

Estimating Photosynthetic Radiation Use Efficiency Using Incident Light and Photosynthesis of Individual Leaves

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Received: 15 November 2002 Returned for revision: 23 December 2002 Accepted: 27 February 2003

It has been theorized that photosynthetic radiation use efficiency (PhRUE) over the course of a day is constant for leaves throughout a canopy if leaf nitrogen content and photosynthetic properties are adapted to local light so that canopy photosynthesis over a day is optimized. To test this hypothesis, 'daily' photosynthesis of individual leaves of *Solanum melongena* plants was calculated from instantaneous rates of photosynthesis integrated over the daylight hours. Instantaneous photosynthesis was estimated from the photosynthetic responses to photosynthetically active radiation (PAR) and from the incident PAR measured on individual leaves during clear and overcast days. Plants were grown with either abundant or scarce N fertilization. Both net and gross daily photosynthesis of leaves were linearly related to daily incident PAR exposure of individual leaves, which implies constant PhRUE over a day throughout the canopy. The slope of these relationships (i.e. PhRUE) increased with N fertilization. When the relationship was calculated for hourly instead of daily periods, the regressions were curvilinear, implying that PhRUE changed with time of the day and incident radiation. Thus, linearity (i.e. constant PhRUE) was achieved only when data were integrated over the entire day. Using average PAR in place of instantaneous incident PAR increased the slope of the relationship between daily photosynthesis and incident PAR of individual leaves, and the regression became curvilinear. The slope of the relationship between daily gross photosynthesis and incident PAR of individual leaves increased for an overcast compared with a clear day, but the slope remained constant for net photosynthesis. This suggests that net PhRUE of all leaves (and thus of the whole canopy) may be constant when integrated over a day, not only when the incident PAR changes with depth in the canopy, but also when it varies on the same leaf owing to changes in daily incident PAR above the canopy. The slope of the relationship between daily net photosynthesis and incident PAR was also estimated from the photosynthetic light response curve of a leaf at the top of the canopy and from the incident PAR above the canopy, in place of that measured on individual leaves. The slope (i.e. net PhRUE) calculated in this simple way did not differ statistically from that calculated using data from individual leaves.

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Key words: Radiation use efficiency, leaf photosynthesis, light, *Solanum melongena*, eggplant, aubergine, modelling, nitrogen.

INTRODUCTION

Light use efficiency models assess canopy productivity based on Monteith's (1972, 1977) observation that net primary productivity (NPP) is proportional to intercepted solar radiation, which represents the ultimate limit to productivity (Cooper, 1970; Loomis *et al.*, 1971; Monteith, 1972). Thus, biomass production can be modelled as a linear function of intercepted photosynthetically active radiation (PAR). The slope of this relationship is the radiation use efficiency (RUE or ϵ), which is approximately constant for forests and natural ecosystems, and particularly for crops when growth is not limited by water or nutrient shortage or adverse climatic conditions that may decrease the efficiency of metabolic and other processes that determine RUE (Monteith, 1977; Ruimy *et al.*, 1995). RUE varies among crops (Sivakumar and Virmani, 1984; Gosse *et al.*, 1986; Prince, 1991), and with plant nitrogen

status (Muchow and Davis, 1988; Sinclair and Horie, 1989; Hammer and Wright, 1994).

Using biomass to study RUE implies long-term experiments since, on a short time-scale (e.g. 1 d or less), biomass increases are difficult to measure. On a short time-scale, RUE can be studied by using gas exchange, though the results are difficult to compare with long-term changes in biomass since crop respiration needs to be assessed and accounted for. Although few studies have been performed, linearity has been found between net CO₂ assimilation of the whole canopy, integrated over a day (daily canopy photosynthesis), and absorbed or incident PAR, implying constant photosynthetic RUE (PhRUE) on a daily basis (Sinclair, 1991; Ruimy *et al.*, 1995; Sinclair and Muchow, 1999). However, instantaneous canopy photosynthesis tends to saturate at high irradiance, and instantaneous PhRUE varies with time of the day (Grace *et al.*, 1995; Ruimy *et al.*, 1995).

The physiological basis for a linear relationship between daily canopy photosynthesis and absorbed or incident PAR is not well understood, and it is not clear why this linearity

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occurs at the canopy level since instantaneous photosynthesis of leaves is curvilinearly related to PAR and tends to saturate. Explanations of this phenomenon are based on the theory that nitrogen content (and thus photosynthetic properties) of leaves is distributed in a canopy in relation to the light gradient, resulting in optimization of daily canopy photosynthesis and in a linear relationship between daily canopy photosynthesis and incident PAR (De Witt, 1965; Charles-Edwards, 1982; Kull and Jarvis, 1995).

Haxeltine and Prentice (1996) and Dewar and co-workers (Dewar, 1996; Dewar *et al.*, 1998) have mathematically simulated this linearity, modelling leaf and canopy photosynthesis over 1 d. Their results implied that all leaves in a canopy have constant PhRUE over 1 d (daily PhRUE), independent of their canopy position and PAR exposure. If all leaves have the same daily PhRUE, then the whole canopy has the same daily PhRUE. This implies that measuring or estimating daily PhRUE on one or a few leaves can provide an estimate of daily PhRUE of the canopy and allow modelling of daily canopy photosynthesis as a simple function of the daily incident PAR integrated over the canopy leaf area index. However, no analysis has been made of possible changes in daily PhRUE with short-term changes in daily incident PAR (e.g. an overcast followed by a clear day), which are too rapid for adjustment of leaf N and photosynthetic properties. Furthermore, even under constant patterns of incident PAR during the day, the simulation studies estimated the PAR incident on the leaves with a modelling approach, which averaged light in space and/or time, and assumed optimal N allocation in the canopy based on the modelled PAR. Real leaves, however, are exposed to a pattern of PAR which is more variable than that predicted by models, and the PAR incident on leaves changes on a time scale which is too rapid for the acclimation of leaf photosynthetic capacity (de Pury and Farquhar, 1999). Indeed, averaging of PAR, whether in space or in time, leads to overestimation of photosynthesis (Sinclair *et al.*, 1976; Spitters, 1986).

