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Modelling the Effect of Diffuse Light on Canopy Photosynthesis in Controlled Environments

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Abstract

A layered canopy model was used to analyze the effects of diffuse light on canopy gross photosynthesis in controlled environment plant growth chambers, where, in contrast to the field, highly diffuse light can occur at high irradiance. The model suggests that high diffuse light fractions (~ 0.7) and irradiance ($1400 \mu\text{mol m}^{-2} \text{s}^{-1}$) may enhance crop life-cycle canopy gross photosynthesis for hydroponic wheat by about 20% compared to direct light at the same irradiance. Our simulations suggest that high accuracy is not needed in specifying diffuse light fractions in chambers between ~ 0.7 and 1, because simulated photosynthesis for closed canopies plateau in this range. We also examined the effect of leaf angle distribution on canopy photosynthesis under growth chamber conditions, as these distributions determine canopy extinction coefficients for direct and diffuse light. We show that the spherical leaf angle distribution is not suitable for modeling photosynthesis of planophile canopies (e.g., soybean and peanut) in growth chambers. Also, the absorption of the light reflected from the surface below the canopy should generally be included in model simulations, as the corresponding albedo values in the photosynthetically active range may be quite high in growth chambers (e.g., ~ 0.5). In addition to the modeling implications, our results suggest that diffuse light conditions should be considered when drawing conclusions from experiments in controlled environments.

INTRODUCTION

Accounting for the amount of diffuse light incident on a canopy is an important component of modeling canopy light absorption, photosynthesis and crop growth rates under field conditions (e.g., De Wit, 1965; Allen et al., 1974; Sinclair et al., 1992). The effects of diffuse light are especially pertinent when modeling plant productivity in controlled environment growth chambers, because highly diffuse lighting conditions often coexist with high irradiance. These conditions are due to the presence of multiple lamps and reflective walls, which cause the light energy to be incident on plant canopies from many angles. Previous work using experimental data and a single-layer canopy model with sunlit and shaded leaf classes suggests that the high fractions of diffuse light encountered in growth chambers (~ 0.7) may enhance crop productivity with respect to optimal field conditions, where high irradiance occurs on clear days (Tubiello et al., 1997).

In this paper, we apply a multi-layer, sun-shade canopy light absorption model to further quantify the effect of diffuse light on canopy gross photosynthesis in controlled environments, and to examine some relevant modeling considerations. Leaf aggregation methods (i.e., canopy layers, and sunlit and shaded leaf classes) are needed to account for the uneven distribution of light within the canopy, and the non-linear response of leaf photosynthesis to irradiance (e.g., Goudriaan, 1988; Reynolds et al., 1992; Boote and Pickering, 1994). Although single-layer, sun-shade models can be modified so that diffuse light absorption at the canopy level approximates that simulated by multi-layer models (Boote and Pickering, 1994; De Pury and Farquhar, 1997), multi-layer models allow analyses of light absorption and photosynthesis with canopy depth.

Canopy extinction coefficients differ for direct and diffuse light, depending on beam direction and leaf angle distribution (Goudriaan, 1988). It has been shown that there is not a strong effect of leaf angle distribution on canopy photosynthesis for overcast skies under field conditions, while the effects under direct sunlight are strongest at midday, diminishing with lower solar elevations (De Wit, 1965). In contrast, the diurnal variations in light extinction coefficients that occur with time of day and with changing overcast conditions in the field do not occur in constant light environments. We therefore examine the effect of leaf angle distribution on canopy photosynthesis under growth chamber conditions, for which the distribution is often taken to be spherical in model simulations.

The multiple extinction of diffuse light is also considered in our analysis, as suggested by Goudriaan (1988). This method calculates diffuse light absorption by summing the contribution of canopy light extinction profiles originating from different beam directions. The result is a higher absorption of diffuse light in the upper canopy layers compared to the use of an average extinction coefficient for diffuse light. Lastly, we consider the absorption of light reflected from the surface below the canopy, as the corresponding albedo values in the photosynthetically active range may be much higher than typical soil values.

MODEL OUTLINE

The model for canopy light absorption and photosynthesis is adapted from Boote and Pickering (1994), which follows the method of Spitters (1986). To summarize, light absorption is calculated for LAI (leaf area index) increments equal to iL/n , where L is total canopy LAI, n is the number of layers in the canopy (here, $n = 10$), and $i = 1, \dots, n$. Differences between cumulative totals of light absorption are used to calculate the light absorbed by sunlit and shaded leaves in each layer (keeping field terminology). Diffuse light (i.e., incident diffuse light, direct light scattered within the canopy, and light reflected from the growth chamber surface) is shared equally by all leaves in a given layer, and sunlit leaves additionally receive direct light.

