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OPTIMIZING THE CANOPY PHOTOSYNTHETIC RATE BY PATTERNS OF INVESTMENT IN SPECIFIC LEAF MASS

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In a recent paper (Gutschick and Wiegel 1984), we developed a general theory for calculating the distribution of light in a vegetative canopy. The canopy is assumed to be laterally homogeneous in a statistical sense (as are most crops, many even-aged stands, and some clonal plants) but otherwise of quite arbitrary architecture and leaf optical properties. Here we study a related problem: Given the total dry mass of leaves in a canopy per unit of ground area, M, how should this mass be distributed with depth to maximize the photosynthetic rate of the canopy? That is, what is the optimal leaf-area index and the optimal dependence of specific leaf mass on cumulative leaf-area index? We may assume that the number of leaves per unit of volume is uniform with depth, because light penetration is a function only of the cumulative leaf-area index,

$$L = \int_{z}^{z_0} dz\, n(z) A_l(z) \,, \tag{1}$$

at least when leaves are randomly placed and their angular distribution does not change with depth (Ross 1981; Gutschick and Wiegel 1984). Here, z and z_0 are the heights of the point of interest and the top of the canopy, respectively; $n(z)$ is the number of leaves per unit of volume; and $A_l(z)$ is the average area of an individual leaf at depth z. The quantity L is dimensionless, since it is an area of leaf per unit of ground area. It measures effectively the optical depth of the canopy, independent of leaf size. One's intuition is that upper leaves should have the highest specific leaf mass (SLM is mass per unit of leaf area, also denoted as $m = m(L)$ in equations). Simply, the greatest photosynthetic capacity and corresponding energy investment in growth should be placed where the average irradiance is highest and the payback is therefore highest. In contrast, SLM should attain some structurally determined minimum after some modest depth: at low (average) irradiances, SLM and other properties become virtually irrelevant to the efficiency of light use by leaves. The quantum efficiency of using low irradiances is almost independent of leaf biochemical investments and the like, at least within each of the three major photosynthetic pathways denoted as C_3, C_4, and CAM

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(Ehleringer and Björkman 1977). Thus, there should be an optimal profile, $m^{\mathrm{opt}}(L)$, at any given leaf-area index, LAI. Second, LAI itself can be optimized. This may be viewed as optimizing the average SLM:

$$\bar{m} = \int_0^{\mathrm{LAI}} dL\,m(L) \bigg/ \int_0^{\mathrm{LAI}} dL = M/\mathrm{LAI}\,. \tag{2}$$

We have derived the formal and numerical methods to solve for $m^{\mathrm{opt}}(L)$ at every L. Our model can be used to generate hypotheses about the evolutionary design and agricultural improvement of canopies. We show that canopies apparently are substantially optimized, and we advance arguments that partial optimization gives high canopy photosynthetic rates while allowing strong shading of competitors.

To date, the regulation of SLM has most often been studied to discover the mechanisms that govern it (e.g., Gourdon and Planchon 1982) rather than to assess its adaptive value. Furthermore, most studies have focused on single leaves without discussing their integration into whole-canopy performance. Models of the optimization of single-leaf performance by choice of SLM, among other parameters, have been proposed (e.g., Givnish 1979; Solbrig 1981). Some recent studies have addressed canopy performance. Tooming and Tammets (1984) measured profiles of SLM with depth in herbaceous crops and argued qualitatively for the adaptive value of SLM variations. Field et al. (1983), deJong and Doyle (1985), and Caldwell et al. (1986) measured the variations in SLM (and related nitrogen content per area) with age or depth in woody species. A number of recent studies, including the last three cited above and one by Hirose and Werger (1987) of an herbaceous perennial, concerned the optimal distribution of leaf nitrogen content, which is loosely tied to SLM. These studies have yielded valuable ecological insights. However, all the studies used models of light interception that were highly simplified in three regards. First, none of the studies resolved the contribution of diffuse skylight to leaf irradiance (seen as critical in assessing leaf-angle effects, below). Second, none could assess the effects of different leaf angles, and some did not even simulate the shallower penetration of light with shallower solar angle. Third, none accounted for the statistical distribution of irradiances on leaves arising from the varied angles between leaf and sun for leaves of different azimuthal angle. Additionally, none of the above studies provided a formalism for calculating the optimal distribution a priori. Rather, they used fixed elementary functions, often exponentials, as guesses, to be partially optimized numerically by altering a choice of parameter. (Meister et al. [1987] performed purely numerical "perturbations" on the SLM distributions observed by Caldwell et al. [1986], concluding that the original distributions were nearly optimal.) Finally, the previous studies treated incompletely the costs of achieving nitrogen distributions. We have striven to provide remedies to these limitations, applying our formalism to the optimization of SLM. A most valuable future study would merge our light-interception model and formalism with considerations of nitrogen distribution so well presented in the publications cited.

