Estimating Canopy Light Interception and Absorption Using Leaf Mass Per Unit Leaf Area in *Solanum melongena*

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Knowledge of canopy light interception and absorption is fundamental for understanding many aspects of crop growth and productivity, and for crop modelling. Light interception is commonly measured with expensive equipment or estimated with elaborate models; simpler and more economical ways of estimation would be advantageous. Since leaf mass per unit leaf area (M_A) is closely related to long-term light interception by leaves, the latter can be estimated by measuring M_A. In this study, partitioning of leaf area into one of six classes of M_A was used to estimate canopy light interception and absorption in aubergine (*Solanum melongena* L.) grown with different amounts of nitrogen fertilizer and with or without artificial shade. Although plants grown with ample fertilizer had a greater leaf area index (LAI) than those grown with less nitrogen, the increase in leaf area occurred in the lower and intermediate M_A classes, while the leaf area in the two highest M_A classes was similar. Artificially shaded plants had more leaf area in the lower M_A classes and less in the higher classes compared to unshaded plants, showing acclimation to low light conditions. The amount of light intercepted daily by leaves in each M_A class was estimated using the previously determined light : M_A relationship. Canopy light interception was calculated as the sum of intercepted light for all M_A classes, and canopy light absorption was estimated from light interception data assuming a constant absorption coefficient (82 %). To validate the results, the estimated values were compared to those calculated from independent measurements of light absorption carried out in the same field. Results indicate that it is possible to estimate canopy light interception and absorption from the partitioning of leaf area into M_A classes. © 2001 Annals of Botany Company

Key words: Canopy light interception and absorption, leaf mass per unit area, specific leaf area, canopy architecture, sun and shade leaves, *Solanum melongena* L., eggplant, aubergine, nitrogen fertilization.

INTRODUCTION

Knowledge of canopy light distribution and absorption is fundamental for understanding many aspects of crop growth and productivity and for modelling whole canopy photosynthesis, which is basic to crop modelling (e.g. Whisler *et al*., 1986). Since direct measurements of light interception and photosynthesis for all leaves are not feasible, the canopy light distribution (i.e. radiation intercepted by leaves at different canopy depths) is typically modelled. Different categories of models are described in the literature. Three dimensional computer models trace light rays and calculate their interception by the foliage after geographical, weather and plant architecture information is entered into the model (e.g. Wang and Jarvis, 1990; Takenaka, 1994; Pearcy and Yang, 1996). These models predict the light intercepted by each leaf. They usually require high parameterization and are suitable for single branches or small canopies only. Other models assume that radiation attenuation through canopies can be described by Beer's Law (Monsi and Saeki, 1953) and predict the irradiance at different depths in the canopy (e.g. de Wit, 1965; Cowan, 1968; Goudriaan, 1977; Ryel *et al*., 1993). The

latter models are suited for large canopies and assume the existence of homogeneous layers within the canopy with constant irradiance at equal cumulative leaf area indexes (LAI). The leaf area of each layer is assessed and multiplied by the estimated or measured irradiance of that layer, then summed for all layers. In this way, the light intercepted by each layer (i.e. light distribution) and the total canopy light interception and absorption can be modelled.

Many tree and vegetable crops have discontinuous canopies, at least during the initial period of growth. Irradiance in such canopy layers is not homogeneous and canopy depth is difficult to assess. This problem can be addressed by comparing canopies to particular geometric shapes; light interception can then be assessed with geometrically based models (Charles-Edwards, 1981).

Although theoretically possible, direct measurement of canopy light distribution by measuring light interception on all leaves of the canopy has not been pursued, partly due to difficulties in handling very large numbers of light sensors. However, daily light interception by single leaves is commonly measured and correlated with leaf nitrogen content and photosynthesis (Field, 1983; DeJong and Doyle, 1985; Hirose and Werger, 1987; Ellsworth and Reich, 1993; Niinemets, 1995, 1997) and leaf mass per unit

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leaf area (M_A) or specific leaf area (SLA = $1/M_A$) ([Lewandowska and Jarvis, 1977](); [Gulmon and Chu, 1981](); [Jurik, 1986](); [Reich and Walters, 1994]()). While the relationships between leaf irradiance and both leaf nitrogen and photosynthesis are affected by soil N availability ([DeJong et al., 1989](); [Walters and Reich, 1989](); [Rosati et al., 1999]()), the relationship between daily light and M_A appears to be independent of plant N nutrition ([Rosati et al., 2000]()). Thus, M_A may be a valuable parameter for estimating long-term leaf light conditions ([Niinemets, 1997]()) even across different N fertilization treatments. Assuming that, for a given genotype under the same environment, leaves of similar M_A intercept similar amounts of light, then dividing canopy leaves into classes of M_A may provide homogeneous 'layers' of leaves with similar light interception.