The objectives of this study were to investigate whether: (1) a linear relationship between daily photosynthesis and incident PAR of individual leaves (i.e. constant daily PhRUE throughout the canopy) results when daily photosynthesis is modelled using the varying incident PAR and photosynthetic properties measured in the field; (2) averaging of PAR affects this linearity; (3) daily PhRUE of leaves changes for overcast *vs.* clear days; and (4) whether daily PhRUE can be estimated simply from the incident PAR above the canopy without measuring incident PAR on individual leaves.

To investigate the effect of N availability on PhRUE, plants were provided with either abundant or scarce nitrogen fertilization. To study the variation in PhRUE on a time-scale shorter than 1 d, leaf photosynthesis and incident PAR were also calculated on an hourly basis.

MATERIALS AND METHODS

Aubergine (*Solanum melongena* L. 'Cima di Viola') plants were grown in the experimental field of the Research Institute for Vegetable Crops, Pontecagnano (SA), Italy,

with split applications of N fertilizer, for total amounts of either 50 ('low N') or 355 ('high N') kg N ha⁻¹, in a randomized complete block design with three replicates (140 plants per replicate). With the exception of N fertilization, plants were grown as a commercial crop would be. Further details on the agronomic management of the crop are given in Rosati *et al.* (2001).

PAR measurements

Photosynthetically active radiation (PAR) incident during one day on individual selected leaves in the crop canopies of plants grown with low and high N fertilization was monitored using GaAsP photosensors (Hamamatsu, Japan). Sensors were placed on the adaxial surface of the leaf (parallel to the leaf lamina) and were kept in place by electrical wires. One sensor was placed horizontally above the canopy to measure incident PAR. The photosensors had been previously calibrated with a quantum sensor (LI-190; LI-COR Inc., Lincoln, NE, USA), and data were recorded every 60 s from 0600 to 2000 h on 10 d (including clear, partially cloudy and overcast days) at the end of July and August 1997, using a battery-operated datalogger (CR21 Micrologger; Campbell Scientific Inc., Logan, UT, USA).

Gas exchange measurements and modelling of photosynthesis and PhRUE

Instantaneous light-saturated net photosynthesis (A_{\max}) was measured on the selected leaves the day after PAR measurements. Measurements were made at ambient temperature and humidity, between 0900 and 1200 h, using a portable gas exchange system (LI-6200; LI-COR Inc.). A_{\max} was relatively constant during the measurement hours (data not shown). In addition to A_{\max} , the net photosynthetic response to PAR was measured on six leaves in the inner canopy and six leaves in the outer canopy, using sunlight and neutral shade cloth to vary the incident PAR. The rate of CO₂ emission at zero PAR was assumed to be the dark respiration rate (R_d) of the leaf. From these data, a linear regression between R_d and A_{\max} was calculated, as well as values for the curvature factor and the apparent quantum yield that best fitted all curves (non-rectangular hyperbola; Thornley, 1976). The net photosynthetic response curve to PAR was then calculated with the Thornley (1976) model for each sampled leaf, using the measured A_{\max} of the leaf, R_d estimated from its A_{\max} , and the curvature factor and apparent quantum yield that best fitted the 12 measured curves. Gross photosynthetic response curves were also calculated, assuming that R_d was constant (i.e. gross photosynthesis = net photosynthesis + R_d). The photosynthetic response curves were then used with the measured incident PAR data of the corresponding leaf to estimate the instantaneous leaf photosynthesis (net and gross). PAR data were not averaged in space or time, but each single value of PAR (one every 60 s) was used to estimate the corresponding photosynthesis. Daily photosynthesis was then calculated as the integral (i.e. from 0600 to 2000 h) of the instantaneous values and was plotted against the PAR

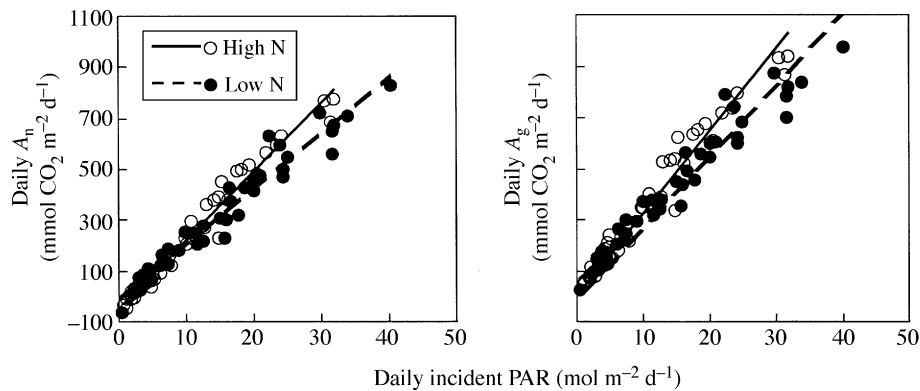


FIG. 1. Relationship between net and gross CO_2 assimilation integrated over a day (Daily A_n and Daily A_g , respectively) and daily incident PAR of individual leaves of aubergine, grown with either low (Low N) or high (High N) nitrogen fertilization. For daily A_n , $Y = 26.8X - 43$, $R^2 = 0.97$ for high N; and $Y = 22.0X - 13$, $R^2 = 0.96$ for low N. For daily A_g , $Y = 32.2X$, $R^2 = 0.96$ for high N; $Y = 27.3X$, $R^2 = 0.93$ for low N. The slope of the regressions increased with N fertilization (for daily A_n , $F_{1,86} = 23.2$; $P < 0.001$; for daily A_g , $F_{1,86} = 26.1$; $P < 0.001$).

incident on the leaf, integrated over the same period (daily incident PAR).

