Modeling Photosynthesis of Row Crop Canopies

K.J. Boote¹ and N.B. Pickering²

Agronomy Department, University of Florida, Gainesville, FL 32611

Most field and horticultural crops are grown in rows rather than in horizontally uniform stands. Thus, it is important to be able to predict light interception and photosynthesis of incomplete hedgerow crops. With improved knowledge of the biochemistry of single-leaf photosynthesis, particularly in response to temperature and CO₂ concentration, it is now possible to model canopy assimilation based on single-leaf characteristics.

The complexity of plant responses to climatic and management factors makes a mechanistic modeling approach attractive for predicting such responses reliably (Reynolds and Acock, 1985). Important plant processes include leaf photochemistry, leaf and canopy gas exchange, growth, and assimilate partitioning. Most efforts to model canopy photosynthesis mechanistically have applied only to closed horizontally uniform crop stands (Denison and Loomis, 1989; de Wit, 1965; Duncan et al., 1967; Norman and Arkebauer, 1991). Horticultural production could benefit from models that predict optimum spacing for fruit and nut tree crops, yield response to various hedgerow arrangements for trellised vineyards or staked tomatoes (*Lycopersicon esculentum* Mill.), and effects of various spacings on productivity of field and greenhouse commodities.

In this paper we describe a light interception–canopy photosynthesis approach that calculates absorption of direct and diffuse irradiance by incomplete hedgerow canopies as a function of canopy height, canopy width, leaf area index (LAI), leaf angle, row direction, latitude, day of year, and time of day. A sunlit and shaded LAI approach was used to simulate absorption of photosynthetic photon flux density (PPFD) by sunlit and shaded leaves. Canopy assimilation is the sum of sunlit and shaded leaf photosynthesis over their respective LAI classes. Photosynthesis of sunlit and shaded leaves was computed with the asymptotic exponential equation, where quantum efficiency (Q_E) and light-saturated photosynthesis rate (P_{max}) were functions of intercellular CO₂ (C_i), O₂, and temperature. The Farquhar and von Caemmerer equations for the ribulose 1,5 bisphosphate (RuBP)-regeneration limited region were used to compute the efficiency of electron conversion to CO₂ fixation. The modeling approach is modular in that various mechanistic leaf photosynthesis equations can be substituted, with each receiving inputs of absorbed PPFD, temperature, and CO₂ for each class of leaves.

Light absorbance, reflectance, and transmittance processes

Photosynthetically active irradiance arrives at leaf surfaces in crop canopies by several pathways: 1) direct beam, 2) diffuse skylight (scattered by atmosphere and clouds), 3) diffuse scattered from other foliage (e.g., reflected from and transmitted through foliage), and 4) diffuse scattered from the soil surface.

Green leaves have a high absorbance for photosynthetically active radiation. The leaf scattering coefficient for direct-beam irradiance (σ = fraction transmitted plus reflected) is ≈ 0.20 (Goudriaan, 1977), with $\approx 10\%$ of incident PPFD reflected, $\approx 10\%$ transmitted, and $\approx 80\%$ absorbed. The scattering coefficient varies somewhat with leaf thickness, leaf chlorophyll content, and angle of incidence of the direct

beam. Scattering of direct-beam irradiance to lower leaves and penetration of diffuse skylight are important to canopy assimilation in two ways. First, in crop canopies, the lower, shaded leaves absorb 10% to 15% of the incident PPFD that is scattered by the sunlit leaves. Second, lower leaves absorb a considerable fraction of the diffuse skylight since it is less directional than the direct beam. Diffuse-light flux absorbed by lower leaves, although fairly small, is important because, at low PPFD, the apparent Q_E will be high for lower leaves.

Light interception by closed crop canopies

For crop canopies that are closed and have their leaves randomly distributed horizontally, there are simple equations for light interception and for PPFD striking a leaf at any given LAI depth. Because the leaves in crop canopies are not contiguous, there are gaps between adjacent leaves through which light penetrates farther down in the canopy. Assuming the gaps are randomly distributed horizontally, the area of direct-beam irradiance penetrating to any depth in the canopy is an exponential function of the cumulative LAI from the top of the canopy (analogous to the Beer–Lambert law):

$$I = I_0 \cdot e^{-(K_d \cdot \text{LAI})} \quad [1]$$

where I and I_0 are the total energies or areas of direct-beam fluxes on a horizontal plane at points within and above the canopy, respectively (Loomis and Williams, 1969; Monsi and Saeki, 1953). In the area context, the direct-beam extinction coefficient (K_d) is the ratio of horizontally projected shadow area per unit land area per unit leaf area. The shadow projection of leaves depends on leaf angle and solar elevation angle (β) from the horizontal. K_d is 1.0 only when all leaves are distributed randomly in the horizontal plane and are perpendicular to the direct beam when the sun is directly overhead. Under these conditions, a canopy of LAI = 1 intercepts 63% of the incident direct irradiance. Since K_d includes $1/\sin(\beta)$, it varies as the solar elevation angle β changes. Leaf angle variations also affect K_d because less light is intercepted when leaves are displayed obliquely to the direct beam. Equation [1] assumes random horizontal distribution of leaf area; however, that assumption does not hold for incomplete row crop stands or regularly spaced but incomplete plant stands. In addition to K_d , total light extinction by a crop canopy requires accounting for scattering (reflectance and transmittance), as was done by Duncan et al. (1967) and Goudriaan (1977, 1982). For these reasons, experimentally determined values for total light extinction would not necessarily be the same as K_d calculated from Eq. [1]. See Loomis and Williams (1969), Ross (1981), and Campbell and Norman (1989) for further information on light interception relative to leaf angle, leaf pattern, LAI, and solar elevation.

Simple models for predicting assimilation of closed canopies

Two simple models for gross canopy assimilation (P_{can}) of horizontally uniform canopies are introduced here, so readers can compare them to the subsequent hedgerow photosynthesis model. Both simple models use light-response curves that can be defined by Q_E and P_{max} . Acock et al. (1978) developed an analytical solution for P_{can} that considers the integral of the Michaelis–Menten equation for leaf photosynthesis over successive LAI depth (L) as PPFD is absorbed:

$$P_{can} = \int_0^{\text{LAI}} P_{leaf} dL \quad [2]$$

Light attenuation through the canopy is assumed to follow the Beer–Lambert law, where I_0 is the PPFD on a horizontal plane above the canopy. The actual PPFD reaching the surface of a leaf and absorbed for

Florida Agricultural Experiment Station Journal Series no. R-03661. We express appreciation to H. Gijzen and J. Goudriaan for their excellent suggestions for adapting the sunlit leaf area index approach for hedgerow canopies. We thank J. Norman for his advice on the model and E.B. Blazey and G. Bourgeois for their assistance with photosynthesis measurements. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

¹Professor of Agronomy. To whom reprint requests should be addressed.

²Visiting Assistant in Agricultural Engineering.

photosynthesis (I_i) at any LAI depth in the canopy requires consideration of σ and K_d (Charles-Edwards, 1981):

$$I_i = K_d / (1 - \sigma) \cdot I_0 \cdot e^{(-K_d \cdot \text{LAI})} \quad [3]$$

I_i is the average irradiance absorbed at any given LAI depth and does not reflect the randomness of sunflecks penetrating to depth in the canopy. Upon combining the Michaelis-Menten leaf light-response equation and Eq. [3] for PFD absorbed by leaf area at any LAI depth, then integrating over LAI depth, the following equation is obtained:

$$P_{\text{can}} = \frac{P_{\text{max}}}{K_d} \ln \frac{(1 - \sigma) \cdot P_{\text{max}} + Q_E \cdot K_d \cdot \text{PFD}}{(1 - \sigma) \cdot P_{\text{max}} + Q_E \cdot K_d \cdot \text{PFD} \cdot e^{(-K_d \cdot \text{LAI})}} \quad [4]$$

Equation [4] tends to overpredict P_{can} slightly, possibly because of the use of average irradiance per layer and because one P_{max} value is used throughout the entire canopy. Reynolds et al. (1992) compared various model approaches and reported that using average irradiance for all leaves within a layer invariably overestimated canopy assimilation. This problem is inherent in the modeling approaches of Acocck et al. (1978), Monsi and Saeki (1953), and Hirose and Werger (1987).

Another simple model for gross assimilation of closed crop canopies is based on the sunlit and shaded LAI approach and the exponential light-response equation (Boote and Jones, 1987; Boote and Loomis, 1991; Sinclair and Horie, 1989). This approach is based on light absorption by sunlit and shaded leaf classes, subsequent photosynthesis of these leaf classes, and summation of rates over the sunlit and shaded LAIs. The exponential light-response equation for leaf photosynthesis (P) is described:

$$P = P_{\text{max}} \cdot [1 - e^{(-Q_E \cdot \text{PFD}/P_{\text{max}})}] \quad [5]$$

First, consider photosynthesis by sunlit leaves. The amount of sunlit LAI (LAI_{sun}) is described analytically from K_d and total LAI (Goudriaan, 1977):

$$\text{LAI}_{\text{sun}} = (1/K_d) \cdot [1 - e^{(-K_d \cdot \text{LAI})}] \quad [6]$$

If $K_d = 1$ (leaves perpendicular to solar beam), then sunlit LAI approaches 1 as LAI approaches infinity. If $K_d < 1$, say 0.5, then the amount of sunlit LAI would approach 2 as LAI approaches infinity. The incident PFD on LAI_{sun} would be $K_d \cdot \text{PFD}$. After accounting for σ due to reflectance and transmittance, the absorbed PFD would be $(1 - \sigma) \cdot K_d \cdot \text{PFD}$. Using the exponential leaf photosynthesis equation, the assimilation rate of sunlit leaves (P_{sun}) becomes

$$P_{\text{sun}} = P_{\text{max}} \cdot [1 - e^{(-Q_E \cdot K_d \cdot (1 - \sigma) \cdot \text{PFD}/P_{\text{max}})}] \quad [7]$$

Next, consider photosynthesis by shaded leaves. Total canopy photosynthesis is increased by the photosynthetic contribution of lower, shaded leaves that absorb diffuse skylight and direct beam scattered and transmitted through the upper leaves. Shaded LAI (LAI_{shd}) is defined as any LAI that is not sunlit.