The objective of this work was to assess whether the partitioning of leaf area into M_A classes (rather than into layers of different depth) is an alternative way of modelling canopy light interception and absorption. The distribution of leaf area into M_A classes was assessed for canopies of field-grown aubergine (*Solanum melongena* L.) treated with different amounts of nitrogen fertilizer and with or without artificial shade. The leaf area distribution into M_A classes was then used to estimate canopy light interception and absorption. To validate the results, estimated values of canopy light absorption were compared to those calculated from independent field measurements carried out in the same field using traditional techniques.

MATERIALS AND METHODS

Experimental set-up

Solanum melongena L. plants were grown outdoors at the Research Institute for Vegetable Crops, Pontecagnano (SA), Italy ($40.7°$ N and $14.8°$ E), with three levels of nitrogen (N) fertilizer corresponding to a total of 50 (N50), 200 (N200) and 355 (N355) kg ha^{-1} N in a randomized, complete block design with three replicates (140 plants per replicate). The field had been fertilized with 60 kg ha^{-1} P and 130 kg ha^{-1} K. Plants were transplanted on 10 May 1997 and black plastic mulch was used to control weeds. Plants were spaced with 1 m between rows and 0.4 m within rows, and were fertilized weekly by application in the irrigation water. Irrigation, pest control and other agronomic practices were carried out as in a commercial crop. On 5 August, three contiguous plants in each replicate plot and for each N treatment were covered with neutral shade cloth (non-woven polypropylene fabric) which decreased light incident on the plants by 22 % as measured under direct sunlight with a quantum sensor (LI-190SA, LI-COR, Inc., Lincoln, NE, USA) placed 10 cm under the cloth and with both the fabric and the sensor held perpendicular to the sun's rays. However, the cloth was placed loosely and directly onto the plants and hung down the sides of the row, thus providing more shade than under standard conditions.

Light and M_A measurements

The photosynthetically active radiation (PAR) intercepted by single leaves during a single cloudless day was measured with GaAsP photosensors (Hamamatsu, Japan). Measurements were taken on several days in July and August, for a total of 65 leaves randomly chosen throughout the canopies of the lowest (N50) and highest (N355) N treatment. Neither young, rapidly growing leaves nor old senescent leaves were used. The photosensors were individually calibrated with a PAR quantum sensor (LI-190SA, LI-COR, Inc.) and placed on the sampled leaf, parallel to the leaf lamina. The sensors were connected to a datalogger (CR10, Campbell Scientific Ltd., Leics, UK) which recorded the radiation every 60 s throughout the day. One sensor was placed horizontally above the canopy to measure incoming PAR. To compare measurements from different days, the leaf light interception data were expressed as a fraction of the daily incoming PAR (FPAR). The day after taking light measurements, the leaves were detached from the plants between 0900 and 1100 h and immediately taken to the laboratory where their area was measured with a leaf area meter (LI-COR 3000, LI-COR, Inc.). Leaves were then dried for at least 3 d at 70 °C and weighed; mass per unit leaf area (M_A) was calculated for each leaf. Since the objective of this study was to estimate FPAR from M_A, FPAR was plotted as the dependent variable against M_A. FPAR data were square root transformed to normalize their distribution, which was skewed. The influence of N treatment on this regression was tested with analyses of covariance.

Leaf area distribution into M_A classes

On 22 July and 19 August, one plant from each replicate plot (three plants per treatment) was removed (except from the N200 treatment on 22 July) and taken to the laboratory where total leaf area (i.e. including all leaves) for each plant was measured. The leaf area index (LAI) was calculated as the total leaf area per plant multiplied by the number of plants per square metre of soil. The effect of both N fertilization and date on LAI was tested with analyses of variance. On 19 August, three more plants per N treatment were sampled among those previously shaded (the central plant of the three shaded plants in each replicate plot). All plants were sampled between 0900 and 1100 h. After measuring total leaf area per plant to calculate LAI, 50 randomly chosen leaves per plant, excluding the young, small leaves and the old, senescent leaves, were sampled and M_A was assessed as above for each leaf. The 50 leaves represented at least half of the total leaf area of a plant. The 50 M_A values were divided into one of six groups: 20–29 g m^{-2}; 30–39 g m^{-2}; ... 70–79 g m^{-2}. For each M_A class, total leaf area was calculated and expressed as a fraction of the total leaf area of the 50 sampled leaves. This fraction of leaf area of each M_A class was then multiplied by the LAI of the corresponding treatment. In this way, the LAI of each M_A class (i.e. the total leaf area of each M_A class per square metre of soil) was calculated and the leaf area distribution into M_A classes was estimated for each sampled plant.