Hourly photosynthesis was obtained similarly for a subset of data, but the instantaneous values of photosynthesis were integrated over each hour, rather than over the whole day, and were plotted against the total hourly PAR incident on the leaf.

Daily photosynthesis (gross and net) was also calculated by integrating over the day the instantaneous photosynthetic response to the daily average PAR incident on the leaf (i.e. average of the instantaneous values measured every 60 s during the day), in place of the actual instantaneous PAR.

Variations in daily PhRUE with changes in incident PAR in the short term (i.e. 1 d) were studied by comparing the relationships between daily photosynthesis and incident PAR of individual leaves obtained using data from an overcast and the subsequent clear day (the light sensors were kept on the same leaves for both days).

To test a simplified method for assessing daily PhRUE, we hypothesized that if all leaves (and thus the whole canopy) have the same daily PhRUE on a net photosynthesis basis, then a hypothetical leaf, placed at the very top of the canopy and thus exposed to the above-canopy incident PAR, should also have the same daily PhRUE. A_{\max} of this leaf would equal that of the leaves at the top of the canopy, which have the highest A_{\max} in the canopy. Thus, we estimated the daily photosynthesis of this hypothetical leaf as was done for actual leaves, but by using the photosynthetic response curve of the leaf with the highest A_{\max} for each data set, and the PAR incident above the canopy (instead of PAR incident on an actual leaf) during the two and three brightest days for the high and low N treatments, respectively. Estimates of daily photosynthesis of the hypothetical leaves were plotted against the corresponding daily PAR, as was done for actual leaves, and the data were fitted with a linear regression, assuming a zero intercept. The slope of these regressions (i.e. the PhRUE) was compared with that of the regressions obtained for actual leaves.

RESULTS

Both net and gross photosynthesis of individual leaves, integrated over the day (daily photosynthesis) were linearly related to the daily PAR incident on the leaf, in both the low and high N fertilization treatments (Fig. 1). The slope of these relationships (i.e. the PhRUE) increased significantly (by about 20–25 %) with N fertilization for both net and gross photosynthesis.

When hourly data were used, the regressions were curvilinear, showing that linearization (i.e. constant PhRUE) occurred only over a time scale greater than 1 h (Fig. 2). A few points were outside of the general curvilinear trend.

Use of average PAR in place of instantaneous data increased the slope of the relationship between daily photosynthesis and incident PAR of individual leaves. The relationships were curvilinear (Fig. 3).

When data for an overcast and the subsequent clear day were compared, the slope of the linear regression between daily photosynthesis and incident PAR of individual leaves remained similar for net photosynthesis, but increased significantly (by about 42 %) for gross photosynthesis (Fig. 4).

Figure 5 shows the pattern of PAR incident above the canopy during the overcast and the subsequent clear day of Fig. 4, and the class frequency distribution of PAR values. Going from a clear to an overcast day resulted in a shorter duration of high incident PAR (i.e. above $400 \mu\text{mol m}^{-2} \text{s}^{-1}$) and a longer duration of low incident PAR. Consequently, on individual leaves, high incident PAR occurred for less time and low PAR for more time during the overcast day (Fig. 6). Instantaneous net photosynthetic response curves to PAR (A_n curves) are given in Fig. 6 for the leaves for which PAR data are shown. The maximum instantaneous PhRUE occurs at an optimal PAR value corresponding to the point where the A_n curve is tangential to a line passing through the origin (dotted line in the figure). The slope of this line is the maximum instantaneous PhRUE. Above this optimal PAR, net instantaneous PhRUE decreased due to saturation of

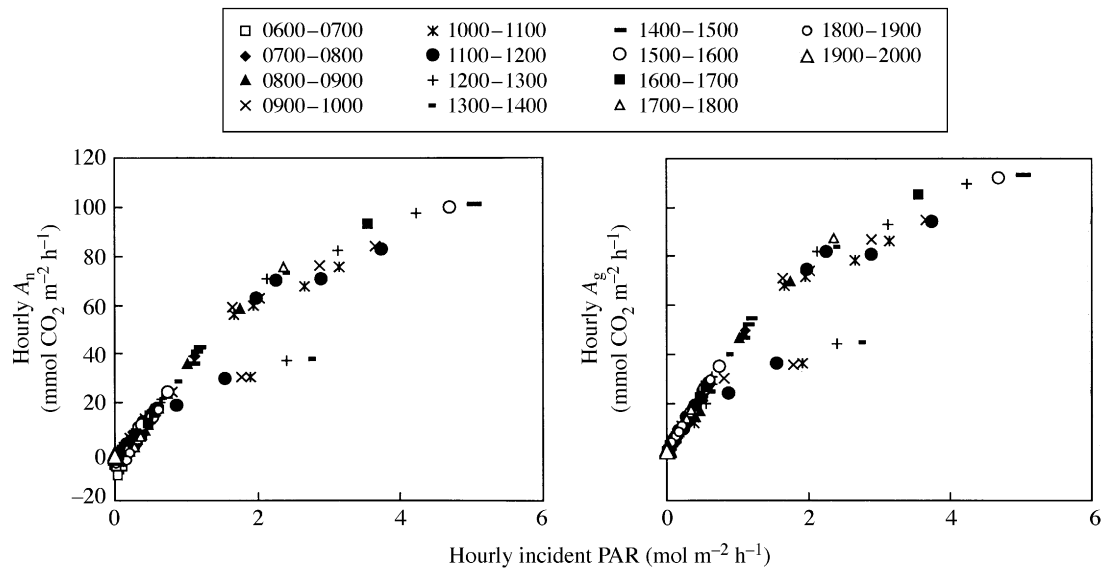


FIG. 2. Relationship between net and gross CO_2 assimilation integrated over one hour (Hourly A_n and Hourly A_g , respectively) and hourly incident PAR for individual leaves and for a subset of the high nitrogen data shown in Fig. 1. Data for each hour (i.e. 0600–0700... 1900–2000 h) are plotted using different symbols. For hourly A_n , $Y = -3.2X^2 + 36.5X - 4.1$; $R^2 = 0.96$; for hourly A_g , $Y = -3.7X^2 + 40.3X$; $R^2 = 0.95$. The regressions (not shown for clarity of graphs) had significant quadratic components (for hourly A_n , $F_{1,151} = 100$, $P < 0.001$; for hourly A_g , $F_{1,151} = 107$, $P < 0.001$).