The actual distribution of direct and diffuse light in growth chambers will depend on the type and arrangement of lamps, and on the shape of the luminaires or reflectors. In analogy to field conditions, the geometry of the light source in growth chambers may be simplified by superimposing direct and diffuse light. However, quantifying the contributions from these components is difficult in growth chambers due to the presence of multiple lamps. This problem is minimal when no preferential direction for the beam radiation exists, as for many closely spaced fluorescent lamps, in which case light is incident on the plant canopy from many angles, and the lighting condition may be taken as totally diffuse. The following simplification is used in this paper to approximate the direct beam for situations where there is a preferential direction for the beam radiation (e.g., under a high intensity discharge lamp).

The direct beam may be defined by the radiation components perpendicular to the horizontal for a representative canopy section directly below a given lamp. This approach assumes uniform lighting at canopy height, and that all canopy sections will grow similarly because of symmetry in lamp positioning within the chamber. All the remaining light of varying incident angles is then defined as diffuse, and includes both non-

perpendicular beam radiation from lamps in adjacent sections, as well as light reflected from the growth chamber walls. In this approach, the canopy extinction coefficient for direct light corresponds to the perpendicular radiation component, and is analogous to a solar elevation of 90° under field conditions. This is a further simplification, as the direction of the beam radiation incident on the representative canopy section will vary over some angular width, depending on lamp spacing and canopy height. As defined here, the direct or diffuse light components may be measured using a point quantum sensor and an opaque shield, which blocks the non-perpendicular components of the incident irradiance, or by blocking the lamp filament, and measuring the irradiance directly under the lamp at canopy height.

Following Goudriaan (1988), canopy extinction coefficients (k) for direct and diffuse light are calculated from leaf angle distributions using three leaf-angle classes (0-30°, 30-60°, and 60-90° from the horizontal). We also compared the use of single (or average) *versus* multiple k values for calculating the absorption of incident diffuse light. We used the following equation for these calculations (Eq. 1):

where $A_{diff(i)}$ is the cumulative absorption of incident diffuse light through the i^{th} LAI layer, ρ

$$A_{diff(i)} = (1 - \rho) * PAR_{diff} * \left\{ a \left(1 - \text{Exp} \left[\sqrt{(1 - \sigma)} K_{15} * i L / n \right] \right) + b \left(1 - \text{Exp} \left[\sqrt{(1 - \sigma)} K_{45} * i L / n \right] \right) + c \left(1 - \text{Exp} \left[\sqrt{(1 - \sigma)} K_{75} * i L / n \right] \right) \right\} \quad (1)$$

is the fraction of incident diffuse light reflected from the canopy, PAR_{diff} is the diffuse component of total incident PAR (photosynthetically active radiation), and σ (= 0.20) is the leaf scattering coefficient. The extinction coefficients K_{15} , K_{45} , and K_{75} correspond to beam directions centered on 15°, 45° and 75° from the horizontal, respectively, and are calculated from a linear combination of extinction coefficients for the three leaf-angle classes.

The coefficients a , b , and c in Eq. 1 are determined by the diffuse radiance. For instance, setting $a = c = 0.25$, and $b = 0.5$ would simulate a “uniform overcast sky,” which corresponds to incident diffuse light with uniform radiance (Goudriaan, 1988). Setting $a = c = 0$, and $b = 1$ in Eq. 1 corresponds to our use of a single k value for diffuse light extinction (K_{45}). For the multiple extinction of diffuse light, we simply use a “uniform overcast sky” as a general approximation for controlled environments. This choice is used to facilitate the comparison of the effect of single *versus* multiple k diffuse values on canopy photosynthesis.