Estimation of canopy light interception

Canopy light interception, expressed as a fraction of incident PAR (CI-FPAR), was estimated for each sampled plant as:

$$\text{CI-FPAR} = \Sigma_{(i=1-6)} \text{ LAI}_{\text{MAi}} \text{ FPAR}_i \qquad (1)$$

where LAI_{MAi} is the LAI of the M_A class *i*, and FPAR_i is the light interception of the M_A class *i* as estimated from the FPAR : M_A relationship. Since the same FPAR : M_A relationship was used for both shaded and unshaded plants, the light intercepted by the shaded plants was also expressed as a fraction of the incident PAR.

To investigate the effects of the treatments on within canopy shading, an index of the average canopy irradiance (CA-FPAR) was calculated as:

$$\text{CA-FPAR} = \text{CI-FPAR/LAI}$$

Estimation of canopy light absorption

Light absorption was estimated for each sampled plant assuming a constant leaf absorptance of 82 % for all leaves and all treatments. Since there are no data available for aubergine, this value was chosen from the range found for most species (Moss and Loomis, 1952; Lee *et al.*, 1986; Heuvelink, 1996).

The light intercepted by leaves in the FPAR : M_A relationship was expressed as a fraction of the daily PAR incident on the canopy so that measurements from different days were comparable. Thus, estimated canopy light interception, absorption and average irradiance were also expressed as fractions of daily incident PAR.

Independent field measurements of canopy light absorption

Light transmission was measured on each replicate plot with a quantum sensor (LI-190SA, LI-COR, Inc.) and a line sensor on which 20 quantum sensors (JYP 1000 SDEC, Reignac sur Indre, France) were aligned along a 35 cm bar. The 20 quantum sensors were calibrated against the LI-COR quantum sensor. The line sensor was moved across the field underneath the canopy along 4 m transects which were arbitrarily chosen before beginning the measurement. Transects were oriented perpendicular to the crop rows (i.e. in an east-west direction) and crossed five rows of plants. Readings were taken every second. The passage along the track took, on average, 44 s, resulting in 44 registered averages of the 20 sensors. Measurements were taken on 3 d (20, 21 and 24 August), several times per day and, each time, on one transect per replicate plot (i.e. three measurements per N treatment). Measurements were not taken on the shade treatments due to the small size of the shaded areas and the presence of the cloth. The transmitted fraction of PAR (f_{trans}) was expressed with respect to the incoming PAR, simultaneously measured with the individual quantum sensor placed horizontally above the canopy. The fraction of incoming PAR reflected by the canopy (f_{rcan}), and the fraction reflected by the soil (f_{rsoil}) were

measured as for transmitted PAR, but with the line sensor respectively above and oriented towards the canopy or beneath the canopy towards the soil.

The fraction of PAR absorbed by the canopy (f_{abs}) was calculated for each measurement time as:

$$f_{\text{abs}} = 1 - f_{\text{rcan}} - f_{\text{trans}} + f_{\text{rsoil}}$$

To calculate the daily fraction of absorbed PAR, data from single measurements were plotted against time of day, separately for each plot, and third order polynomial fits were obtained. These regressions, together with the measured incident PAR (recorded every minute), were used to calculate the time course of the fraction of PAR absorbed by the canopy for three different days (23, 24 and 26 August). The daily fraction of absorbed PAR was calculated for each day as the ratio between the daily integral of absorbed PAR and the daily integral of incident PAR and the values for the 3 d were averaged, thus obtaining one value per replicate plot. The three values per N treatment (i.e. one per replicate plot) were then averaged.

RESULTS

FPAR : M_A relationship and LAI

The square root of daily light interception by leaves (FPAR) was linearly correlated with mass per unit leaf area (M_A) (Fig. 1 and Table 1). Since there was no significant effect of N fertilization on this relationship, the following relationship was obtained by fitting all data:

$$\text{Square root(FPAR)} = 0\cdot015M_A - 0\cdot29 \qquad (2)$$

$$(n = 65; \text{ SER} = 0\cdot11; \ R^2_{\text{adj.}} = 0\cdot66; \ P < 0\cdot001)$$

Crop leaf area index (LAI) increased both with time (from 22 July to 19 August) and with increasing N fertilization (Table 2).
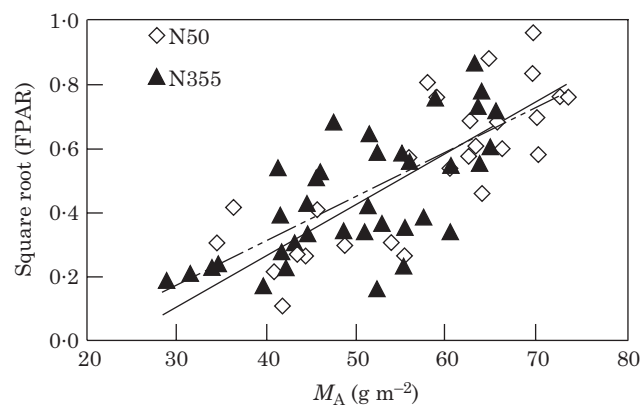