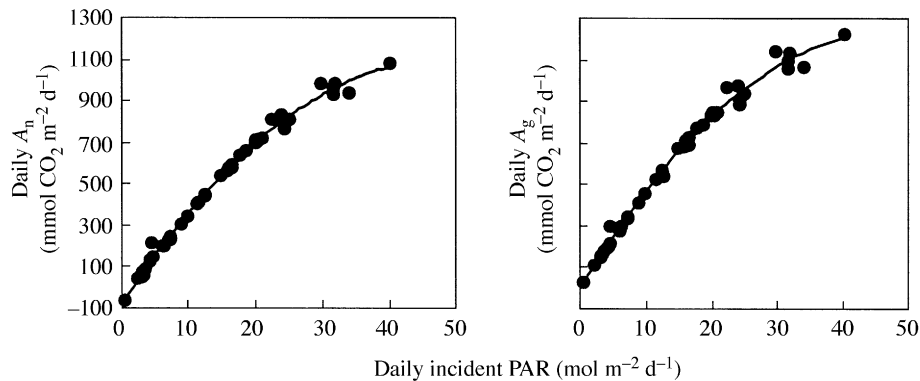


FIG. 3. Relationship between net and gross CO_2 assimilation integrated over a day (Daily A_n and Daily A_g , respectively) and daily incident PAR for individual leaves of aubergine grown with low nitrogen fertilization, using incident PAR averaged over the day, rather than the instantaneous PAR, to model assimilation. For daily A_n , $Y = -0.51X^2 + 48.9X - 77.8$, $R^2 = 0.99$; for daily A_g , $Y = -0.56X^2 + 52.6X$, $R^2 = 0.99$. The regressions had significant quadratic components (for daily A_n , $F_{1,42} = 211$; $P < 0.001$; for daily A_g , $F_{1,42} = 207$; $P < 0.001$).

photosynthesis, whereas below it PhRUE decreased owing to respiration, approaching zero at the light compensation point. Compared with the clear day, leaves were generally exposed to PAR values above the point of maximum instantaneous net PhRUE for less time on the overcast day and to PAR values below it for more time.

When the linear relationship between daily net photosynthesis and incident PAR of individual leaves was calculated from the daily photosynthesis of a hypothetical leaf exposed to above-canopy PAR, the slope of the regression (i.e. daily net PhRUE) was not statistically different from the slope obtained by plotting data for actual leaves (Fig. 7).

DISCUSSION

Linearity of the photosynthesis vs. light relationship

The linear relationship found between photosynthesis and incident PAR of individual leaves, integrated over the day (daily photosynthesis and daily PAR), agrees with the simulations of Haxeltine and Prentice (1996) and Dewar and co-workers (Dewar, 1996; Dewar *et al.*, 1998). Our data for the clear day show that leaves were exposed to a large range of PAR values and, most of the time, were either at very low or high PAR (Fig. 6). Since instantaneous PhRUE changes with incident PAR (Fig. 6), as previously reported by Hirose and Bazzaz (1998), the daily PhRUE of leaves, which was

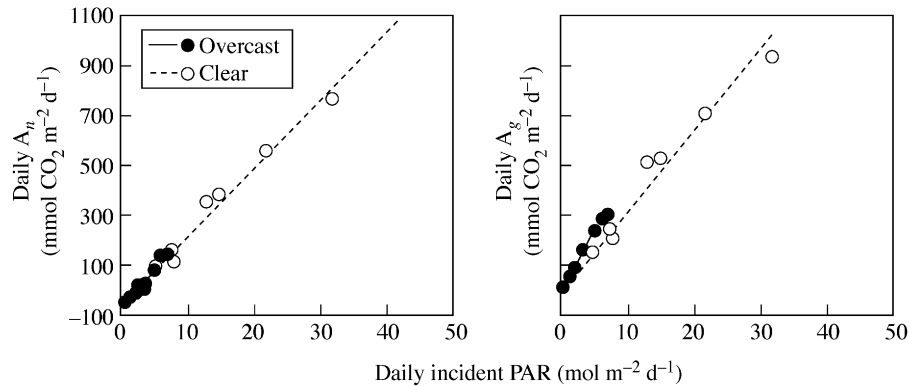


FIG. 4. Relationship between net and gross CO_2 assimilation integrated over a day (Daily A_n and Daily A_g , respectively) and daily incident PAR of individual leaves of aubergine, grown with high nitrogen fertilization. Data are for an overcast day and the subsequent clear day (PAR sensors were kept on the same leaves for both days). For daily A_n , $Y = 29.0X - 58.7$, $R^2 = 0.97$ for the overcast day; $Y = 26.6X - 33.8$, $R^2 = 0.98$ for the clear day. For daily A_g , $Y = 45.9X$, $R^2 = 0.99$ for the overcast day; $Y = 32.2X$, $R^2 = 0.96$ for the clear day. The slope of the regression increased with N fertilization for daily A_g ($F_{1,18} = 8.6$; $P = 0.009$) but not for daily A_n ($F_{1,18} = 0.55$; $P = 0.47$).