Canopy gross photosynthesis (PG_{CAN}) is calculated by summing leaf gross photosynthesis for sunlit and shaded leaves in each canopy layer. The response of leaf gross photosynthesis (PG_{LEAF}) to absorbed irradiance is calculated using a non-rectangular hyperbola (Eq. 2) (see, for instance, Johnson and Thornley, 1984):

$$PG_{LEAF} = \frac{(Q_E PAR_{LF} + P_{MAX}) - \sqrt{(Q_E PAR_{LF} + P_{MAX})^2 - (4 \Theta Q_E PAR_{LF} P_{MAX})}}{2\Theta} \quad (2)$$

where PAR_{LF} = PAR absorbed per unit leaf area by sunlit or shaded leaves ($\mu\text{mol m}^{-2} \text{s}^{-1}$), Q_E = Quantum efficiency of leaf photosynthesis ($\mu\text{mol CO}_2$ fixed μmol^{-1} absorbed PAR), P_{MAX} = Light-saturated leaf photosynthesis rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and Θ = Dimensionless curvature parameter ($0 \leq \Theta \leq 1$). A three-point Gaussian integration of leaf photosynthesis is used for sunlit leaves to account for leaf angle distribution (Goudriaan, 1988), in order not to over predict canopy photosynthesis at low diffuse light fractions and high irradiance.

For crop life-cycle simulations of hydroponic wheat, the above model components were integrated into a modified CERES-Wheat model (Tubiello et al., 1995). We used an erectophile leaf angle distribution in these simulations based on effective canopy extinction coefficients, defined by the Beer-Lambert law, calculated for hydroponic wheat

at high planting densities (Smart et al., 1994). While numerous canopy models exist, some more elaborate than the one used in this paper, the model presented is considered appropriate to quantify the effects of interest for this study.

RESULTS

The simulated response of PG_{CAN} to the diffuse fraction of incident PAR (f_D) is shown in Figure 1 for LAI = 2 and 6, and PAR = 500 and 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. These values for LAI and irradiance were chosen to simulate different responses, and were otherwise arbitrary. We showed model sensitivity to leaf angle distribution by comparing planophile (e.g., peanut, soybean) and erectophile (e.g., wheat, rice) canopies to the spherical leaf angle distribution. These simulations used single k values for diffuse light extinction, and a PAR albedo of zero for the surface below the canopy. The k values for direct and diffuse light used in the simulations are given in the caption to Figure 1 for reference.

The increases of PG_{CAN} with f_D shown in Figure 1 depended on the combined effects of a more uniform distribution of light among sunlit and shaded leaves per canopy layer as f_D increases, and on changes in canopy light absorption profiles. These changes occurred due to the different extinction coefficients for direct and diffuse light. The fractional increases in PG_{CAN} between $f_D = 0$ and 1 for the different canopies are also given in Figure 1, and are denoted by I (e.g., I_P for the planophile canopy). These increases ranged from approximately 10 to 45% depending on canopy type, LAI and irradiance. At low LAI and moderate irradiance (Figure 1A), the increase in PG_{CAN} with f_D for the spherical and erectophile canopies was primarily a result of increased light absorption due to the higher k values for diffuse light, rather than from the more efficient distribution of diffuse light. It may also be seen that PG_{CAN} plateaued at high LAI and irradiance for f_D greater than ~ 0.7 (Figure 1B). The simulations indicated that the spherical leaf angle distribution was generally a suitable default for erectophile canopies, but not for planophile canopies. For example, at $f_D = 0.5$, the largest absolute difference in PG_{CAN} between the spherical and erectophile canopies was about 4%, whereas the largest difference between spherical and planophile canopies was about 10% (Figure 1A, LAI = 2; Figure 1B, LAI = 6).

Model sensitivity to using single *versus* multiple k diffuse values for diffuse light absorption is shown in Table 1A, by comparing the fractional increases in PG_{CAN} between $f_D = 0$ and 1. In general, there were only small differences between the use of the single (or average) *versus* multiple k diffuse values (approximately 2 to 3% at $f_D = 1$). At high LAI and irradiance, the effect of multiple k diffuse values was to increase the plateaus in PG_{CAN} with f_D somewhat compared to those obtained using single k diffuse values (not shown). This occurred since the use of multiple k diffuse values resulted in a higher, but less efficient absorption of light in the upper canopy layers compared to the use of an average k value (Goudriaan, 1988). This effect eventually outweighed that of uniformly distributing diffuse light within canopy layers. At high LAI and irradiance, the use of multiple *versus* single k diffuse lowered the fractional increase in PG_{CAN} between $f_D = 0$ and 1 by about 6% (Table 1A). This result applied to simulating incident diffuse light with uniform radiance (see section 2).