FIG. 1. Relationship between light interception, expressed as a fraction of daily incident photosynthetically active radiation (FPAR), and leaf mass per unit leaf area (M_A) in leaves of aubergine grown with 50 (N50) or 355 (N355) kg ha^{-1} nitrogen. FPAR data were square root transformed to normalize their distribution. Solid line represents a linear fit to N50; broken line represents a linear fit to N355. Nitrogen fertilization had no significant effect on the regression (see Table 1).

TABLE 1. *Fit of the analyses of covariance for the square root (FPAR) :* M_A *linear relationship shown in Fig. 1*

Variable	Coefficient	t ratio	Prob $|t|$
Intercept	−0·310	−4·03	<0·001
N	0·062	0·81	0·422
M_A	0·015	10·59	0·001
N × M_A	−0·001	−0·72	0·472

$n = 65$; SER = 0·11; $R^2_{adj.} = 0.65$.
N, Nitrogen treatment; M_A, leaf mass per unit leaf area.

TABLE 2. *Leaf area index (LAI) on different dates for canopies of aubergine grown with 50 (N50), 200 (N200) or 355 (N355) kg ha^{-1} nitrogen*

Nitrogen treatment	22 July	19 August
LAI		
N50	1·76	2·38
N200	2·60	3·00
N355	3·09	3·48
Prob $|F|$		
N(linear)	< 0·01	
N(quadratic)	0·62	
Date	0·07	
Date × N	0·90	

Leaf area distribution into M_A classes

The partitioning of leaf area into M_A classes is shown in Fig. 2. On 22 July, the N50 and N355 treatments had similar leaf area in the two highest M_A classes, but the lower N treatment had much less leaf area in the lower and intermediate M_A classes (no data for N200). The lower fertilization treatment had the highest fraction of leaf area in the 60–69 M_A class while the higher N treatment had more leaf area in the 50–59 M_A class. Thus, the reduction of LAI, which resulted from reduced N fertilization (Table 2), occurred at the expense of the lowest and intermediate M_A classes.

The results on 19 August were similar to those of 22 July. Partitioning of leaf area into M_A classes in the intermediate N treatment (N200) resembled that of the N355 treatment. However, decreasing N supply from 355 to 200 kg ha^{-1} reduced LAI at the expense of the lower and intermediate M_A classes.

On 19 August, the plants that had been shaded for the previous 14 d had a greater leaf area in the lower M_A classes than the unshaded plants. All N treatments had the greatest fraction of leaf area in the 40–49 M_A class. A reduction in LAI with decreasing N fertilization occurred at the expense of the lowest and intermediate M_A classes. The N50 treatment had no leaves in the lowest M_A class, the N200 treatment had no leaves in the highest M_A class, and the N355 treatment had no leaves in the two highest M_A classes.
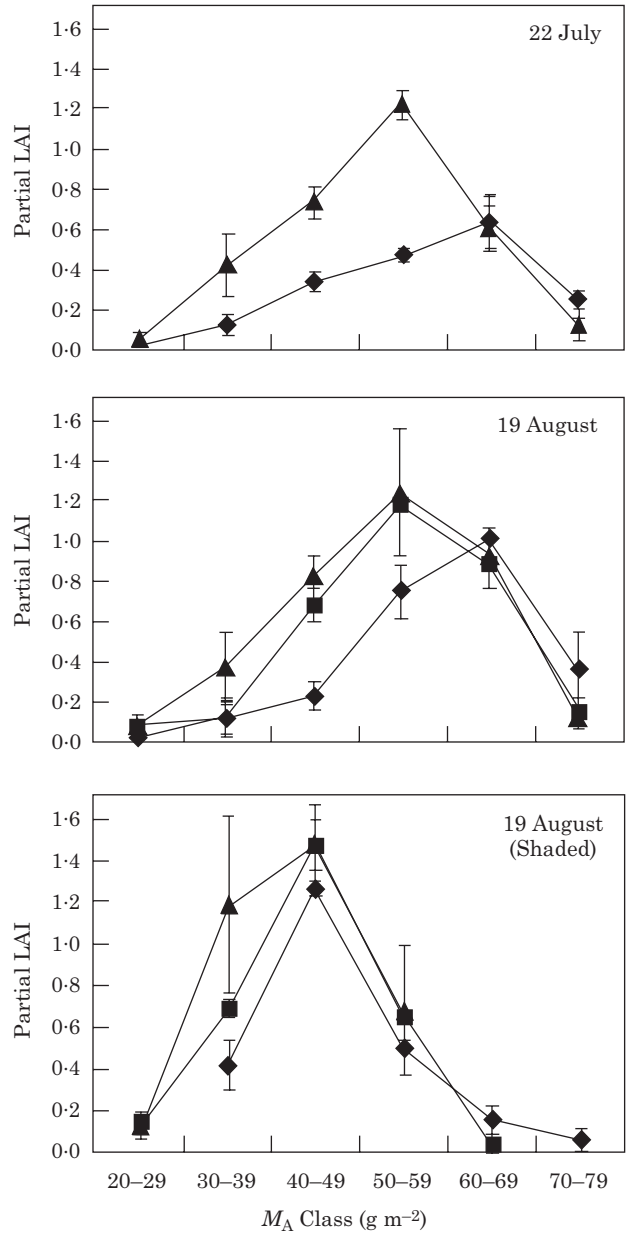