$$\text{LAI}_{\text{shd}} = \text{LAI} - \text{LAI}_{\text{sun}} \quad [8]$$

In a typical situation, $\approx 10\%$ to 20% of the direct beam is scattered through sunlit leaves to shaded leaves. In the simple examples in Boote and Loomis (1991), scattered direct beam ($\sigma = 0.20$) was assumed to include some diffuse skylight. As an approximation, Boote and Jones (1987) assumed that LAI_{shd} intercepted this scattered light using the same K_d as for LAI_{sun} , and that all shaded LAI shared equally in the use of this scattered PFD, once intercepted. Thus, PFD incident on, and available for, photosynthesis per unit shaded LAI (PFD_{shd}) is

$$\text{PFD}_{\text{shd}} = \sigma \cdot \text{PFD} \cdot [1 - e^{(-K_d \cdot \text{LAI}_{\text{shd}})}] / \text{LAI}_{\text{shd}} \quad [9]$$

and assimilation by shaded leaves (P_{shd}) is

$$P_{\text{shd}} = P_{\text{max}} \cdot [1 - e^{(-Q_E \cdot \text{PFD}_{\text{shd}}/P_{\text{max}})}] \quad [10]$$

The total canopy assimilation summed over both leaf categories is

$$P_{\text{can}} = P_{\text{sun}} \cdot \text{LAI}_{\text{sun}} + P_{\text{shd}} \cdot \text{LAI}_{\text{shd}} \quad [11]$$

Given inputs of field measurements of leaf P_{max} , K_d , and LAI, the sunlit plus shaded LAI photosynthesis model has adequately predicted total canopy assimilation response to PFD measured on closed canopies of soybean (*Glycine max* L.), peanut (*Arachis hypogaea* L.), and common bean (*Phaseolus vulgaris* L.) (Boote and Jones, 1987; Boote et al., 1988). Predictions with the sunlit plus shaded LAI approach (Eqs. [6–11]) have generally been closer to observed total canopy photosynthesis than predictions with the analytical equation of Acocck et al. (1978). The analytical equation (Eq. [4]) gives comparable, but slightly higher, predictions than the sunlit plus shaded LAI approach (same K_d and σ). These two approaches are satisfactory for closed crop canopies but do not work well for incomplete hedgerow canopies and lack a separate accounting for interception of direct beam and diffuse skylight. The sunlit plus shaded LAI approach has the advantage that any leaf photosynthesis equation (simple or complex) can be used.

Row crop canopies and nonrandom horizontal distribution of LAI

Many field and horticultural crops are grown in rows and the foliage is confined within a hedgerow. Even under equidistant plant spacing, leaves are usually clumped about the main axis of the plant. The canopy leaf area is then nonrandomly distributed horizontally, allowing greater light capture in clumped regions and greater light penetration to the soil where gaps in the canopy exist. If one looks at the canopy hedgerows at midday with the sun directly overhead, the impression may be that considerable light is not captured. Nevertheless, the effects of time of day and day of year on solar elevation causes considerably greater capture for lower solar elevations. It is possible to simulate the light interception by a hedgerow using three-dimensional geometry if one considers hedgerow dimensions, latitude, day of year, and time of day (Allen, 1974; Boote and Loomis, 1991; Gijzen and Goudriaan, 1989; Mutsaers, 1980).

ASSIMILATION BY HEDGEROW CANOPIES

A model to predict assimilation of row crop canopies was developed by Boote et al. (1988, 1989) based on a simplification of the hedgerow approach of Gijzen and Goudriaan (1989). The approach considers sunlit and shaded LAI similar to that for a horizontally uniform canopy, but with adaptations that apply to hedgerows. A simplified version of this approach is described by Boote and Loomis (1991). The version described below is a component of our crop growth simulation model, CROPGRO (Hoogenboom et al., 1992).

Canopy envelope and light extinction coefficients

The crop model predicts plant height and width over time, as a function of rate of increase in vegetative stage (V ; main stem node number) and internode length, which depends on temperature, water deficit, PFD, photoperiod, and plant vegetative stage (length per internode varies with V stage). Figure 1 illustrates prediction of width, height, and vegetative stage for a peanut crop canopy over the season. Plant canopy envelope is assumed to have an elliptical shape defined by the height and width. On an hourly basis, the shadow projected by individual plants is computed as a function of canopy height (H), canopy width (W), time of day, day of year, latitude, and row azimuth. The shadow projections account for row spacing and spacing between plants in the row to allow computation of the fraction of the soil surface shaded by plant canopy at least once (f_{sh}).

Solar azimuth and elevation are computed from standard equations as a function of latitude, day of year, and time of day (Spitters, 1986). Parameters such as latitude, row azimuth, row spacing, plant spacing in the row, leaf angle distribution, leaf scattering coefficient, soil albedo, and cultivar potential P_{max} are assumed to remain constant during the season. Daily changes occur in day of year, height, width, LAI, leaf N concentration, specific leaf weight, and actual P_{max} .

The direct-beam extinction coefficient, K_d , is computed hourly as

Fig. 1. (A) Predicted hedgerow width and height and (B) predicted vegetative stage of 'Florunner' peanut in 1990 at Gainesville, Fla. Solid points are field observations and line represents values simulated by PNTGRO model—hedgerow version. V = vegetative.

a function of solar elevation and approximate leaf angle distribution among three angle classes (0 to 30, 30 to 60, and 60 to 90 degrees) using the approach of Goudriaan (1988). A similar, alternative approach has been proposed by Campbell and Norman (1989), whereby an ellipsoidal leaf angle distribution with a single parameter (0.1 = vertical, 10 = horizontal) can be used to compute the proportion of leaves in each of three leaf angle classes. For simplicity, a spherical leaf-angle distribution could also be used, where the average horizontal projection of leaves relative to the direct-beam path is a constant 0.5. Experience has shown that leaf angle distribution has only small effects on daily canopy photosynthesis, although a spherical leaf-angle distribution can underestimate light interception at midday for soybean and peanut. K_d varies with β , because β affects the effective pathlength through the canopy.

Light interception, photosynthesis, and LAI are restricted to the fraction of the soil surface shaded by the canopy (f_{sh}), which depends on overlapping shadows of plant ellipses relative to row spacing and plant spacing.

The sunlit and shaded LAI are computed for the hedgerow canopy as

$$LAI_{sun} = (f_{sh}/K_d) \cdot [1 - e^{(-K_d \cdot LAI/f_{sh})}] \quad [12]$$

$$LAI_{shd} = LAI - LAI_{sun} \quad [13]$$

Calculating hourly weather data

Class A weather station data generally consist of daily maximum and minimum temperatures, daily rainfall, and, for a few stations, daily solar radiation and relative humidity. Hourly weather data are frequently not available, but can be used to drive the model if available. A function from Spitters (1986) is used to compute the hourly radiation values from daily values to distribute solar radiation and PFD throughout the day. Hourly temperatures are calculated from daily maximum and minimum air temperatures using a combined sine-exponential

curve vs. time of day (Kimball and Bellamy, 1986; Parton and Logan, 1981). Hourly total and photosynthetic irradiance are split into direct (PFD_{dir}) and diffuse (PFD_{dif}) components using an algorithm for fraction diffuse vs. atmospheric transmission (Erbs et al., 1982; Spitters et al., 1986).

Radiation absorption

The PFD absorbed by sunlit and shaded LAI is computed as described by Spitters (1986). In this algorithm, a proportion of the direct-beam PFD is converted to diffuse within the canopy by scattering processes. The scattering coefficient (σ) includes transmittance and reflectance down through the foliage. Reflectance (δ_{dir} and δ_{dif}) from the canopy to the sky depends on σ and solar elevation. The use of f_{sh} limits absorption of direct-beam PFD to the shaded soil surface area at any time of day. The relative LAI in the shaded zone is increased by dividing LAI by f_{sh} as shown below:

$$A_{dir,dir} = f_{sh} \cdot (1 - \sigma) \cdot PFD_{dir} \cdot [1 - e^{(-K_d \cdot LAI/f_{sh})}] \quad [14]$$

$$A_{dir,tot} = f_{sh} \cdot (1 - \delta_{dir}) \cdot PFD_{dir} \cdot \{1 - e^{[-K_d \sqrt{(1-\sigma)} \cdot LAI/f_{sh}]} \} \quad [15]$$

$$A_{dir,dif} = A_{dir,tot} - A_{dir,dir} \quad [16]$$

$$\delta_{dif} = [1 - \sqrt{(1-\sigma)}] / [1 + \sqrt{(1-\sigma)}] \quad [17]$$

$$\delta_{dir} = \delta_{dif} \cdot 2 / [1 + 1.6 \cdot \sin(\beta)] \quad [18]$$

Absorption of diffuse skylight (A_{dif}) depends on row spacing (R), plant spacing within the row (S), canopy height (H), and canopy width (W), based on an adaptation of Goudriaan (1977). The approach computes the path width [gap (G) between hedges = $R - W$] or the path width (G) between plants in the row ($S - W$) to compute the view factor (fraction of sky seen by the plants) for incomplete canopies. A diffuse extinction coefficient of 0.8 is assumed.

$$\text{If } W < R, G = R - W \quad [19]$$

$$DelR = G + H - \sqrt{(G^2 + H^2)} \quad [20]$$

$$f_r = \text{MIN}[1.0, (W + DelR)/R] \quad [21]$$

$$\text{If } W < S, G = S - W \quad [22]$$

$$DelG = G + H - \sqrt{(G^2 + H^2)} \quad [23]$$

$$f_p = \text{MIN}[1.0, (W + DelG)/S] \quad [24]$$

$$A_{dif} = f_r f_p \cdot (1 - \delta_{dif}) \cdot PFD_{dif} \cdot \{1 - e^{[-K_{dif} \sqrt{(1-\sigma)} \cdot LAI/(f_r f_p)]} \} \quad [25]$$

This approach assumes that diffuse irradiance originates from a uniformly overcast sky and that an incomplete canopy has a view factor > 1 . It is important that diffuse-light capture be computed in the two-dimensional manner above when plant canopy envelopes do not overlap within the row. This requirement was discovered by simulating single widely spaced plants, where, theoretically and in practice, photosynthesis and yield should reach a constant maximum per plant at some spacing at which single plants no longer compete for light.