Including the absorption of light reflected from the surface below the canopy in the PG_{CAN} calculations had the general effect of decreasing the sensitivity of PG_{CAN} to f_D . This is shown in Table 1B for the different canopies and PAR albedo values of zero and 0.5, again by comparing the fractional increases in PG_{CAN} between $f_D = 0$ and 1. Actual PAR albedo values depended on the particular surface below the canopy, and may range, for instance, from 0.25 for diatomaceous earth to 0.85 for white plastic. Typical soil values are about 0.1–0.2 by contrast. The decreased sensitivity of PG_{CAN} to f_D occurred since k for direct light is less than that for diffuse light, which resulted in more light transmission to the substrate at $f_D = 0$ than at $f_D = 1$. Consequently, the greatest relative increase in PG_{CAN} from the reflected light absorption was at $f_D = 0$, flattening the response of PG_{CAN} to f_D . This effect was more pronounced for the spherical and erectophile canopies at lower LAIs (Table 1B).

The model was applied by simulating canopy gas-exchange data from a hydroponic wheat (*Triticum aestivum* L., cv. Veery-10) experiment conducted at Utah State University (USU) (Monje and Bugbee, 1998). The lighting conditions for this particular experiment, where four 1000-W high-pressure sodium lamps were evenly spaced over a 1 m² growing area, corresponded to both high diffuse light fraction ($f_D \sim 0.7$) and high irradiance (1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The reflective, aluminum-coated walls in the chamber used for this experiment contributed to the diffuse lighting conditions. The value for f_D was estimated by blocking the lamp filaments, and measuring the irradiance at canopy height (see section 2). Other experimental conditions are given in the caption to Figure 2.

For the data, PG_{CAN} was calculated by adding canopy respiration during the dark-cycle (4h) to apparent photosynthesis during the light-cycle. This derivation assumed that canopy respiration during the light-cycle equaled that measured during the dark-cycle at the same temperature (as in Monje and Bugbee, 1998). Model simulations of daily PG_{CAN} for $f_D = 0$ and 0.7 are compared with that calculated for the USU experiment in Figure 2. Multiple k diffuse values were used in the simulation for $f_D = 0.7$ due to the high diffuse irradiance (see Table 1A). As shown in the figure, using the diffuse conditions in the USU experiment in our model resulted in reasonable agreement between simulation and the data. Integrated canopy photosynthesis for the simulation in Figure 2 with $f_D = 0.7$ was about 20% greater than that assuming all light to be direct (i.e., $f_D = 0$), and was within 2% of the data.

DISCUSSION

A comparison of crop life-cycle canopy gross photosynthesis simulations with growth chamber data suggests that high diffuse light fractions coexistent with high irradiance may enhance canopy photosynthesis by about 20% compared to direct light for hydroponic wheat. This result emphasizes the need to properly account for the diffuse light conditions in growth chambers for modeling canopy photosynthesis. Our simulations also suggest that high accuracy is not needed in specifying diffuse light fractions in chambers between ~ 0.7 and 1, because simulated photosynthesis for closed canopies plateau in this range.

The modeling considerations examined here indicate that the spherical leaf angle distribution is not a suitable default for planophile canopies (e.g., soybean, peanut) for the light conditions in growth chambers. In addition, the absorption of the light reflected from the surface below the canopy should generally be included in model simulations, as the corresponding albedo values in the photosynthetically active range may be quite high in growth chambers (e.g., ~ 0.5). This especially applies to lower planting densities. It was also shown that the use of multiple extinction coefficients for diffuse light absorption instead of average values generally has only a small effect on simulated canopy photosynthesis. However, the use of multiple values is perhaps warranted under conditions of high LAI and high diffuse irradiance. In such cases, a suitable diffuse radiance distribution should be chosen for specific applications.

In conclusion, our results suggest that diffuse light conditions should be considered when drawing conclusions from experiments in controlled environments. The modeling approach presented here may thus provide a baseline for growth chamber applications, and other situations where diffuse conditions predominate.

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Tables

Table 1. Simulated fractional increase in PG_{CAN} between f_D = 0 and 1. ^a

	PAR = 500 μmol m ⁻² s ⁻¹		PAR = 1500 μmol m ⁻² s ⁻¹					
	LAI = 2	LAI = 6	LAI = 2	LAI = 6				
A. Single versus multiple k diffuse values.								
Single (average) k diffuse	1.26	1.11	1.43	1.32				
Multiple k diffuse	1.29	1.08	1.40	1.24				
B. The effect of substrate PAR albedo for different canopy types.								
<i>PAR albedo</i>	0	0.5	0	0.5	0	0.5	0	0.5
Planophile canopy	1.12	1.11	1.12	1.12	1.39	1.30	1.44	1.44
Spherical canopy	1.26	1.16	1.11	1.08	1.43	1.25	1.32	1.27
Erectophile canopy	1.34	1.18	1.12	1.07	1.46	1.24	1.29	1.22

a. Other modeling parameters are as in Figure 1.