FIG. 2. Partitioning of leaf area distribution into classes of leaf mass per unit leaf area (M_A classes) on different dates and, on 19 August, with or without artificial shade, for canopies of aubergine grown with 50 (N50, ◆), 200 (N200, ■) or 355 (N355, ▲) kg ha^{-1} nitrogen. The partitioning of leaf area is expressed as leaf area index of each M_A class (Partial LAI). Bars indicate s.e.

Estimated canopy light interception

Light interception for each M_A class was calculated from the LAI of that M_A class and from the FPAR : M_A relationship (Fig. 3), and the sum of all M_A classes provided an estimate of the total canopy light interception (Table 3). On 22 July, the leaf area corresponding to the two lowest M_A classes (Fig. 2) resulted in very little light interception by those classes in either N treatment (Fig. 3). Estimated canopy light interception was 35 % greater for the high N treatment than for the N50 treatment, while LAI was 76 %
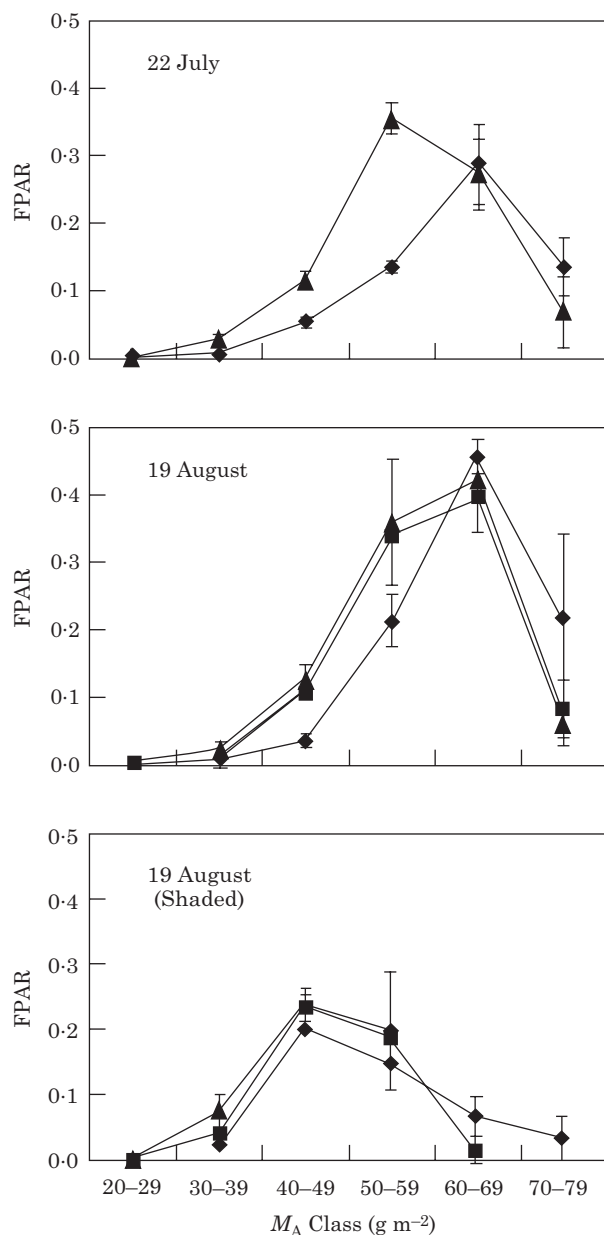
FIG. 3. Estimated light interception by all leaves of each M_A (leaf mass per unit leaf area) class on different dates and, on 19 August, with or without artificial shade, for canopies of aubergine grown with 50 (N50, ◆), 200 (N200, ■) or 355 (N355, ▲) kg ha^{-1} nitrogen. Light interception is expressed as a fraction of the daily incident photosynthetically active radiation (FPAR). Values were calculated from the partitioning of leaf area into M_A classes (Fig. 2) and from the FPAR : M_A relationship [eqn (2)]. Bars indicate s.e.

greater. Results from 19 August were similar to those of 22 July, but differences in total estimated canopy light interception between the N50 and N355 treatments were smaller (+7 % instead of +35 %) while the LAI increased by a similar amount. The N200 treatment had intermediate values.