Absorption of PFD reflected from soil (A_{ref}) is handled in a similar manner to Eq. [25], based on total PFD incident on the soil surface (both direct and diffuse) and assuming that diffuse soil reflectance to PFD (δ_{soil}) is 0.25.

$$PFD_{int} = A_{dir,dir} + A_{dir,dif} + A_{dif} + f_{sh} \delta_{dir} \cdot PFD_{dir} + f_r f_p \cdot \delta_{dif} \cdot PFD_{dif} \quad [26]$$

$$PFD_{soil} = PFD - PFD_{int} \quad [27]$$

$$A_{ref} = f_r f_p \cdot (1 - \delta_{dif}) \cdot \delta_{soil} \cdot PFD_{soil} \cdot \{1 - e^{[-K_{dif} \sqrt{(1-\sigma)} \cdot LAI/(f_r f_p)]} \} \quad [28]$$

$$PFD_{abs} = A_{dir,dir} + A_{dir,dif} + A_{dif} + A_{ref} \quad [29]$$

Fig. 2. Simulated and observed percent light interception at midday for 'Florunner' peanut canopies grown at Gainesville in (A) 46- and 91-cm row spacing in 1987 and (B) 61-cm row spacing in 1990. Plant population was 22.4 plants/m² for both row spacings in 1987, and 15 plants/m² in 1990.

Comparison to canopy light interception

Canopy light absorption (PFD_{abs}) is calculated in Eq. [29] as the sum of direct-beam PFD absorbed by sunlit leaves, direct beam converted to diffuse and absorbed by all LAI, skylight absorbed by sunlit and shaded leaves, and light reflected and absorbed from the soil. Canopy light interception (PFD_{in}) is the sum of the first three components above and also includes reflectance of direct and diffuse from the canopy (Eq. [26]). Predicted and observed light interception is illustrated in Fig. 2 for peanut canopies with different row spacings. This figure illustrates that the hedgerow approach will predict light interception correctly if the geometry is adequately described (canopy height and width over time had been calibrated to field measurements).

Allocation of diffuse PFD among LAI layers

The PFD absorbed by the sunlit and shaded classes of leaves is computed for leaves in three LAI layers (each layer is one-third of total LAI). The flux of diffuse PFD absorbed by leaves in a given stratum, $PFD_{shd(i)}$, is calculated from direct beam converted to diffuse within the canopy ($A_{dir,dif}$), absorbed skylight (A_{dif}), and diffuse reflected from the soil, applying Eqs. [14, 15, 16, 25, and 28] over one-third, two-thirds, and three-thirds of the total LAI, respectively, then using differences to calculate PFD absorbed per layer and per unit LAI in each layer. The average flux of PFD absorbed by the shaded leaves in a given stratum is $PFD_{shd(i)}$, whereas sunlit leaves additionally receive direct beam, $(1 - \sigma) \cdot K_d \cdot PFD_{dir}$, as shown in Eq. [30].

The need for layering diffuse-light absorption was documented by Reynolds et al. (1992) and is also supported by our comparison of model predictions to field data. We found canopy assimilation to be overpredicted 10% to 15% when nonlayered diffuse-light capture was used for high LAI canopies and when the Spitters' (1986) fraction

Table 1. Influence of number of canopy layers for diffuse-light absorption and the resulting effect on assimilation by sunlit leaves, shaded leaves, and the total canopy. Light-saturated photosynthesis rate (P_{max}) = 26 $\mu\text{mol CO}_2/\text{m}^2$ per sec and leaf area index = 5.

Layers (no.)	Assimilating leaves ($\mu\text{mol CO}_2/\text{m}^2$ per sec)			Deviation (%)
	Sunlit	Shaded	Total	
<i>Midday, PFD² = 1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 0.245 fraction diffuse</i>				
1	27.8	17.8	45.6	8.9
2	28.3	14.8	43.2	3.0
3	28.5	14.0	42.4	1.4
5	28.6	13.4	42.1	0.4
10	28.6	13.2	41.9	0
1 (SL/SH) ^y	29.2	11.4	40.6	-3.2
<i>Midday, PFD = 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 0.245 fraction diffuse</i>				
1	30.7	23.0	53.7	11.0
2	31.2	19.0	50.2	3.6
3	31.3	17.9	49.2	1.6
5	31.4	17.3	48.7	0.5
10	31.4	17.0	48.4	0
1 (SL/SH)	31.8	14.8	46.7	-3.7
<i>Midday, PFD = 1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 0.490 fraction diffuse</i>				
1	25.0	26.5	51.5	13.7
2	26.3	21.1	47.4	4.6
3	26.7	19.5	46.2	2.0
5	26.9	18.7	45.6	0.6
10	27.0	18.4	45.3	0
1 (SL/SH)	28.3	15.6	43.9	-3.0
<i>Midday, PFD = 2000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 0.490 fraction diffuse</i>				
1	28.4	33.6	62.0	16.6
2	29.5	26.4	55.9	5.2
3	29.8	24.6	54.3	2.2
5	29.9	23.6	53.5	0.7
10	30.0	23.2	53.2	0
1(SL/SH)	31.2	20.2	51.4	-3.3

^aPFD = photon flux density.

^bSL/SH assumes sunlit leaves over shaded leaves.

diffuse approach was followed. The overprediction was less pronounced on clear days and was minor in our earlier models in which we had arbitrarily limited the fraction of diffuse light and compared the models to data measured only on clear days (Boote et al., 1988, 1989). Reynolds et al. (1992) reported errors up to 15% when a single-layer model with one sunlit and one shaded leaf class was used, whereas a multilayer model with one sunlit and shaded leaf class per layer gave reasonable results. This finding indicates the need for layering LAI for diffuse-light absorption. We compared numbers of layers for diffuse-light absorption (Table 1) and concluded that a model with three to five layers is adequate. A single-layer model (with sunlit and shaded leaves) gives 9% to 11% overprediction when the fraction of diffuse is low (0.245), but gives larger errors of 14% to 17% if the fraction of diffuse is higher. An assumption of sunlit leaves physically above shaded leaves for diffuse-light absorption underestimates P_{can} by 3% to 4% compared to a 10-layer model. Ignoring sunlit and shaded leaf classes in each LAI layer and computing average PFD absorbed per unit LAI was a poor option, giving a 0% to 19% higher estimate of P_{can} than versions with sunlit and shaded leaf classes. These results concur with those of Reynolds et al. (1992), who reported that modeling approaches using average irradiance for all leaves within a layer invariably overestimated canopy assimilation. We conclude that canopy assimilation models must have layering for diffuse PFD absorption and must have sunlit vs. shaded leaf classes. In our approach, the multilayer strategy is valuable primarily for diffuse-light absorption, because the sunlit leaves, by definition, receive direct beam regardless of canopy position. Layering has a minor effect on total PFD absorbed by sunlit leaves because the diffuse PFD on sunlit leaves varies by layer.

Summation of canopy rate over sunlit and shaded leaves

Leaf photosynthesis is computed with single-leaf equations, described below, for sunlit and shaded leaf classes within each of three canopy layers ($i = 1$ to 3). Because using an average leaf projection

angle slightly overestimates leaf photosynthesis, we use a three-point Gaussian approach (Goudriaan, 1986) to integrate photosynthesis of sunlit leaves over the range of leaf angles expected. For simplification, we show only a constant leaf angle projection in Eq. [30]. This layering approach requires computing sunlit and shaded LAI within each stratum and then summing up assimilation over all layers (Eq. [33]). Using layers also allows using variation in $P_{\max(i)}$ with canopy depth.

$$PFD_{sl(i)} = PFD_{shd(i)} + (1 - \sigma) \cdot K_d \cdot PFD_{dir} \quad [30]$$

$$P_{sl(i)} = P_{\max(i)} \cdot \{1 - e^{[-Q_E \cdot PFD_{sl(i)} / P_{\max(i)}]}\} \quad [31]$$

$$P_{shd(i)} = P_{\max(i)} \cdot \{1 - e^{[-Q_E \cdot PFD_{shd(i)} / P_{\max(i)}]}\} \quad [32]$$

$$P_{can} = \sum_{i=1}^3 [P_{sun(i)} \cdot LAI_{sun(i)} + P_{shd(i)} \cdot LAI_{shd(i)}] \quad [33]$$

Use of class divisions to reduce aggregation error

One cannot merely compute leaf photosynthesis rate at the average leaf PFD and then multiply by the total LAI to obtain P_{can} . This approach does not work because the photosynthetic light response is nonlinear and most leaves are either at higher or lower PFD. Light penetration into the crop canopy is nonlinear with canopy depth and time of day. Rastetter et al. (1992) described this as the "fallacy of the averages" (from Wagner, 1969) and illustrated the problem nicely and discussed ways to reduce aggregation error in predicting canopy photosynthesis. We approach the nonlinear integration (aggregation) from leaf-to-canopy photosynthesis in several ways: sunlit vs. shaded leaf classes, leaf angle classes, canopy layers, and hourly computations within the day. In our opinion, the sunlit and shaded leaf classes (and time of day) are the most important aggregation techniques, while leaf-angle classes are the least important. Canopy layers are useful for diffuse-light absorption and allowing $P_{\max}$ to vary with depth. In the terminology of Rastetter et al. (1992), we have primarily partitioned the fine-scale components into relatively homogeneous subaggregates with respect to PFD and $P_{\max}$. We discussed the relative importance of these techniques for minimizing aggregation error in the previous section on allocation of diffuse PFD among LAI layers and in a subsequent section on variation in $P_{\max}$, specific leaf weight (SLW), and N concentration with LAI depth.