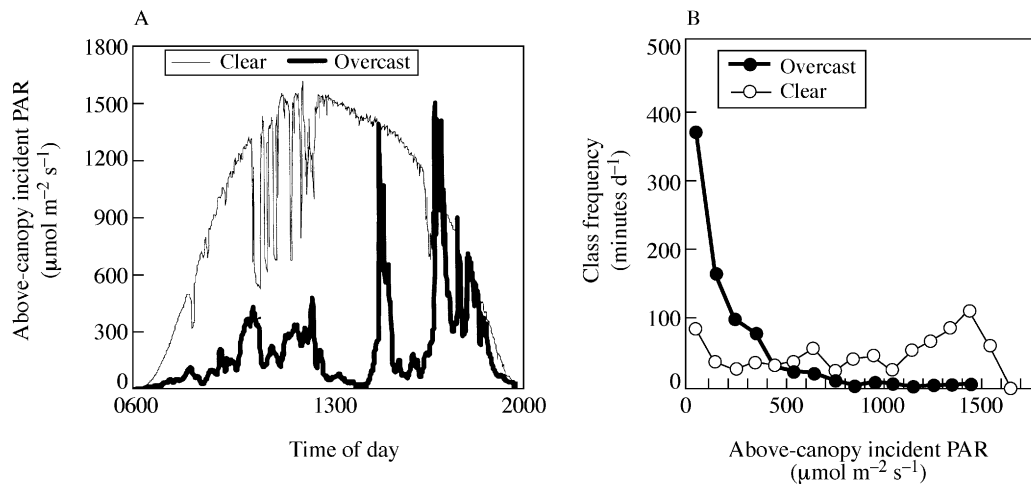


FIG. 5. Pattern of above-canopy incident PAR during the overcast and clear days of Fig. 4 (A) and class frequency distribution of PAR values (B) represented by the number of minutes per day during which PAR was within a given class of values (i.e. 0–100, 100–200 . . . 1600–1700 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

constant among all leaves (i.e. linear regression between daily photosynthesis and incident PAR), derived from integration over the day of variable instantaneous PhRUE. Integration over a shorter time period (i.e. 1 h) did not result in linearization of the relationship between photosynthesis and incident PAR of individual leaves, as the regression was curvilinear (Fig. 2). The curvature implies variation in hourly PhRUE during the day, with greater PhRUE occurring during hours of lower light (except at very low light for net photosynthetic RUE, due to respiration). Although our data represent photosynthesis of single leaves and not of the whole canopy, saturation of photosynthesis of single leaves also implies saturation at the whole-canopy level. Therefore, our data agree with field measurements showing saturation of instantaneous canopy photosynthesis at high PAR (Grace *et al.*, 1995; Ruimy *et al.*, 1995). The

few data points that fall outside the general curvilinear trend of the hourly relationship represent leaves that had low A_{max} but still received high incident PAR during certain hours of the day, which resulted in marked saturation of photosynthesis. However, this only occurred on a few leaves at certain times and, when data were integrated over the day instead of over the hour, these leaves had similar PhRUE values to those of all other leaves.

The large range of PAR values recorded on individual leaves (Fig. 6) supports the assertion of de Pury and Farquhar (1999) that real leaves are exposed to a pattern of incident PAR during the day that differs from the modelled patterns, and the radiation received by leaves changes on a time scale that is too rapid to allow acclimation of their photosynthetic capacity. This does not imply that photosynthetic properties do not adjust to local irradiance, thus

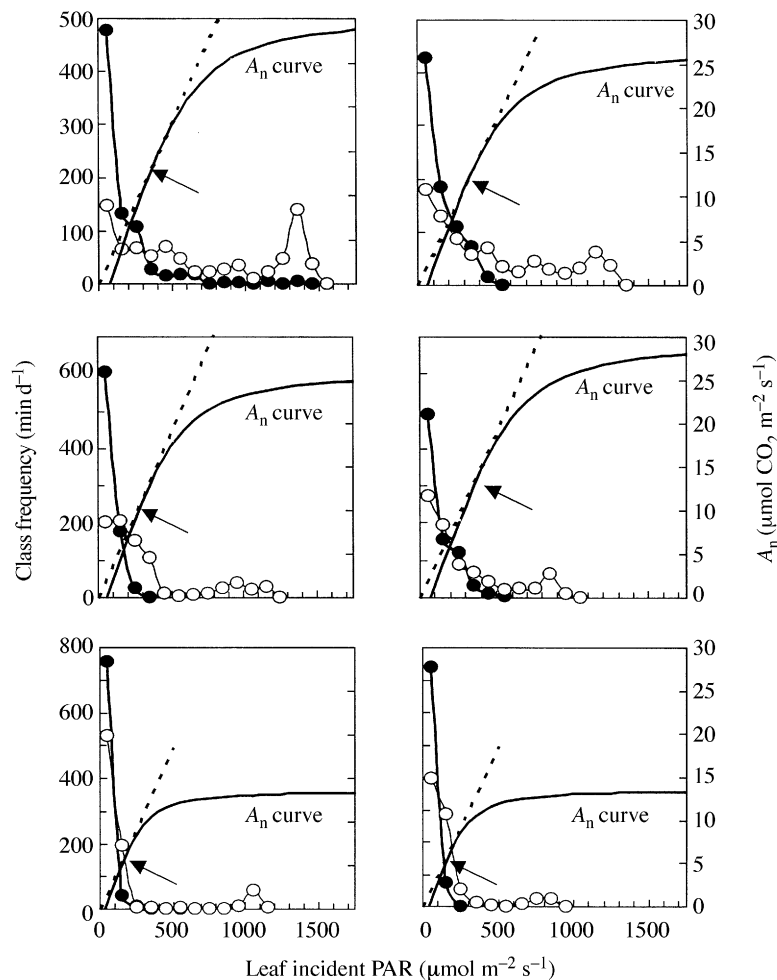


FIG. 6. Class frequency distribution of the PAR incident on each of the six most illuminated leaves among those shown in Fig. 4, during the overcast (closed circles) and clear (open circles) days shown in Fig. 5. Each point represents the number of minutes per day during which the PAR incident on the leaf was within a given class of PAR. The response curve of instantaneous net CO₂ assimilation to incident PAR (A_n curve), as modelled for the same leaf, is also shown. The PAR value corresponding to the point where the dotted line is tangential to the A_n curve (arrows) is that at which the leaf achieves maximum instantaneous net PhRUE. Above and below this PAR value, instantaneous net PhRUE diminishes.