Within each N treatment, the greater LAI on 19 August resulted in higher estimated values of canopy light

interception compared to the previous date, while average irradiance was similar (Table 3). On the same date, the shaded plants had a much lower estimated canopy light interception (about half) and average irradiance compared to unshaded plants. Canopy light interception of shaded plants was similar for all treatments, but average irradiance was lower with increasing N fertilization.

Canopy light absorption

Estimated canopy light absorption on 19 August, calculated by multiplying the light interception estimated on that date (Table 3) by a constant absorption coefficient (82 %), was 0·76, 0·77 and 0·82 (expressed as fractions of incoming PAR) respectively for the N50, N200 and N355 treatments. These values were all within 2 % of those obtained from the independent field measurements on the same crop (Table 4).

DISCUSSION

Leaf area distribution into M_A classes, light interception and FPAR : M_A relationship

LAI increased both with time (from 22 July to 19 August) and with increasing N fertilization (Table 2). Partitioning leaf area into different M_A classes allowed visualization and understanding of the changes in leaf area and leaf mass distribution with increasing LAI. On each date, increasing LAI with N fertilization resulted in a greater leaf area (and thus leaf mass) of the lower and intermediate M_A classes (Fig. 2), which intercepted little light (Fig. 3), while the area of the top two M_A classes, which intercepted most light, was about the same in all N treatments. Thus, increasing LAI with N fertilization increased light interception but also increased shading (lower average irradiance, Table 3) so that light interception increased less than the increase in LAI, in accordance with Beer's law (Monsi and Saeki, 1953). However, increasing LAI from 22 July to 19 August within each N treatment increased intercepted light without decreasing the average irradiance (Table 3). Thus, N fertilization probably increased canopy density (i.e. shading) while the increase in LAI with time probably increased ground cover (the canopy was discontinuous) improving light interception without increasing shading.

On 19 August, plants which had been shaded for the previous 14 d, had more leaf area in lower M_A classes than unshaded plants, showing adaptation to the lower light environment. As a result, when light interception was estimated for shaded plants from the leaf area distribution into M_A classes, lower values (about 50 %) were obtained than for unshaded plants (Table 3). The difference in estimated light interception between shaded and unshaded plants provided an estimate of the shading effect of the cloth. Light interception was expected to be reduced by over 22 % (measured under standard conditions) since the shade cloth was placed loosely and directly onto the plants and hung down the sides of the row. Thus, much of the fabric was in a non-perpendicular position with respect to incoming light (i.e. increasing light reflection), and about 2 m^2 of cloth per square metre of crop was used, providing

TABLE 3. *Estimated intercepted photosynthetically active radiation (PAR) of the canopy and canopy average irradiance (canopy intercepted radiation/canopy LAI), expressed as fractions of daily incident PAR (FPAR), on different dates and, on 19 August, with or without artificial shade (As), for aubergine grown with 50, 200 or 355 kg ha^{-1} nitrogen (N)*

N Treatment	Canopy intercepted radiation			Canopy average irradiance		
	22 July	19 August	19 August (As)	22 July	19 August	19 August (As)
Kg ha^{-1}	FPAR					
50	0·64 (0·02)	0·93 (0·05)	0·48 (0·03)	0·36 (0·01)	0·39 (0·02)	0·20 (0·01)
200	—	0·94 (0·04)	0·49 (0·00)	—	0·31 (0·01)	0·16 (0·00)
355	0·84 (0·04)	1·00 (0·04)	0·51 (0·03)	0·27 (0·01)	0·29 (0·01)	0·15 (0·01)

Values of canopy intercepted radiation are the sums of the values shown in Fig. 3 [calculated using eqn (1)]. Standard errors in parentheses.