LEAF PHOTOSYNTHESIS EQUATIONS USED IN THE HEDGEROW MODEL

Equations for light response

A common equation used for single-leaf photosynthesis response to light is the nonrectangular hyperbola given below, including parameters, $P_{\max}$, Q_E , and a curvature factor (Θ):

$$P = \{Q_E \cdot PFD + P_{\max} - \sqrt{[(Q_E \cdot PFD + P_{\max})^2 - 4\Theta \cdot Q_E \cdot PFD \cdot P_{\max}]}\} / (2\Theta) \quad [34]$$

Johnson and Thornley (1984) reviewed the use of the nonrectangular hyperbola for predicting photosynthetic response to PFD. When $\Theta = 0$, the equation becomes a rectangular hyperbola (Michaelis-Menten equation). With $\Theta = 1.0$, the equation is a Blackman response of two intersecting straight lines. The asymptotic exponential equation (Eq. [5]) is similar to, but not exactly the same as, a nonrectangular hyperbola having a Θ of ≈ 0.7 . Most evidence suggests that the asymptotic exponential or a nonrectangular hyperbola with $\Theta = 0.7$ to 0.9 provides a better fit than the Michaelis-Menten equation (Marshall and Biscoe, 1980; Peat, 1970). Evans and Farquhar (1991) used $\Theta = 0.7$ to describe electron transport or photosynthesis response to PFD. The above equations are defined by initial slope, Q_E , and the asymptote ($P_{\max}$ at light saturation). Thus, it would be convenient if we could define environmental effects on Q_E and $P_{\max}$.

Incorporating leaf photosynthesis response to CO₂ and temperature

The Farquhar and von Caemmerer (1982) approach is commonly

used to predict leaf photosynthetic response to C_i . In their model, leaf CO₂ assimilation rate takes the minimum of two equations: 1) rubisco-limiting equation (primarily at low C_i , where CO₂ assimilation responds almost linearly to increasing C_i and rate is limited by rubisco activity), and 2) RuBP-limiting equation (at ambient to superambient C_i , where assimilation responds less rapidly to increasing C_i because rate is limited by electron transport). We use an adaptation based only on the RuBP-limiting equations for several reasons. First, the transition to the RuBP-limiting region begins near ambient CO₂ and continues to higher CO₂ levels. We are primarily interested in predictions only at and above ambient CO₂. Second, assimilation in crop canopies is limited by light availability during much of the day, and lower parts of the crop canopy are light-limited all the time; thus, the RuBP-limiting equations apply more often. Last, our approach eliminates the need for independent estimates of the rubisco's maximum rate and its Michaelis constants.

In our hedgerow canopy photosynthesis model, we predict Q_E as a function of CO₂, O₂, and temperature, while $P_{\max}$ is modeled as a function of CO₂, O₂, temperature, SLW, and N concentration. In our approach, CO₂, O₂, and temperature effects on Q_E and $P_{\max}$ follow the approach of Farquhar and von Caemmerer (1982), assuming that RuBP is limiting; this includes the temperature effects on specificity factor (τ) and CO₂ compensation point (Γ^*) in absence of mitochondrial respiration.

Under limiting low light, where Q_E is defined, the Farquhar and von Caemmerer (1982) equations, assuming electron transport is limiting, approach the limit of

$$Q_E = \frac{(C_i - \Gamma^*)}{4C_i + 8\Gamma^*} \cdot \frac{1}{2.1} \quad [35]$$

where the latter part of the equation (1/2.1) represents 1 electron per 2.1 photons, and the first part of the equation is the efficiency of using electrons to fix and reduce CO₂. This limiting equation for Q_E is equation 16.63 of Farquhar and von Caemmerer (1982), assuming electron transport is limiting. At light saturation, the same equation holds for efficiency of using electrons for CO₂ assimilation:

$$Q_E = \frac{(C_i - \Gamma^*)}{4C_i + 8\Gamma^*} \cdot \frac{1}{QR_{sat}} \quad [36]$$

Fewer electrons, however, are produced per photon absorbed (1/QR_{sat}). In a practical sense, 1/QR_{sat} is related to the light-saturated rate of electron transport, $J_{\max}$.

Equations [35] and [36] essentially describe the efficiency of electron use for CO₂ fixation, from zero to saturating PFD. To calculate the effect of CO₂ and temperature on Q_E , we use Eq. [35] with a scalar of 6.225 to compute a relative effect, CO₂ Q_E (1.0 at 30C and 350 ppm). CO₂ Q_E is then multiplied by 0.0541 (mol CO₂ fixed/mol PFD), which is the Q_E (adjusted from 0.0524 at 325 ppm CO₂) from observations on many C₃ species (Ehleringer and Björkman, 1977; Ehleringer and Pearcy, 1983).

$$CO_2Q_E = 6.225 \cdot \frac{(C_i - \Gamma^*)}{4C_i + 8\Gamma^*} \quad [37]$$

$$Q_E = 0.0541 \cdot CO_2Q_E \quad [38]$$

To compute Γ^* and C_i , we need to know τ , the specificity factor of rubisco for CO₂ vs. O₂. Harley and Tenhunen (1991) used the following exponential energy of activation equation to describe the response of τ to temperature based on data of Jordan and Ogren (1984):

$$\tau = \exp \{-3.9489 + 28990/[8.31 (TEMP + 273)]\} \quad [39]$$

The τ value decreases and Γ^* increases similarly with temperature for most C₃ species (Brooks and Farquhar, 1985; Jordan and Ogren, 1984). Then Γ^* can be computed as a function of O₂ concentration (0.21 mol·mol⁻¹) and τ :

$$\Gamma^* = 1000000 \cdot 0.5 \cdot 0.21/\tau \quad [40]$$

Fig. 3. Predicted quantum efficiency (Q_E) at CO_2 concentration of 350 and 700 ppm as affected by temperature. Point represents reference Q_E of 0.0541 at 350 ppm CO_2 based on Ehleringer and Björkman (1977).

Fig. 4. Predicted quantum efficiency (Q_E) at 30°C as affected by CO_2 concentration.

Fig. 5. Relative rate of electron transport ($E_{\max}$) vs. temperature. $J_{\max}$ and $V_{c\max}$ are electron transport and rubisco rate from Harley et al. (1985). All responses are normalized to 1.0 at 30°C.

Equation [36] is used to describe C_i and temperature effects on the relative efficiency of CO_2 fixation ($\text{CO}_{2\max}$) in saturating light (at $P_{\max}$) as follows:

$$\text{CO}_{2\max} = 7.179 \cdot \frac{(C_i - \Gamma^*)}{(4C_i + 8\Gamma^*)} \quad [41]$$

Equation [41] is scaled to a relative effect of 1.0 at 30°C and 350 ppm CO_2 . This requires $P_{\max}$ input to the model to be described as CO_2 fixation rate measured at saturating PFD, 30°C, 350 ppm CO_2 , and 21% O_2 .

Fig. 6. Leaf photosynthesis response to intercellular CO_2 (C_i) with and without CO_2 -substrate limitations on electron transport. Simulated at 30°C and a photon flux density of $1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ using light-saturated photosynthesis rate ($P_{\max}$) = $28 \mu\text{mol CO}_2/\text{m}^2$ per sec. Harley equation was parameterized as described by Harley et al. (1985).

At the light compensation point, C_i is assumed equal to C_a . In contrast, at high PFD, C_i is computed with the following equation, where the ratio of 0.7 is the rate of change of C_i with respect to C_a , which has held over a wide range of environmental conditions for many C_3 species (Morison, 1987).

$$C_i = 0.7C_a + 0.3\Gamma^* \quad [42]$$

The Q_E response to temperature and CO_2 , based on Eqs. [35–40], is shown in Figs. 3 and 4. The responses closely mimic the sensitivity of Q_E to temperature and CO_2 reported for C_3 species by Ehleringer and Björkman (1977). The shape of $\text{CO}_{2\max}$ vs. temperature and CO_2 is very similar, but is normalized to 1.0 at 30°C and 350 ppm CO_2 .

Effect of temperature on $J_{\max}$

The $\text{CO}_{2\max}$ equation essentially describes the relative efficiency of converting electrons to CO_2 fixed at high light intensity as influenced by C_i , O_2 , and temperature, but does not address temperature effects on electron transport itself. Temperature effects on light-saturated, CO_2 -saturated leaf photosynthesis of soybean have been described with energy of activation–deactivation equations by Harley et al. (1985) and Harley and Tenhunen (1991). Since responses obtained by Harley et al. (1985) for soybean and by Tenhunen et al. (1976) for common bean (*Phaseolus vulgaris* L.) were almost linear and there were no data below 15°C, we used a straight line function, shown in Fig. 5, for increasing electron transport between 8 and 40°C, scaled to a relative value of 1.0 at 30°C (Pickering et al., 1995). Exponentially increasing heat damage to photosystem II is assumed, which reduces the rate 1.5% at 36°C, 6% at 40°C, 25% at 44°C, and 100% (to zero) at 48°C. Figure 5 compares our combined function to that of Harley et al. (1985).

Effect of CO_2 on electron transport

If electron acceptors become limiting, as when CO_2 declines below ambient, then electron transport is decreased because of inadequate CO_2 or O_2 to be fixed. Electron transport of *P. vulgaris* in high light flux (PFD > $380 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was reported to decrease as C_i fell below 300 ppm CO_2 , but there was no C_i effect at a PFD of $175 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Sharkey et al., 1988). The authors explained this as the regulation of electron transport to match the rate of rubisco activity at low C_i in the presence of high PFD. The excess energy was lost as chlorophyll fluorescence. Applying RuBP-limited equations to data on rice (*Oryza sativa* L.) canopy assimilation at 160 to 900 ppm CO_2 and solving for $P_{\max}$ showed that $P_{\max}$ declined as C_a dropped below 330 or 500 ppm (Boote et al., 1992).

To address this problem, we added an asymptotic equation [$1 - e(-z^*C_i)$] that decreases $P_{\max}$ as a function of C_i . This term describes substrate limitation for electron transport–RuBP generation. The 50% response

level was reached between $C_i = 83$ to 137 ppm for rice. This function accounts for the effects of the rubisco-limited phase in a simple way that is normalized to the original P_{max} term. As illustrated in Fig. 6, this causes a sharper transition in response to CO_2 than our original function, but gives an A : C_i curve that is more similar to the Farquhar and von Caemmerer approach [as parameterized by Harley et al. (1985)].

