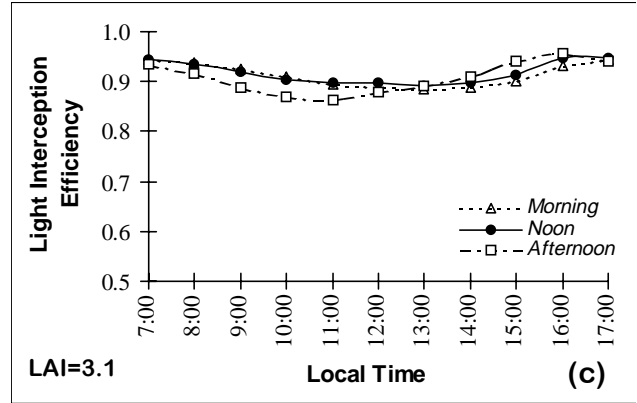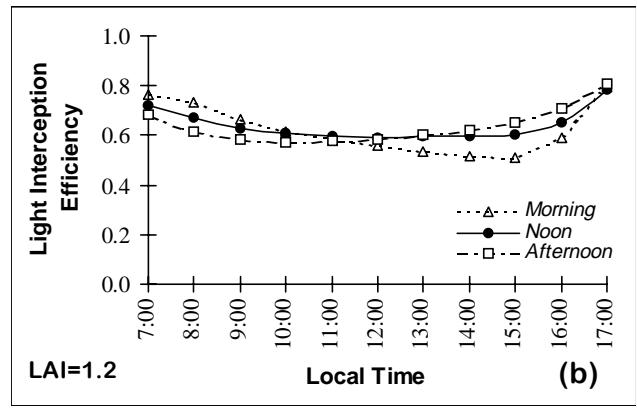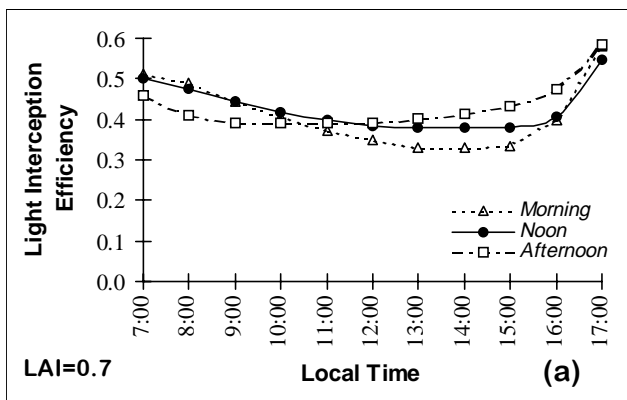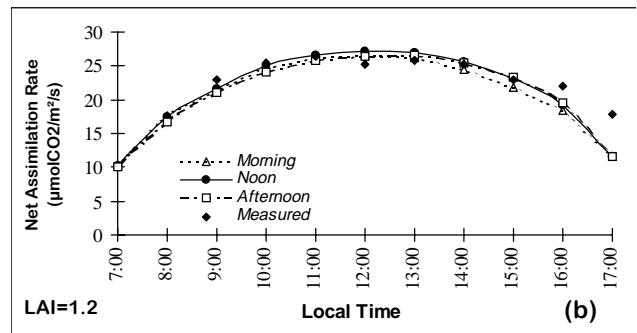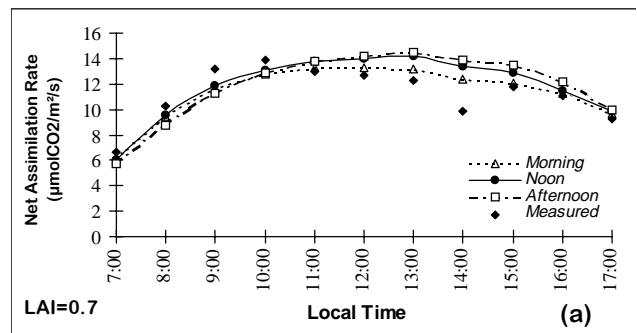

Figure 3. Diurnal variations of Light Interception Efficiency (LIE) for 3 different canopy structures : morning, noon and afternoon, at 3 stages of development of cotton : (a) LAI=0.7, (b) LAI=1.2, and (c) LAI=3.1.
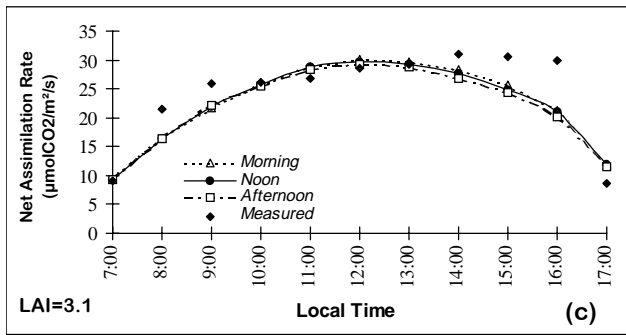
Figure 4. Diurnal variations of net assimilation rate (μmol CO_2 s^{-1}) of a 1-m² cotton canopy simulated by the model for 3 different canopy structures : morning, noon and afternoon canopy, compared to the measured canopy photosynthesis at 3 stages of development : (a) LAI=0.7, (b) LAI=1.2, and (c) LAI=3.1