TABLE 4. *Photosynthetically active radiation absorbed by the canopy, expressed as a fraction of daily incident PAR (FPAR), calculated from field measurements or estimated from the partitioning of leaf area into classes of leaf mass per unit leaf area (M_A) and from the FPAR : M_A relationship assuming a leaf absorptance value of 82%, in aubergine grown with 50, 200 or 355 kg ha^{-1} nitrogen*

Nitrogen treatment	Absorbed radiation	
	Measured	Estimated
Kg ha^{-1}	FPAR	
50	0·77 (0·003)	0·76 (0·039)
200	0·79 (0·009)	0·77 (0·029)
355	0·82 (0·011)	0·82 (0·033)

Standard errors in parentheses.

more shade than measured with standard techniques. However, these results must not be taken quantitatively since the shade cloth may have affected light quality (i.e. the ratio between diffuse and direct light) in addition to light intensity, possibly altering the PAR : M_A ratio and thus the FPAR : M_A relationship. Unfortunately, the technique used did not allow field measurement of light absorption under shade for validation of the estimation. Further research is needed to assess whether the PAR : M_A relationship remains constant under shade or other field conditions, including cloudiness, which might interact with light quality. Since M_A reflects long-term light conditions experienced by the leaf (Niinemets, 1997), any PAR : M_A relationship should be calculated using integrated PAR interception determined during some days previous to M_A measurement. If this is not possible, leaf irradiance can be measured on 1 d and expressed as a fraction of incoming PAR (FPAR) so that measurements from different days are comparable, as was done in this experiment. However, the FPAR : M_A relationship is valid only for the light conditions under which it is calculated. Under different light conditions (e.g. cloudy weather, shorter days), M_A should change (diminish) in proportion to the total available PAR while FPAR should remain almost constant, thus changing the FPAR : M_A relationship. To estimate light interception and absorption by partitioning leaf area into M_A classes, independent of the light conditions of a given experiment or period of measurements, the PAR : M_A and not the FPAR : M_A relationship must be used.

Other factors affecting the PAR : M_A relationship

The PAR : M_A relationship may be affected by temperature (Bell *et al.*, 1992) and leaf age as M_A increases with leaf age and season (Reich *et al.*, 1991). In our study, the PAR : M_A relationship was used to estimate light interception over a relatively short period. Furthermore, *S. melongena* plants produced new leaves continuously throughout the season, unlike deciduous trees or crops that produce most of their leaves at the beginning of the growing season. New shoots sprouted from the bottom of aubergine canopies forming new young leaves in shaded positions while other new leaves were formed at the top of the canopy. Older leaves at the bottom of the canopy tended to senesce and abscise, unlike those of deciduous trees which are retained for the whole season. Consequently, as the season progressed, the average age of the leaves remained similar, with young and older leaves distributed in all layers of the canopy. Thus, it seems unlikely that aging or time significantly affected the PAR : M_A relationship over the short period of this experiment. However, if the approach presented here is used to model light interception and absorption by other crops or over longer periods, seasonal effects on the PAR : M_A relationship must be considered.

Daily fluctuations of the leaf sugar content may affect M_A and change the PAR : M_A relationship. In tree species, the structural M_A (i.e. leaf weight excluding non-structural carbohydrates) has a different, but never the less significant, relationship with daily PAR than total M_A (Niinemets, 1997). In aubergine, total non-structural carbohydrate content of leaves increases with time after the onset of illumination (Claussen and Biller, 1977) and with light intensity (Claussen and Lenz, 1979). However, the increase after 4 h of high illumination is only about 10–15 % of leaf dry matter while in this experiment the variation in M_A from the bottom to top leaves was about 300 %. Thus, fluctuations in M_A due to variation in the sugar content appear to be of only marginal significance. However, when establishing the PAR : M_A relationship, sampling the leaves

before sunrise or at the same time of day, as in this experiment, may help to obtain a better fit.

Canopy light absorption

When light interception data were used to estimate canopy light absorption, assuming a leaf absorptance of 82 % for all leaves, the estimated values were within 2 % of those obtained from field measurements (Table 4). The value of 82 % was chosen because it gave the best results when comparing estimated and measured light absorption. Leaf absorptance has been reported to be between 80 and 90 % for most species (Moss and Loomis, 1952; Lee *et al.*, 1986; Heuvelink, 1996), thus the value of 82 % used in this work is within the range found in the literature. Using a different value would only change the results slightly (e.g. using 85 % would increase the difference between estimated and measured values by only about 3·5 %) and it would not change the difference between the treatments since all values would change proportionally.

Leaf absorptance varies with leaf age, position and N content (Schultz, 1996; Sinha *et al.*, 1996). Thus leaf absorptance was probably not homogeneous within the canopies of each N treatment or between treatments. However, the contribution to canopy light interception by the leaves in the lower M_A classes (more shaded leaves) was very low, indeed the three lowest M_A classes intercepted less than 15 % of the total light (Fig. 3). Thus, using a different absorptance value for the leaves of the lower M_A classes would not significantly alter results (e.g. using 85 % for the three lowest M_A classes would change values by less than 0·5 %). Instead, using lower leaf absorptance values with reduced N availability would have produced a greater difference in estimated light absorption between N treatments. However, at the canopy level, only a variation in the upper-canopy leaves would have had a significant effect for the reasons discussed above.