Leaf and canopy photosynthesis response to temperature

Leaf response to temperature. Despite a linear effect of temperature on J_{max} , leaf photosynthesis response to temperature shows a curvilinear trend with a broad optimum, even at high CO_2 and a PFD of $1500 \mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 7A). At ambient CO_2 (350 ppm), the response becomes flatter, with broad optimum between 32 and 40C. The leaf P response to CO_2 increases with temperature.

Canopy response to temperature. Simulated instantaneous canopy photosynthesis is illustrated in Fig. 7B for a closed canopy at solar noon (LAI = 5.0, PFD = $1500 \mu mol \cdot m^{-2} \cdot s^{-1}$ on 1 July at lat. 30°N). Note that the optimum temperature for photosynthesis is quite broad, between 25 to 37C at 350 ppm CO_2 , but the optimum temperature increases as CO_2 concentration increases. The broad temperature optimum for P_{can} at ambient CO_2 is caused by two features: 1) in a canopy, many leaves operate at low light flux, which increases the effect of Q_E , and 2) leaf photosynthesis depends on temperature functions that influence Q_E and P_{max} , and these two temperature functions operate in opposite directions. Using similar modeling approaches, Long (1991) also found broad optimums for daily P_{can} that shifted up several degrees with CO_2 enrichment. The broad temperature optimum for P_{can} is consistent with field data showing little variation on crop growth rates despite variation in air temperature. It

is also supported by measurements in sunlit controlled-environment chambers, which showed no difference in P_{can} for rice at air temperatures of 25 to 37C (Baker and Allen, 1993) and for soybean at 28 to 35C (Jones et al., 1985a). The present model assumes that leaf temperature is equal to air temperature. When the model is used with canopy energy balance and stomatal sensitivity to CO_2 and foliage temperature is predicted (Pickering et al., 1990, 1995), the optimum air temperature range becomes even broader because leaf temperature tends to be above air temperature if air temperature is low, and leaf temperature tends to be below air if air temperature is high.

Leaf and canopy photosynthesis response to CO_2

Leaf response to CO_2 . Figure 8A illustrates leaf photosynthesis response to CO_2 for leaves at 10, 20, 30, and 40C, where the equations include the CO_2 effect on electron transport as described above. Photosynthetic response to CO_2 increases with temperature. These equations reproduce the well-known increase in CO_2 compensation point as temperature increases.

Canopy response to CO_2 . The simulated P_{can} response to CO_2 in Fig. 8B shows that the response to CO_2 depends on temperature and is limited at low temperature. The simulated P_{can} at 30C increased 35% as CO_2 increased from 330 to 660 ppm. This compares to measured increases in P_{can} of 35% to 40% for rice (Baker et al., 1992, Boote et al., 1992) and 50% to 60% for soybean exposed to 660 vs. 330 ppm CO_2 at 31C (Campbell et al., 1990). Jones et al. (1985b) observed that midday P_{can} of soybean measured at 800 ppm CO_2 was 75% greater than the same canopy measured at 330 ppm CO_2 (both at 31C). Predicted response for that comparison was a 42% increase. The predicted canopy responses to CO_2 in these chambers appear to be somewhat less than those observed.

Fig. 7. (A) Leaf photosynthesis and (B) gross canopy assimilation (P_{can}) response to leaf temperature at three CO_2 concentrations. Response simulated for leaf area index = 5.0, closed canopy, at a photon flux density of $1500 \mu mol \cdot m^{-2} \cdot s^{-1}$, at solar noon on 1 July at lat. 30°N, assuming fraction diffuse of 0.49. Light-saturated photosynthesis rate (P_{max}) = $26 \mu mol CO_2 / m^2$ per sec at 350 ppm CO_2 and 30C.

Fig. 8. (A) Leaf photosynthesis and (B) gross canopy assimilation response to CO_2 at four temperatures. Response simulated for leaf area index = 5.0, closed canopy, at a photon flux density of $1500 \mu mol \cdot m^{-2} \cdot s^{-1}$, at solar noon on 1 July at lat. 30°N, assuming fraction diffuse of 0.49. Light-saturated photosynthesis rate (P_{max}) = $26 \mu mol CO_2 / m^2$ per sec at 350 ppm CO_2 and 30C.

$P_{\max}$ as influenced by leaf N status and growth environment

Under normal conditions, $P_{\max}$, $J_{\max}$, and maximum RuBP carboxylase activity ($V_{\max}$) on a leaf-area basis are reasonably well correlated to each other and are proportional to N concentration, N content per unit area, chlorophyll concentration, and leaf thickness (Field, 1983; Harley et al., 1992; Seemann et al., 1987). Evans and Farquhar (1991) proposed that $J_{\max}$ and $P_{\max}$ are proportional to the chlorophyll and N content per unit leaf area because these variables reflect the amount of photosynthetic apparatus per unit leaf area. Also, within a species, the amount of rubisco per unit leaf area is proportional to the amount of leaf N per unit leaf area. Sinclair and Horie (1989) proposed that $P_{\max}$ strongly depends on specific leaf N content (SLN).

Effects of growth environment (climate, nutrition, and CO_2) are expressed at the morphological and biochemical level, e.g., SLW, N concentration of leaf tissue, and the amount of chlorophyll, thylakoid membranes, and rubisco per unit leaf area. Second-order environmental effects also occur. The portion of N in rubisco decreased under N deficiency and as irradiance declined (Seemann et al., 1987). Decline in total N per unit leaf mass and decline in rubisco per unit leaf area have been reported in response to increasing CO_2 (Harley et al., 1992; Rowland-Bamford et al., 1991). Furthermore, Harley et al. (1992) observed a decline in the ratio of protein allocated to rubisco as CO_2 increased.

In our modeling approach, $P_{\max}$ (at standard 30C, 350 ppm CO_2 , and optimum N concentration) is allowed to be a linear function of SLW, based on the data of Dornhoff and Shibles (1970), adjusted to 350 ppm CO_2 , and assuming a zero intercept (zero $P_{\max}$ at zero SLW, and a CO_2 uptake slope of $0.65 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ per gram leaf mass). $P_{\max}$ is reduced

if N concentration is not at optimum concentration (Fig. 9) (K.J. Boote, unpublished data).

Variation in $P_{\max}$, SLW, and N concentration with LAI depth

SLW and leaf N concentration vary with depth in the crop canopy and, in turn, influence $P_{\max}$ variation with depth in the canopy. Modeling vertical distribution in leaf photosynthetic characteristics is important for canopy assimilation models (Reynolds et al., 1992). Optimization analysis has shown higher P_{can} for closed crop canopies that have higher SLN (and $P_{\max}$) for upper leaf layers at the cost of lower SLN and lower $P_{\max}$ for lower leaf layers (Field, 1983; Hirose and Werger, 1987). Interestingly, crop canopies already tend toward an optimum distribution of SLN and SLW. Shiraiwa and Sinclair (1993) reported that SLN of soybean foliage declined linearly with increasing LAI depth, the slope ranging from 0.19 to 0.29 ($\text{g N}/\text{m}^2$ per unit LAI). Using a similar approach, we model decline in SLW and N concentration, each as linear functions of LAI depth. In our simulation examples, SLW declines $3.6 \text{ g}\cdot\text{m}^{-2}$ and N concentration declines $3.0 \text{ g}\cdot\text{kg}^{-1}$ per unit LAI depth increment. As a result of both features, we obtain variation in $P_{\max}$ with LAI depth. For simulation purposes, standard light-saturated $P_{\max}$ is defined at 30C and 350 ppm CO_2 and at a defined SLW ($40 \text{ g}\cdot\text{m}^{-2}$) and N concentration ($52 \text{ g}\cdot\text{kg}^{-1}$) for soybean. These values are typical for upper soybean leaves and correspond to the calculated values for the upper third of the LAI of a soybean canopy (LAI = 5.0) when average SLW = $34 \text{ g}\cdot\text{m}^{-2}$, average N concentration = $47 \text{ g}\cdot\text{kg}^{-1}$, and SLW and N decline with LAI depth as described above.

For the subsequent simulation examples, the input $P_{\max}$ is assumed to apply to the upper one-third of the LAI, and $P_{\max}$ of lower layers declines with LAI depth according to the functions described. In our crop model, canopy average SLW and N concentration are state variables and are used to compute SLW and N of the LAI layers. Layering SLW and N concentration increases P_{can} by 3% to 8% over an unlayered, uniform canopy that uses canopy average $P_{\max}$, SLW, and N (Table 2). Researchers generally measure $P_{\max}$ only for upper, sunlit leaves, which have greater SLW and higher N concentration than the canopy average. These upper leaves are the most relevant ones to measure because upper sunlit leaves receive most of the PFD and generate over half of the canopy CO_2 assimilation. Using an input of $P_{\max}$ for upper leaves and applying it to all LAI depths resulted in only a 1% to 4% overestimate of P_{can} . This result could be an argument that vertical gradient in $P_{\max}$ is not really necessary, provided the input is upper-leaf $P_{\max}$. Definitions of variables and abbreviations are provided in Table 3.

Fig. 9. Relative light-saturated photosynthesis rate ($P_{\max}$) response to leaf N concentration.

Evaluating the hedgerow photosynthesis model

Light interception and photosynthesis vs. time of day for closed and incomplete canopies. Crop canopies that are not closed are less able to respond to the high PFD at solar noon when the sun is directly

Table 2. Influence of vertical gradient in light-saturated photosynthesis rate ($P_{\max}$) upon canopy assimilation response to photon flux density (PFD). The conditions are leaf area index (LAI) = 5.0, canopy average specific leaf weight (SLW) = $34 \text{ g}\cdot\text{m}^{-2}$, and N concentration = $47 \text{ g}\cdot\text{kg}^{-1}$. The gradients in SLW and N concentration are $3.6 \text{ g}\cdot\text{m}^{-2}$ and $3.0 \text{ g}\cdot\text{kg}^{-1}$ per unit LAI depth increment. For a three-layer canopy, $P_{\max}$ of the upper one-third of LAI is $26 \mu\text{mol CO}_2/\text{m}^2$ per sec defined at SLW = $40 \text{ g}\cdot\text{m}^{-2}$ and N concentration = $52 \text{ g}\cdot\text{kg}^{-1}$. The comparison is made with canopies where all leaves are like upper leaves ($P_{\max} = 26$) vs. canopies where all leaves are like average leaves ($P_{\max} = 21$).