Fig.1. Simulated canopy gross photosynthesis (PG_{CAN}) vs. diffuse light fraction (f_D) for the planophile (—), spherical (---), and erectophile (—) leaf angle distributions. I_P (planophile), I_S (spherical), and I_E (erectophile) are the fractional increases in PG_{CAN} between $f_D = 0$ and 1 for the different canopy types. A. PAR = $500 \mu\text{mol m}^{-2} \text{s}^{-1}$; B. PAR = $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. $Q_E = 0.0524 \text{ mol mol}^{-1} \text{s}^{-1}$; $P_{MAX} = 26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$, all leaves like upper canopy layers (e.g., see Boote and Pickering, 1994); $\Theta = 0.8$; Surface PAR albedo = 0. The canopy extinction coefficients (k) used for the leaf angle distributions are (k direct; average k diffuse): (0.81; 0.83) for planophile; (0.50; 0.71) for spherical; (0.43; 0.69) for erectophile.

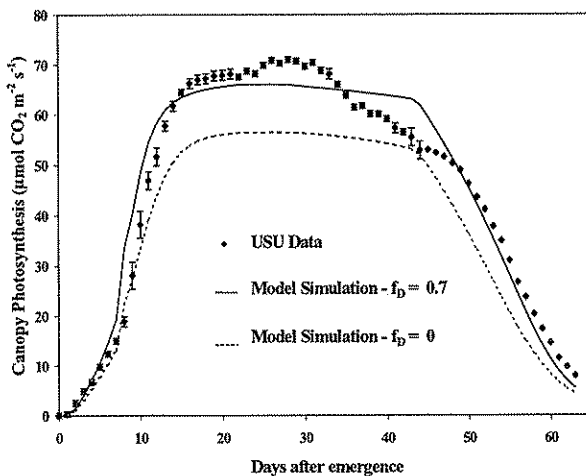
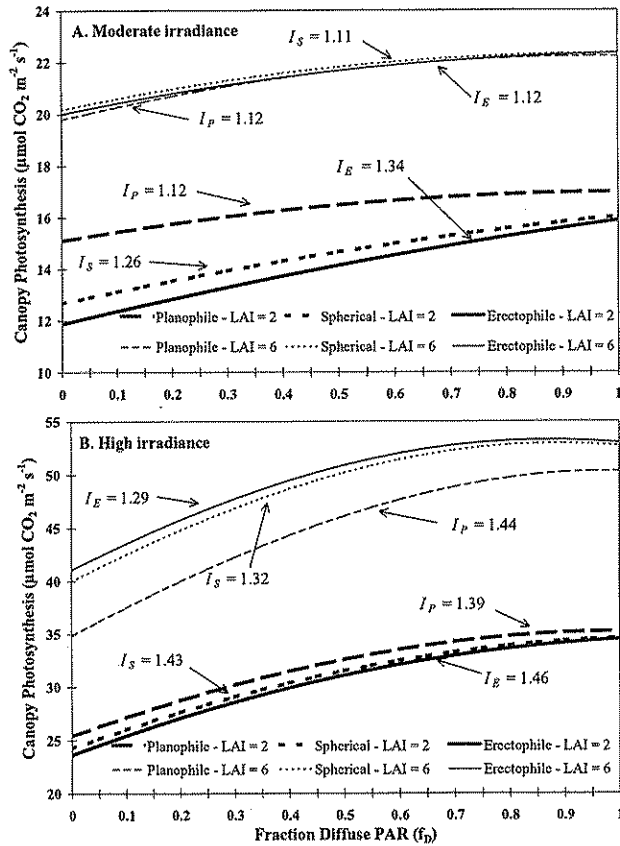


Fig. 2. Simulated daily PG_{CAN} vs. USU wheat data. Data are the mean and standard error for three replicates (where applicable). $Q_E = 0.0587 \text{ mol mol}^{-1}$ at 23°C (adjusted for temperature as in Boote and Pickering, 1994); $P_{MAX} = 33 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ (O. Monje, unpublished data); $\Theta = 0.9$. Experimental conditions: PAR: $1400 \mu\text{mol m}^{-2} \text{s}^{-1}$; $[\text{CO}_2]$: $330 \mu\text{mol mol}^{-1}$; Temperature: 23°C (constant); Photoperiod: 20 h; PAR albedo: 0.25. Planting density: $720 \text{ plants m}^{-2}$.