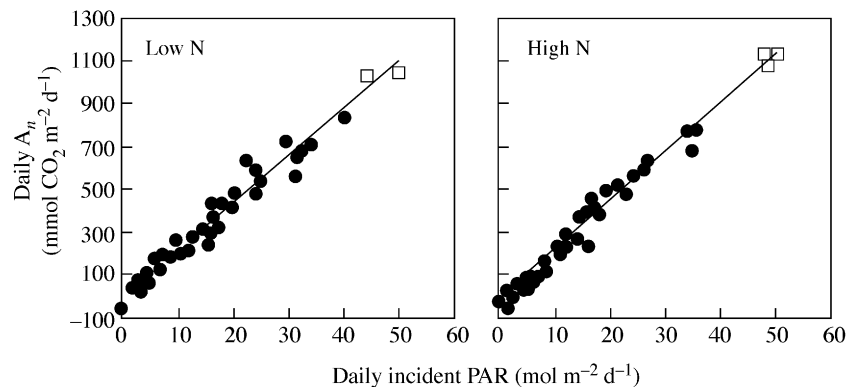


FIG. 7. Relationship between net CO₂ assimilation integrated over a day (Daily A_n) and daily incident PAR for hypothetical leaves (open squares). Daily A_n values for the hypothetical leaves were calculated from the photosynthetic properties of a leaf at the top of the canopy and from the above-canopy incident PAR on the two or three brightest days for the Low and High N datasets, respectively. Lines are fits, imposing a zero intercept, to the estimates of daily A_n of the hypothetical leaves: $Y = 22.0X$, $R^2 = 0.99$ for Low N; $Y = 25.3X$, $R^2 = 0.99$ for High N. Closed circles are data for actual leaves, as in Fig. 1 (for Daily A_n), which are plotted for comparison. The slopes of the regressions for the hypothetical leaves were not statistically different to those obtained by fitting data for actual leaves as in Fig. 1 ($F_{1,44} = 0.01$, $P = 0.92$ for Low N; $F_{1,45} = 1.56$, $P = 0.22$ for High N).

optimizing canopy photosynthesis and achieving constant daily PhRUE. However, to understand the physiological mechanisms of such optimization, it may be necessary to consider the varying light conditions experienced by leaves in the field. For instance, when using average PAR in place of the instantaneous data, the slope of the relationship between daily photosynthesis (both net and gross) and daily incident PAR of individual leaves increased, and the regressions became curvilinear (Fig. 2). Curvilinearity implies that PhRUE is greater with lower light, at least on a gross photosynthesis basis. Thus, use of average light appears not only to overestimate daily photosynthesis and PhRUE (Sinclair *et al.*, 1976; Spitters, 1986), but also the overestimation increases with decreasing light within the canopy, masking the nature of the physiological mechanisms that lead to constant PhRUE of leaves. Similarly, when daily photosynthesis was calculated using an average value of light-saturated leaf net photosynthesis (A_{\max}) for all leaves in place of the value measured in the field for each leaf, the relationship of daily photosynthesis vs. incident PAR was also curvilinear (data not shown).

The slope of the linear relationships between daily photosynthesis and incident PAR of individual leaves (i.e. daily PhRUE) increased significantly with N fertilization (Fig. 1). Although calculated in different ways and not easily comparable, RUE has also been found to increase with N fertilization in other crops (Green, 1987; Muchow and Davis, 1988; Gimenez *et al.*, 1994), as predicted by modelling work (Sinclair and Horie, 1989; Hammer and Wright, 1994). This contrasts with the conclusions of Haxeltine and Prentice (1996) and Dewar and co-workers (Dewar, 1996; Dewar *et al.*, 1998) that N status changes canopy photosynthesis only via canopy leaf area (i.e. light interception), but does not change PhRUE. The present results show that nitrogen fertilization greatly increased canopy leaf area and light interception (Rosati *et al.* 2001) as well as leaf N content and assimilation rates (data not shown), resulting in greater daily PhRUE. This supports previous theories that PhRUE, calculated in various ways, increases with increasing leaf N and photosynthesis (De Witt, 1965; Monteith, 1977; Murata, 1981; Sinclair and Horie, 1989). Whilst the slope of the regressions between daily photosynthesis and PAR incident on individual leaves increased with N fertilization, the relationships remained linear (Fig. 1), suggesting that daily PhRUE increased with N fertilization but remained constant within the canopy. This provides a basis for modelling canopy photosynthesis under variable N conditions using PhRUE models.