PFD ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Assimilation example ($\mu\text{mol CO}_2/\text{m}^2$ per sec)			Loss if lower leaf $P_{\text{max}} < \text{upper}$ (%)	Benefit from layering vs. avg (%)
	All like upper ($P_{\text{max}} = 26$)	Layered canopy f(SLW, N)	All like avg ($P_{\text{max}} = 21$)		
		0.245 fraction diffuse			
500	20.1	19.8	19.2	1.4	3.2
1000	33.3	32.5	30.8	2.5	5.5
1500	42.5	41.1	38.4	3.2	7.0
2000	49.2	47.4	43.9	3.7	7.9
		0.490 fraction diffuse			
500	20.8	20.6	20.0	0.9	3.0
1000	35.5	34.9	33.1	1.7	5.2
1500	46.2	45.1	42.3	2.4	6.7
2000	54.3	52.7	48.9	3.0	7.7

overhead, and a fraction of the PFD is lost directly to the soil. Figures 10 and 11 illustrate how incomplete peanut canopies (92-cm row spacing) intercepted a smaller fraction of the PFD toward midday and tended to light-saturate at a lower PFD than the closed canopies (46-cm row spacing). As the canopy grew wider and increased in LAI, a greater fraction of PFD was intercepted. The diurnal time course of percent light interception (Fig. 10, top) and P_{can} (Fig. 10, center) are reasonably predicted for the different times of day and treatments. Despite a constant number of plants per square meter in both row spacings, there were persistent row-spacing effects on light interception and P_{can} until the widely spaced crop canopy closed at or about 29 July (57 days after planting). The Spitters (1986) function for PFD distribution (Fig. 10, bottom) adequately describes actual PFD mea-

Fig. 10. (A) Light interception, (B) gross canopy assimilation, and (C) photon flux density (PFD) on 1 and 29 July 1987 for peanut canopies in 46- and 92-cm row spacing as the crop canopy closed. Canopy assimilation was simulated for actual experimental conditions [leaf area index, canopy width and height, and light-saturated photosynthesis rate (P_{max}) measured on sunlit leaves], but using instantaneous PFD from the Spitters function, given a PFD of $58 \text{ mol}\cdot\text{day}^{-1}$ as input. Solid line for modeled PFD (bottom) is for 1 July. Points represent observed light interception, gross canopy assimilation (P_{can}), and PFD.

surements, although it is a bit high near dawn or sunset and a bit low at midday. The alternative full-sine function of Charles-Edwards and Acock (1977) would underpredict near dawn and overpredict at midday. Because P_{can} and PFD point measurements were manually taken only for clear sunny conditions, the points are compared to a line predicted for a clear day in July with high daily PFD ($58 \text{ mol}\cdot\text{m}^{-2}$) and minimum cloud cover.

Assimilation response to PFD at various degrees of canopy closure. Data for the above measurement dates are plotted in Fig. 11 as P_{can} vs. PFD. As expected, the incomplete canopies on 1 July were less able to respond to high PFD, whereas the closed canopies on 29 July increased P_{can} to the highest PFD value. The early season row spacing effects on P_{can} nearly disappeared with canopy closure. These results show that the hedgerow model will successfully predict canopy assimilation response to PFD for different row spacings, canopy widths, LAIs, times of day, and temperatures, based on only one input (P_{max} measured on upper leaves). We conclude that P_{can} can be predicted from single-leaf P_{max} . Actually, measured peanut P_{max} was quite repeatable over seven successive dates in this study and over much of the season in data of Bennett et al. (1993), thus one P_{max} value could have been used with only a small loss in accuracy.

Daily assimilation response to LAI at various degrees of canopy closure. Figure 12 illustrates the importance of degree of canopy closure on daily assimilation. With 80% apparent ground cover [width : row spacing ($W : R$) = 0.8], there is only a small reduction (4.2%) in P_{can} even at high LAI. With progressively smaller canopy width (ratio

Fig. 11. Gross canopy assimilation (P_{can}) response to photon flux density (PFD) on 1 and 29 July 1987 for peanut in 46- and 92-cm row spacings. P_{can} was simulated for actual experimental conditions [leaf area index, canopy width and height, time of day, instantaneous PFD, and light-saturated photosynthesis rate (P_{max}) measured on sunlit leaves].

Fig. 12. Daily canopy assimilation vs. leaf area index at five degrees of canopy closure (W/R = canopy width/row spacing). Simulated at 30°C , $\text{CO}_2 = 350 \text{ ppm}$, light-saturated photosynthesis rate (P_{max}) = $26 \mu\text{mol CO}_2/\text{m}^2$ per sec, photon flux density = $45 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, in east-west rows, at lat. 30°N , on 1 July.

Table 3. Definition of variables, symbols, and abbreviations used. Fluxes and rates are per square meter of land area, unless clearly stated as per unit leaf area.

Symbol/ abbreviation	Definition
A_{ref}	Photosynthetic photon flux density (PPFD) reflected from soil that is absorbed by canopy, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
A_{dif}	Diffuse skylight that is absorbed by canopy, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$A_{dir,dif}$	Component of direct-beam PFD that strikes sunlit leaves but is scattered (becomes diffuse) and is absorbed by all leaf area of canopy, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$A_{dir,dir}$	Component of direct-beam PFD that strikes sunlit leaves and is absorbed by sunlit leaves only, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$A_{dir,tot}$	Total direct-beam PFD that strikes sunlit leaves, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
β	Solar elevation angle from horizontal, degrees
C_a	Ambient CO_2 concentration, $\mu\text{mol CO}_2/\text{mol}$
C_i	Leaf intercellular CO_2 concentration, $\mu\text{mol CO}_2/\text{mol}$
CO_2	Carbon dioxide, usually meaning concentration, $\mu\text{mol CO}_2/\text{mol}$
CO_{2max}	Relative effect of CO_2 , O_2 , and temperature on efficiency of electron use for CO_2 fixation at light saturation, normalized to 1.0 at 350 $\mu\text{mol CO}_2/\text{mol}$, 0.21 $\text{mol O}_2/\text{mol}$, and 30C
CO_2QE	Relative effect of CO_2 , O_2 , and temperature on quantum efficiency, normalized to 1.0 at 350 $\mu\text{mol CO}_2/\text{mol}$, 0.21 $\text{mol O}_2/\text{mol}$, and 30C
E_{max}	Relative rate of light-saturated electron transport
f_p	Effective fraction of soil surface shaded from diffuse PFD by plants within the hedgerow in direction parallel to the row, when plant width is less than plant spacing in the row
f_r	Effective fraction of soil surface shaded from diffuse component of PFD by hedgerow in direction perpendicular to the row, when plant width is less than row spacing
f_{sh}	Fraction of the soil surface shaded from direct-beam PFD by plant canopy at least once
G	Gap between plants in the row (S-W), or alley between hedgerows (R-W), meter
Γ^*	CO_2 compensation point in absence of mitochondrial respiration, $\mu\text{mol CO}_2/\text{mol}$
H	Plant height to top of canopy envelope, meter
I_i	Average PFD reaching the surface of a leaf and absorbed for photosynthesis at any leaf area index depth in the canopy, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
I_o	PFD incident on a horizontal plane above the canopy, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
J_{max}	Light-saturated rate of electron transport, $\mu\text{mol electrons}/\text{m}^2$ leaf area per sec
K_d	Direct-beam extinction coefficient (ratio of horizontally projected shadow area per unit land area per unit leaf area)
K_{dif}	Extinction coefficient for diffuse component of PFD
LAI	Leaf area index, m^2 leaf area/ m^2 ground area
LAI_{shd}	LAI that is not sunlit, m^2 leaf area/ m^2 ground area
LAI_{sun}	Sunlit LAI, m^2 leaf area/ m^2 ground area
$\text{LAI}_{shd(i)}$	Amount of shaded LAI in canopy layer i , m^2 leaf area/ m^2 ground area
$\text{LAI}_{sun(i)}$	Amount of sunlit LAI in canopy layer i , m^2 leaf area/ m^2 ground area
O_2	Oxygen concentration, $\text{mol}\cdot\text{mol}^{-1}$
P	Leaf photosynthesis rate, $\mu\text{mol CO}_2/\text{m}^2$ per sec
P_{can}	Gross canopy assimilation rate, $\mu\text{mol CO}_2/\text{m}^2$ ground area per sec
PFD	Incident total photosynthetic photon flux density, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
PFD_{abs}	Total PFD absorbed by canopy, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
PFD_{dif}	Diffuse component of total incident PFD, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
PFD_{dir}	Direct component of total incident PFD, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
PFD_{int}	PFD intercepted by canopy, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
PFD_{shd}	PFD absorbed per unit shaded leaf area, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
PFD_{sun}	PFD absorbed per unit sunlit leaf area, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$\text{PFD}_{shd(i)}$	(Diffuse) PFD absorbed per unit shaded leaf area for canopy layer i , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$\text{PFD}_{sl(i)}$	PFD absorbed per unit sunlit leaf area for canopy layer i (sum of direct and diffuse PFD absorbed), $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
PFD_{soil}	PFD incident per unit soil surface area, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
P_{max}	Light-saturated leaf photosynthesis rate, $\mu\text{mol CO}_2/\text{m}^2$ per sec
$P_{max(i)}$	Light-saturated leaf photosynthesis rate for leaves in canopy layer i , $\mu\text{mol CO}_2/\text{m}^2$ per sec
ppm	Parts per million by volume, for CO_2 concentration, $\mu\text{mol CO}_2/\text{mol}$
P_{shd}	Assimilation rate per unit shaded leaf area, $\mu\text{mol CO}_2/\text{m}^2$ per sec
P_{sun}	Assimilation rate per unit sunlit leaf area, $\mu\text{mol CO}_2/\text{m}^2$ per sec
$P_{shd(i)}$	Assimilation rate per unit shaded leaf area for shaded leaves in canopy layer i , $\mu\text{mol CO}_2/\text{m}^2$ per sec
$P_{sun(i)}$	Assimilation rate per unit sunlit leaf area for sunlit leaves in canopy layer i , $\mu\text{mol CO}_2/\text{m}^2$ per sec
Q_E	Quantum efficiency, $\text{mol}\cdot\text{mol}^{-1}$
$Q_{R_{sat}}$	Photons absorbed per electron transported at light saturation, $\text{mol}\cdot\text{mol}^{-1}$
R	Row spacing, meters
RuBP	Ribulose 1,5-bisphosphate, usually meaning concentration, μmol
σ	Leaf scattering coefficient for PFD, fraction
δ_{dif}	Reflectance of diffuse component of PFD from the canopy to the sky, fraction
δ_{dir}	Reflectance of direct component of PFD from the canopy to the sky, fraction
δ_{soil}	Reflectance of direct component of PFD from the soil, fraction
S	Spacing between plants in the row, meters
SLN	Specific leaf nitrogen, $\text{g}\cdot\text{m}^{-2}$
SLW	Specific leaf weight, $\text{g}\cdot\text{m}^{-2}$
τ	Specificity factor of RuBP carboxylase-oxygenase for CO_2 vs. O_2 , ratio
Θ	Curvature factor for nonrectangular hyperbola equation describing photosynthetic response to PFD, dimensionless
V_{cmax}	Maximum RuBP carboxylase activity, $\mu\text{mol CO}_2/\text{m}^2$ per sec
W	Plant width, apparent envelope width at widest dimension, meters