Effect of N fertilization on canopy growth and light distribution

Our results agree with previous findings that the main effect of N fertilization is an increase in canopy LAI and intercepted light (Gulmon and Chu, 1981; DeJong *et al.*, 1989; Walters and Reich, 1989), derived from a lower average contribution of single leaves (lower average irradiance, Table 3), which is more than compensated for by the greater LAI (Rosati *et al.*, 1999). The optimal LAI for carbon-gain by the complete canopy increases with increasing N availability, while optimal M_A diminishes (Dingkuhn *et al.*, 1990; Anten *et al.*, 1995; Hirose *et al.*, 1997). Although the light : M_A relationship is independent of N fertilization (Rosati *et al.*, 2000), larger canopies following N fertilization are associated with reductions in average M_A of the canopy (Gulmon and Chu, 1981; Jurik *et al.*, 1982) which is probably due to increased shading.

Modelling canopy light interception and absorption

Modelling canopy photosynthesis requires estimation of the interception and absorption of radiation (de Wit, 1965; Norman, 1979; Hirose *et al.*, 1997). This can be achieved by measuring cumulative leaf area and light extinction in the canopy profile. These measurements are complex or, especially in the case of non-homogeneous canopies or single plants, impossible tasks. Our alternative approach bypasses the calculation of radiation penetration. The canopy was divided into M_A classes instead of layers of different depth. Given the good correlation between M_A and the light environment of the leaf, at least under the conditions of this experiment, M_A classes represented homogeneous 'layers' with similar daily irradiance. Thus, this approach may be one way of overcoming the difficulties in assessing canopy depth and average irradiance in non-homogeneous canopies, as is often the case in crop stands, without using geometrically based models. However, it should be noted that this approach provides an estimate of daily (thus not instantaneous) irradiance without distinction between direct and diffuse radiation with consequent limitations for modelling canopy photosynthesis (Sinclair *et al.*, 1976; Spitters, 1896).

Biometrical parameters such as M_A have been used in the past to estimate plant functions [e.g. Oren *et al.* (1986) used M_A to characterize leaves for photosynthetic studies]. In particular, Cermak (1989) defined a biometrical parameter, called solar equivalent leaf area, which is defined with an equation [see his eqn (13), p. 275] equivalent to our eqn (1). Although the solar equivalent leaf area provides an estimate of light interception by the canopy, Cermak used it to estimate tree transpiration. We used eqn (1) to estimate canopy light interception and compared the estimates with field measurements.

The relative simplicity of the M_A class approach is advantageous. Once the PAR : M_A relationship is determined for a given species (or genotype) under given growing conditions, all that is needed to estimate canopy light interception is the crop LAI and a representative sample of canopy leaves to estimate leaf area distribution into M_A classes. There is no need to harvest all leaves separately for each layer or to calculate the light extinction coefficient to estimate (or to measure directly) irradiance at each layer. Even where direct measurements of the PAR : M_A relationship are not available, this approach should serve as a relative measure of canopy light interception and absorption. Cermak (1989) suggested that the FPAR : M_A relationship could be estimated by measuring M_A in the most shaded and most sunlit leaves without measuring light interception, assuming intercepted FPAR to be 100 % in the most sunlit leaves and 1–4 % (depending on species) in the most shaded ones.

Our approach could be further simplified whenever the FPAR : M_A relationship can be adequately described by a linear regression, as found in many species. In this case, eqn (1) can be simplified, as shown by Cermak [1989, eqns (22) and (15)], becoming:

$$\text{CI-FPAR} = \text{LAI} \times \text{AvFPAR}$$

where AvFPAR is the canopy average irradiance, which can be estimated from the FPAR : M_A relationship using average M_A (total leaf mass/total leaf area). Thus, once a linear FPAR : M_A relationship is obtained, intercepted irradiance by the canopy (CI-FPAR) can be estimated from the total leaf area and mass of sampled plants (i.e. without needing to partition leaf area into M_A classes), which are easy to measure on annual crops. When we used this simplified approach, we obtained estimates of intercepted irradiance which were similar (within 7 %) but not identical to those obtained with the M_A class approach, due to the non-linearity of our FPAR : M_A relationship [eqn (2)].

Our approach could be particularly advantageous in crops where spacing is regular and plant material is genetically uniform. Under these conditions, sampling of a few plants is often representative of the whole canopy. In our research, assessing the leaf area distribution into M_A classes on three plants per treatment resulted in estimates of canopy light absorption which were comparable to independent field measurements of light absorption. Thus, this approach should provide a simple approximate method of studying canopy light interception and absorption. Further validation across different environments and genotypes is desirable.

ACKNOWLEDGEMENTS

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