Daily PhRUE for overcast vs. clear days

The slope of the relationship between gross daily photosynthesis and incident PAR of individual leaves (i.e. daily PhRUE) increased by about 42 % for an overcast compared with a clear day (Fig. 4). This does not contrast with theoretical explanations for the constant daily PhRUE provided by Haxeltine and Prentice (1996) and Dewar and co-workers (Dewar, 1996; Dewar *et al.*, 1998) since their simulations were based on the assumption that leaves adjust their photosynthetic properties to the local light environ-

ment. Thus, if PAR changes above the canopy and, thus, on individual leaves in the short term (e.g. 1 d), before any reallocation of N or change in photosynthetic properties can occur, then PhRUE on a gross photosynthesis basis increases with decreasing light, reflecting the curvature of the leaf photosynthetic response to PAR. However, when net photosynthesis was considered, PhRUE did not change significantly for a clear or an overcast day (Fig. 4). This resulted from the fact that going from a clear to an overcast day results in a shorter duration of high PAR and a longer duration of low PAR incident on the leaves, and that instantaneous net PhRUE at low and high PAR can be similar (Fig. 6), as reported by Hirose and Bazzaz (1998). Thus, the present data suggest that daily net PhRUE of all leaves (and thus of the canopy) may be constant, not only when leaves are acclimated to a given pattern of incident PAR, but also when incident PAR changes in the short term (e.g. 1 d), before reallocation of N can occur. This agrees with field data showing linearity between daily canopy photosynthesis and incident PAR, which implies constant daily PhRUE (Sinclair, 1991; Ruimy *et al.*, 1995; Sinclair and Muchow, 1999).

These results contrast with predictions by some models that daily net PhRUE of leaves and canopy should increase with decreasing daily incident PAR (De Witt, 1965; Norman and Arkebauer, 1991; Sinclair *et al.*, 1992; Hammer and Wright, 1994). This difference may arise from the use of averaged (in space and/or time) incident PAR in such models. Use of averaged PAR, as discussed above, may result in erroneous estimated variability of PhRUE (i.e. curvature of the photosynthesis vs. PAR relationship). Furthermore, some models (e.g. Sinclair and Horie, 1989; Sinclair *et al.*, 1992; Hammer and Wright, 1994) assume that both growth and maintenance respiration are proportional to gross photosynthesis. Thus, net photosynthesis becomes a fixed fraction of gross photosynthesis, and PhRUE is calculated to increase with lower PAR, as it did on a gross photosynthesis basis in the present study (i.e. during the overcast compared with the clear day; Fig. 4). While the assumption of proportionality between maintenance respiration and photosynthesis is acceptable in the long term (Ryan *et al.*, 1994), it is not acceptable in the short term (Medlyn, 1998), and respiration does not diminish proportionally with gross photosynthesis at lower PAR. Therefore, in the short term, the assumption of proportionality increasingly underestimates respiration and overestimates net photosynthesis and PhRUE with decreasing PAR. When PAR is zero, both the estimated maintenance respiration and net photosynthesis of such models are also zero, but in fact the former should be positive and the latter negative.

There is experimental evidence that RUE based on biomass is enhanced under low incident PAR (Horie and Sakuratani, 1985; Stirling *et al.*, 1990; Bange *et al.*, 1997). Even though it is difficult to compare results when RUE is calculated on a different basis, these findings appear to contrast with a constant RUE calculated on a net photosynthetic basis. However, the results cited above were obtained in continuous shade experiments. Under prolonged shade, plants may grow less and have altered root : shoot ratios, so that higher RUE may result from increased

nutrient availability (particularly nitrogen), smaller root biomass, reduced respiration rates, and a higher ambient CO₂ concentration as a result of lower canopy photosynthesis in the shade (Ludlow *et al.*, 1974; Wilson and Ludlow, 1991).

Simplified estimation of PhRUE

When the linear relationship between daily net photosynthesis and incident PAR was calculated using photosynthesis of a hypothetical leaf exposed to above-canopy incident PAR, the slope of the regression (i.e. daily net PhRUE) was not statistically different from that obtained by plotting data for actual leaves (Fig. 7). This suggests that daily net PhRUE of all leaves (and thus of the whole canopy) could be calculated simply from above-canopy incident PAR, which can be obtained from weather stations, and from the photosynthetic properties of one leaf at the top of the canopy, without measuring incident PAR and the photosynthetic properties of individual leaves. This would provide a fast and easy method of estimating daily net photosynthesis of leaves and canopies using a RUE model. However, further work on whole-canopy gas exchange using field data is required to validate this approach prior to field application. Furthermore, this approach does not consider the effects of temperature, vapour pressure deficit or other stresses that might affect photosynthesis and PhRUE during the day. Thus, its potential field application would be limited to non-stress conditions.

ACKNOWLEDGEMENT

We thank Filippo Piro for assistance with statistics.