from 0.8 to 0.2), P_{can} is progressively reduced. A nonhedgerow model would follow the line for $W : R = 1.0$ and would be in error by the difference between that line and the line for the given $W : R$ ratio. Figure 12 probably gives an overly optimistic impression of photosynthesis at incomplete cover, because it assumes that hedgerows with low $W : R$ ratio can achieve the same land-area LAI as a closed canopy.

The latter is not likely; thus, the reduction in P_{can} will be somewhat more than represented in Fig. 12.

Response to row spacing. Figure 13 illustrates response of daily assimilation to variation in row spacing while holding a constant LAI (solid line) or leaf area (LA) per unit of canopy width (long dash line). In conjunction with the crop model, the hedgerow photosynthesis

Fig. 13. Daily canopy assimilation vs. row spacing for a crop canopy 0.5 m tall and 0.5 m wide. Gross canopy assimilation (P_{can}) is expressed 1) per unit of canopy width (per row basis) for constant LAI of 5 per unit canopy width (-----), 2) on a land-area basis with constant land-area-based leaf area index (LAI) of 5 (—), or 3) on land-area basis with constant LAI of 5 per unit canopy width (---). Simulated under same conditions as Fig. 12.

approach creates a somewhat more gradual decline in yield at the row spacing, where the canopy just begins to close. The curve labeled "PG / row basis" is the P_{can} per row where the LA is held constant at 5 per unit of canopy width. Constant LA per unit canopy width is probably the more realistic example, because the situation of a constant land-area LAI of 5 in a 5-m spacing would, for example, force a LA of 50 within the canopy envelope of 0.5 m. The upper line of Fig. 13 also illustrates the maximum P_{can} possible for a 0.5-m-tall $\times$ 0.5-m-wide canopy with no competition. In this case, lack of a border or competition effects increased P_{can} by 77%.

SUMMARY OF HEDGEROW MODEL FEATURES

The proposed hedgerow canopy photosynthesis approach offers the needed ability to model assimilation of incomplete canopies, yet allows use of leaf-level photosynthesis equations that mimic rubisco kinetics. Predicted leaf and P_{can} responses to CO_2 were reasonable, but predicted response at subambient CO_2 was improved by allowing electron transport to be limited as a function of C_i . Single-leaf P_{max}/J_{max} was modeled as a linear function of SLW and as a quadratic function of leaf N concentration. As expected, predicted canopy assimilation response to PFD was limited by incomplete canopies, even at high land-area-based LAI. Canopy assimilation, parameterized for soybean at 350 ppm CO_2 , showed a broad temperature optimum between 25 and 37°C, even though leaf P_{max} has a more pronounced peak between 32 to 40°C.

The sunlit and shaded LAI photosynthesis approach appears to be adaptable to the hedgerow model, provided diffuse-light absorption is handled in a multilayered manner. The sunlit and shaded LAI approach is simpler and less demanding of computer time than the mechanistic hedgerow photosynthesis model of Gijzen and Goudriaan (1989), which uses a ray-tracing approach and LAI layering. We conclude that canopy assimilation models must have layering for diffuse PFD absorption and must have sunlit and shaded leaf classes. Stockle (1992) and Reynolds et al. (1992) compared multilayered canopy photosynthesis models to a single-layer model and proposed that, in many instances, a single-layer model divided into sunlit and shaded LAI fractions yielded reasonable results with <5% error. Their results support the sunlit and shaded LAI approach we have taken. Reynolds et al. (1992) confirmed the importance of including leaf energy balance and distinguishing between sunlit and shaded leaves. They provided evidence that a multilayered approach is best. We agree with this need, particularly for diffuse-light absorption. We conclude that the problem with the single-layer models is primarily related to diffuse-light absorption. We also agree with Reynolds et al. (1992) that leaf energy balance is needed. Including an energy balance actually makes the predicted air temperature optimum for photosynthesis even broader in most cases.

Application to horticultural crops. Horticultural commodities are probably grown more often in hedgerow or limited plant spacing than field crops. There are a number of application examples for using such a hedgerow photosynthesis model: 1) predicting optimum spacing for fruit and nut tree crops; 2) predicting yield effects of various hedgerow arrangements for trellised vineyards, staked tomatoes, or dwarfed dense hedgerow apples; 3) evaluating productivity of sweet corn (*Zea mays* L.), beans, and potatoes (*Solanum tuberosum* L.) grown in rows; and 4) evaluating productivity of single plants in response to various spacings in the field and greenhouse.

Literature Cited

- Acocck, B., D.A. Charles-Edwards, D.J. Fitter, D.W. Hand, L.J. Ludwig, J. Warren Wilson, and A.C. Withers. 1978. The contribution of leaves from different levels within a tomato crop to canopy net photosynthesis: An experimental examination of two canopy models. *J. Expt. Bot.* 29:815–827.
- Allen, Jr., L.H. 1974. Model of light penetration into a wide-row crop. *Agron. J.* 66:41–47.
- Baker, J.T. and L.H. Allen, Jr. 1993. Effects of CO_2 and temperature on rice: A summary of five growing seasons. *J. Agr. Meteorol.* 48:575–582.
- Baker, J.T., L.H. Allen, Jr., and K.J. Boote. 1992. Response of rice to CO_2 and temperature. *Agr. For. Meteorol.* 60:153–166.
- Bennett, J.M., T.R. Sinclair, L. Ma, and K.J. Boote. 1993. Single leaf carbon exchange and canopy radiation use efficiency of four peanut cultivars. *Peanut Sci.* 20:1–5.
- Boote, K.J., G. Bourgeois, and J. Goudriaan. 1988. Light interception and photosynthesis of incomplete hedgerow canopies of soybean and peanut. 1988 *Agron. Abstr.* p. 105.
- Boote, K.J. and J.W. Jones. 1987. Equations to define canopy photosynthesis from quantum efficiency, maximum leaf rate, light extinction, leaf area index, and photon flux density, p. 415–418. In: J. Biggins (ed.). *Progress in photosynthesis research*. vol. 4. Martinus Nijhoff Publ., The Netherlands.
- Boote, K.J., J.W. Jones, and G. Hoogenboom. 1989. Simulating crop growth and photosynthesis response to row spacing. 1989 *Agron. Abstr.* p. 11.
- Boote, K.J. and R.S. Loomis. 1991. The prediction of canopy assimilation, p. 109–140. In: K.J. Boote and R.S. Loomis (eds.). *Modeling crop photosynthesis—From biochemistry to canopy*. Crop Sci. Soc. Amer. Spec. Publ. 19. Amer. Soc. Agron., Madison, Wis.
- Boote, K.J., N. Pickering, J.T. Baker, and L.H. Allen. 1992. Predicting canopy assimilation of rice in response to carbon dioxide concentration and temperature, p. 831–834. In: N. Murata (ed.). *Research in photosynthesis*. vol. 4. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Brooks, A. and G.D. Farquhar. 1985. Effect of temperature on the CO_2/O_2 specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. Estimates from gas-exchange measurements on spinach. *Planta* 165:397–406.
- Campbell, G.S. and J.M. Norman. 1989. The description and measurement of plant canopy structure, p. 1–19. In: G. Russell, B. Marshall, and P.G. Jarvis (eds.). *Plant canopies: Their growth, form and function*. Cambridge Univ. Press, England.
- Campbell, W.J., L.H. Allen, Jr., and G. Bowes. 1990. Response of soybean canopy photosynthesis to CO_2 concentration, light, and temperature. *J. Expt. Bot.* 41:427–433.
- Charles-Edwards, D.A. 1981. *The mathematics of photosynthesis and productivity*. Academic, London.
- Charles-Edwards, D.A. and B. Acocck. 1977. Growth response of a *Chrysanthemum* crop to the environment. II. A mathematical analysis relating photosynthesis and growth. *Ann. Bot.* 41:49–58.
- Denison, R.F. and R.S. Loomis. 1989. An integrative physiological model of alfalfa growth and development. *Bul. Div. Agr. Natural Resources, Univ. of California, Oakland*.
- de Wit, C.T. 1965. Photosynthesis of leaf canopies. *Agr. Res. Rpt.* 663. PUDOC, Wageningen, The Netherlands.
- Dornhoff, G.M. and R.M. Shibles. 1970. Varietal differences in net photosynthesis of soybean leaves. *Crop Sci.* 10:42–45.
- Duncan, W.G., R.S. Loomis, W.A. Williams, and R. Hanau. 1967. A model for simulating photosynthesis in plant communities. *Hilgardia* 38:181–205.
- Ehleringer, J. and O. Björkman. 1977. Quantum yields for CO_2 uptake in C_3 and C_4 plants: Dependence on temperature, $[CO_2]$, and $[O_2]$ concentration. *Plant Physiol.* 59:86–90.
- Ehleringer, J. and R.W. Pearcy. 1983. Variation in quantum yield for CO_2 uptake among C_3 and C_4 plants. *Plant Physiol.* 73:555–559.
- Erbs, D.G., S.A. Klein, and J.A. Duffie. 1982. Estimation of the diffuse

- radiation fraction for hourly, daily and monthly-average global radiation. *Solar Energy* 28:293–302.
- Evans, J.R. and G.D. Farquhar. 1991. Modeling canopy photosynthesis from the biochemistry of the C_3 chloroplast, p. 1–15. In: K.J. Boote and R.S. Loomis (eds.). *Modeling crop photosynthesis—From biochemistry to canopy*. Crop Sci. Soc. Amer. Spec. Publ. 19. Amer. Soc. Agron., Madison, Wis.
- Farquhar, G.D. and S. von Caemmerer. 1982. Modelling of photosynthetic response to environment, p. 549–587. In: O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler (eds.). *Encyclopedia of plant physiology*. new series. vol. 12B. Physiological plant ecology II. Springer-Verlag, Berlin.
- Farquhar, G.D., S. von Caemmerer, and J.A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* 149:78–90.
- Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program. *Oecologia (Berlin)* 56:341–347.
- Gijzen, H. and J. Goudriaan. 1989. A flexible and explanatory model of light distribution and photosynthesis in row crops. *Agr. For. Meteorol.* 48:1–20.
- Goudriaan, J. 1977. *Crop micrometeorology: A simulation study*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Goudriaan, J. 1982. Potential production processes, p. 98–113. In: F.W.T. Penning de Vries and H.H. van Laar (eds.). *Simulation of plant growth and crop production*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Goudriaan, J. 1986. A simple and fast numerical method for the computation of daily totals of crop photosynthesis. *Agr. For. Meteorol.* 38:249–254.
- Goudriaan, J. 1988. The bare bones of leaf-angle distribution in radiation models for canopy photosynthesis and energy exchange. *Agr. For. Meteorol.* 43:155–169.
- Harley, P.C. and J.D. Tenhunen. 1991. Modeling the photosynthetic response of C_3 leaves to environmental factors, p. 17–39. In: K.J. Boote and R.S. Loomis (eds.). *Modeling crop photosynthesis—From biochemistry to canopy*. Crop Sci. Soc. Amer. Spec. Publ. 19. Amer. Soc. Agron., Madison, Wis.
- Harley, P.C., R.B. Thomas, J.F. Reynolds, and B.R. Strain. 1992. Modelling photosynthesis of cotton grown in elevated CO_2 . *Plant Cell Environ.* 15:271–282.
- Harley, P.C., J.A. Weber, and D.M. Gates. 1985. Interactive effects of light, leaf temperature, $[CO_2]$ and $[O_2]$ on photosynthesis in soybean. *Planta* 165:249–263.
- Hirose, T. and M.J.A. Werger. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia (Berlin)* 72:520–526.
- Hoogenboom, G., J.W. Jones, and K.J. Boote. 1992. Modeling growth, development, and yield of grain legumes using SOYGRO, PNUTGRO, and BEANGRO: A review. *Trans. Amer. Soc. Agr. Eng.* 35:2043–2056.
- Johnson, I.R. and J.H.M. Thornley. 1984. A model of instantaneous and daily canopy photosynthesis. *J. Theoretical Biol.* 107:531–545.
- Jones, P., L.H. Allen, Jr., and J.W. Jones. 1985a. Responses of soybean canopy photosynthesis and transpiration to whole-day temperature changes in different CO_2 environments. *Agron. J.* 77:242–249.
- Jones, P., L.H. Allen, Jr., J.W. Jones, and R. Valle. 1985b. Photosynthesis and transpiration responses of soybean canopies to short- and long-term CO_2 treatments. *Agron. J.* 77:119–126.
- Jordan, D.B. and W.L. Ogren. 1984. The CO_2/O_2 specificity of ribulose 1,5-bisphosphate carboxylase/oxygenase. Dependence on ribulose-bisphosphate concentration, pH, and temperature. *Planta* 161:308–313.
- Kimball, B.A. and L.A. Bellamy. 1986. Generation of diurnal solar radiation, temperature, and humidity patterns. *Energy Agr.* 5:185–197.
- Long, S.P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? *Plant Cell Environ.* 14:729–739.
- Loomis, R.S. and W.A. Williams. 1969. Productivity and the morphology of crop stands: Patterns with leaves, p. 27–51. In: J.D. Eastin, F.A. Haskins, C.Y. Sullivan, and C.H.M. Van Bavel (eds.). *Physiological aspects of crop yield*. Amer. Soc. Agron., Madison, Wis.
- Marshall, B. and P.V. Biscoe. 1980. A model for C_3 leaves describing the dependence of net photosynthesis on irradiance. *J. Expt. Bot.* 31:29–39.
- Monsi, M. and T. Saeki. 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jpn. J. Bot.* 14:22–52.
- Morison, J.I.L. 1987. Intercellular CO_2 concentration and stomatal response to CO_2 , p. 229–251. In: E. Zeiger, G.D. Farquhar, and I.R. Cowan (eds.). *Stomatal function*. Stanford Univ. Press, Stanford, Calif.
- Mutsaers, H.J.W. 1980. The effect of row orientation, date and latitude on light absorption by row crops. *J. Agr. Sci.* 95:381–386.
- Norman, J.M. and T.J. Arkebauer. 1991. Predicting canopy photosynthesis and light-use efficiency from leaf characteristics, p. 75–94. In: K.J. Boote and R.S. Loomis (eds.). *Modeling crop photosynthesis—From biochemistry to canopy*. Crop Sci. Soc. Amer. Spec. Publ. 19. Amer. Soc. Agron., Madison, Wis.
- Parton, W.J. and J.A. Logan. 1981. A model for diurnal variation in soil and air temperature. *Agr. For. Meteorol.* 23:205–216.
- Peat, W.E. 1970. Relationships between photosynthesis and light intensity in the tomato. *Ann. Bot.* 34:319–328.
- Pickering, N.B., J.W. Jones, and K.J. Boote. 1990. A moisture- and CO_2 -sensitive model of evapotranspiration and photosynthesis. Paper 90-2519. Amer. Soc. Agr. Eng., St. Joseph, Mich.
- Pickering, N.B., J.W. Jones, and K.J. Boote. 1995. Adapting SOYGRO V5.42 for prediction under climate change conditions. In: C. Rosenzweig, S. Hollinger, J. Jones, and L. Harper (eds.). *Climate change in agriculture: Analysis of potential international impacts*. Spec. Publ., Amer. Soc. Agron., Madison, Wis. (In press.)
- Rastetter, E.B., A.W. King, B.J. Cosby, G.M. Hornberger, R.V. O'Neill, and J.E. Hobbie. 1992. Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. *Ecol. Applications* 2:55–70.
- Reynolds, J.F. and B. Acock. 1985. Modeling approaches for evaluating vegetation responses to carbon dioxide concentration, p. 33–51. In: B.R. Strain and J.D. Cure (eds.). *Direct effects of increasing carbon dioxide on vegetation*. U.S. Dept. of Energy, Carbon Dioxide Res. Div., DOE/ER-0283, Washington, D.C.
- Reynolds, J.F., J. Chen, P.C. Harley, D.W. Hilbert, R.L. Dougherty, and J.D. Tenhunen. 1992. Modeling the effects of elevated CO_2 on plants: Extrapolating leaf response to a canopy. *Agr. For. Meteorol.* 61:69–94.
- Ross, J. 1981. *The radiation regime and architecture of plant stands*. Tasks for vegetative sciences. no. 3. Dr. W. Junk, The Hague, The Netherlands.
- Rowland-Bamford, A.J., J.T. Baker, L.H. Allen, Jr., and G. Bowes. 1991. Acclimation of rice to changing atmospheric carbon dioxide concentration. *Plant Cell Environ.* 14:577–583.
- Seemann, J.R., T.D. Sharkey, J.L. Wang, and C.B. Osmond. 1987. Environmental effects on photosynthesis, nitrogen-use-efficiency, and metabolite pools in leaves of sun and shade plants. *Plant Physiol.* 84:796–802.
- Sharkey, T.D., J.A. Berry, and R.F. Sage. 1988. Regulation of photosynthetic electron-transport in *Phaseolus vulgaris* L., as determined by room-temperature chlorophyll *a* fluorescence. *Planta* 176:415–424.
- Shiraiwa, T. and T.R. Sinclair. 1993. Distribution of nitrogen among leaves in soybean canopies. *Crop Sci.* 33:804–808.
- Sinclair, T.R. and T. Horie. 1989. Leaf nitrogen, photosynthesis, and crop radiation use efficiency: A review. *Crop Sci.* 29:90–98.
- Spitters, C.J.T. 1986. Separating the diffuse and direct component of global radiation and its implication for modeling canopy photosynthesis. Part II. Calculation of canopy photosynthesis. *Agr. For. Meteorol.* 38:231–242.
- Spitters, C.J.T., H.A.J.M. Toussaint, and J. Goudriaan. 1986. Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. I. Components of incoming radiation. *Agr. For. Meteorol.* 38:217–229.
- Stockle, C.O. 1992. Canopy photosynthesis and transpiration estimates using radiation interception models with different levels of detail. *Ecol. Modeling* 60:31–44.
- Tenhunen, J.D., J.A. Weber, C.S. Yocum, and D.M. Gates. 1976. Development of a photosynthesis model with an emphasis on ecological applications. II. Analysis of a data set describing the P_n surface. *Oecologia* 26:101–109.
- Wagner, H.M. 1969. *Principles of operations research*. Prentice-Hall, Englewood Cliffs, N.J.