LITERATURE CITED

- Bange MP, Hammer GL, Rickert KG. 1997. Effect of radiation environment on radiation use efficiency and growth of sunflower. *Crop Science* **37**: 1208–1214.
- Charles-Edwards DA. 1982. *Physiological determinants of crop growth*. Sydney: Academic Press.
- Cooper JP. 1970. Potential production and energy conversion in temperate and tropical grasses. *Herbage Abstracts* **40**: 1–13.
- DePury DGG, Farquhar GD. 1999. A commentary on the use of a sun/shade model to scale from the leaf to a canopy. *Agricultural and Forest Meteorology* **95**: 257–260.
- Dewar RC. 1996. The correlation between plant growth and intercepted radiation: an interpretation in terms of optimal plant nitrogen content. *Annals of Botany* **78**: 125–136.
- Dewar RC, Medlyn BE, McMurtrie RE. 1998. A mechanistic analysis of light and carbon use efficiencies. *Plant Cell and Environment* **21**: 573–588.
- De Witt CT. 1965. *Photosynthesis of leaf canopies*. Agricultural Research Report No. 663. Wageningen, The Netherlands: Institute for Biological and Chemical Research on Field Crops and Herbs.
- Gimenez C, Connor DJ, Rueda F. 1994. Canopy development, photosynthesis and radiation use efficiency in sunflower in response to nitrogen. *Field Crops Research* **38**: 15–27.
- Gosse G, Varlet-Grancher C, Bonhomme R, Chartier M, Allirand JM, Lemaire G. 1986. Maximum dry matter production and solar radiation intercepted by a canopy. *Agronomie* **6**: 47–56.
- Grace J, Lloyd J, McIntyre J, Miranda A, Meir P, Miranda H, Moncrieff J, Massheder J, Wright I, Gash J. 1995. Fluxes of carbon dioxide and water vapor over an undisturbed tropical forest in south-west Amazonia. *Global Change Biology* **1**: 1–12.
- Green CF. 1987. Nitrogen nutrition and wheat growth in relation to absorbed solar radiation. *Agricultural and Forest Meteorology* **41**: 207–248.
- Hammer GL, Wright GC. 1994. A theoretical analysis of nitrogen and radiation effects on radiation use efficiency in peanut. *Australian Journal of Agricultural Research* **45**: 575–589.
- Haxeltine A, Prentice IC. 1996. A general model for the light-use efficiency of primary production. *Functional Ecology* **10**: 551–561.
- Hirose T, Bazzaz FA. 1998. Trade off between light- and nitrogen-use efficiency in canopy photosynthesis. *Annals of Botany* **82**: 195–202.
- Horie T, Sakuratani T. 1985. Studies on crop-weather relationship model in rice. (1) Relation between absorbed solar radiation by the crop and the dry matter production. *Journal of Agricultural Meteorology* **40**: 331–342.
- Kull O, Jarvis PG. 1995. The role of nitrogen in a simple scheme to scale up photosynthesis from leaf to canopy. *Plant, Cell and Environment* **18**: 1174–1182.
- Loomis RS, Williams WR, Hall AE. 1971. Agricultural productivity. In: Machlis L, Briggs WR, Park RB, eds. *Annual review of plant physiology*. Palo Alto, CA: Annual Reviews Inc., 431–441.
- Ludlow MM, Wilson GL, Heselhurst MR. 1974. Studies on the productivity of tropical pasture plants. V. Effect of shading on growth, photosynthesis, and respiration in two grasses and two legumes. *Australian Journal of Agricultural Research* **25**: 425–433.
- Medlyn BE. 1998. Physiological basis of the light use efficiency model. *Tree Physiology* **18**: 167–176.
- Monteith JL. 1972. Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology* **9**: 747–766.
- Monteith JL. 1977. Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London, Series B* **281**: 277–294.
- Muchow RC, Davis R. 1988. Effect of nitrogen supply on the comparative productivity of maize and sorghum in a semi-arid tropical environment. II. Radiation interception and biomass accumulation. *Field Crops Research* **18**: 17–30.
- Murata Y. 1981. Dependence of potential productivity and efficiency for solar energy utilization on leaf photosynthetic capacity in crop species. *Japanese Journal of Crop Science* **50**: 223–232.
- Norman JM, Arkebauer TJ. 1991. Predicting canopy photosynthesis and light-use-efficiency from leaf characteristics. In: Boote KJ and Loomis RS, eds. *Modeling crop photosynthesis—from biochemistry to canopy*. CSSA special publication 19. Madison, WI: American Society of Agronomy: Crop Science Society of America, 75–94.
- Prince SD. 1991. A model of regional primary production for use with coarse resolution satellite data. *International Journal of Remote Sensing* **12**: 1313–1330.
- Rosati A, Badeck FW, DeJong TM. 2001. Estimating canopy light interception and absorption using leaf mass per unit leaf area in *Solanum melongena*. *Annals of Botany* **88**: 101–109.
- Ruimy A, Jarvis PG, Baldocchi DD, Saugier B. 1995. CO₂ fluxes over plant canopies and solar radiation: a review. *Advances in Ecological Research* **26**: 1–68.
- Ryan MG, Linder S, Vose JM, Hubbard RM. 1994. Dark respiration in Pinaceae. In: Gholz HL, Linder S, McMurtrie RE, eds. *Environmental constraints on the structure and productivity of pine forest ecosystem: a comparative analysis*. Ecological Bulletins. Copenhagen: Munksgaard International, 50–63.
- Sinclair TR. 1991. Predicting carbon assimilation and crop radiation-use efficiency dependence on leaf nitrogen content. In: Boote KJ and Loomis RS, eds. *Modeling crop photosynthesis—from biochemistry to canopy*. CSSA special publication 19. Madison, WI, USA: American Society of Agronomy: Crop Science Society of America, 95–107.
- Sinclair TR, Horie T. 1989. Leaf nitrogen, photosynthesis, and crop radiation use efficiency: a review. *Crop Science* **29**: 90–98.
- Sinclair TR, Muchow RC. 1999. Radiation use efficiency. *Advances in Agronomy* **65**: 215–265.
- Sinclair TR, Murphy CE, Knoerr KR. 1976. Development and evaluation of simplified models for simulating canopy photosynthesis and transpiration. *Journal of Applied Ecology* **13**: 813–829.
- Sinclair TR, Shirawa T, Hammer GL. 1992. Variation in crop radiation-use efficiency with increased diffused radiation. *Crop Science* **32**: 1281–1284.

- Sivakumar MVK, Virmani SM. 1984.** Crop productivity in relation to interception of photosynthetically active radiation. *Agricultural and Forest Meteorology* **31**: 131–141.
- Spitters CJT. 1986.** Separating the diffuse and direct component of global radiation and its implication for modeling canopy photosynthesis. Part II. Calculation of canopy photosynthesis. *Agricultural and Forest Meteorology* **38**: 231–242.
- Stirling CM, Williams JH, Black CR, Ong CK. 1990.** The effect of timing of shade on development, dry matter production and light-use efficiency in groundnut (*Arachis hypogaea* L.) under field conditions. *Australian Journal of Agricultural Research* **25**: 171–181.
- Thornley JHM. 1976.** *Mathematical models in plant physiology*. London: Academic Press.
- Wilson JR, Ludlow MM. 1991.** The environment and potential growth of herbage under plantations. In: Shelton HM, Stur WW, eds. *Forages for plantation crops*. Proceedings of a workshop, Sanur Beach, Bali, Indonesia, 27–29 June 1990. Canberra: ACIAR, 10–24.