The complementary study of the optimization of light distribution in a canopy by choice of leaf-angle distribution is well developed (the erect-leaf hypothesis, reviewed in Trenbath and Angus 1975); again, there has been no accounting for the role of SLM. Notwithstanding the lack of study, SLM profiles with depth are observable in crops (see "Results and Discussion"). Our model can be used to attribute adaptive and agricultural benefits to these nontrivial profiles and to explain their dependence on LAI, that is, on the stage of plant development and on solar irradiance patterns. In practical terms, our model could identify suboptimal profiles for improvement through breeding. (Historically, suboptimal profiles and mean SLM have been perpetuated because of a lack of quantitative understanding such as we promulgate here; see the review in Wallace et al. 1972.) We also can develop explicit hypotheses about the adaptive values of imperfect photosynthetic optimization, as noted above.

MODEL AND FORMAL SOLUTION PROCEDURE

The simplest realistic case is that of an overhead sun providing a direct beam of irradiance I_{00} normal to its direction of propagation, with no diffuse sky radiation. Assume that all the leaves have the same zenith angle, θ_l ($\cos\theta_l = x_l$), and random azimuths. Elementary arguments found in all discussions of light propagation in canopies (e.g., Ross 1981) indicate that the probability $\mathcal{P}$ of the direct beam's penetrating to a given location at depth L is simply exponential when leaves are located at random in space, that is, not clumped:

$$\mathcal{P}_{\text{sun}} = e^{-KL} = e^{-x_l L}. \tag{3}$$

Here, e is the base of the natural logarithms, and K is the extinction coefficient, which equals the leaf cosine x_l in our simple case; a more general formulation is given after equation (18), below. We discuss the effect of clumping and ways to model it in "Results and Discussion," below. Because leaves are sufficiently absorptive in the photosynthetically active region of the spectrum (>80%; Gausman 1985), the first interception of sunlight provides the major irradiance on leaves; we ignore light scattered diffusely from other leaves and soil. We also ignore the minor variation of leaf absorbance with SLM; our alfalfa simulations are limited to the normal range of SLM, above 20 g m^{-2}, at which we observed visible absorbances exceeding 85%. (We can generalize the model to treat leaf-absorbance variations and scattered light in later studies.) The irradiance on any leaf is either $I_l = I_{00}x_l$ in sun-flecked areas or zero in shaded areas. Implicitly, we are ignoring penumbral effects—the gradation of shadowing because the sun has a finite angular size—as discussed by E. Miller and Norman (1971). We expect no significant quantitative effect with broad-leaved species and no change in our conclusions about optimization.

The leaf photosynthetic rate per unit of area, $P_{l,\text{a}}$, responds to irradiance in an initially linear, ultimately saturating fashion, representable with good accuracy by a three-parameter equation (Johnson and Thornley 1984; notation modified here):

$$\gamma P_{l,\text{a}}^2 - (I_l/Q_0 + P_{l,\text{a}}^{\max})P_{l,\text{a}} + I_l P_{l,\text{a}}^{\max}/Q_0 = 0, \tag{4}$$

which has the explicit solution

$$P_{l,\text{a}}(I_l) = \{I_l/Q_0 + P_{l,\text{a}}^{\max} - [(I_l/Q_0 + P_{l,\text{a}}^{\max})^2 - 4\gamma I_l P_{l,\text{a}}^{\max}/Q_0]^{1/2}\}/(2\gamma). \tag{5}$$

Here, $P_{l,\mathrm{a}}^{\max}$ is the light-saturated photosynthetic rate, Q_0 is the initial quantum yield ($dP_{l,\mathrm{a}}/dI_l$ as $I_l \to 0$), and γ is a "rectangularity" parameter. When $\gamma = 0$, equation (5) reduces to the rectangular hyperbola, long used to fit experimental data with moderate success:

$$P_{l,\mathrm{a}}(I_l) = P_{l,\mathrm{a}}^{\max} I_l/(I_l + I_\mathrm{s}), \tag{6}$$

where $I_\mathrm{s} = P_{l,\mathrm{a}}^{\max}/Q_0$ is the irradiance at which photosynthesis is half-saturated. As γ approaches one, $P_{l,\mathrm{a}}$ becomes a ramp function: at irradiances of up to $I_\mathrm{m} = P_{l,\mathrm{a}}^{\max}/Q_0$, it is a straight line of slope Q_0, suddenly terminating at I_m in the horizontal line $P_{l,\mathrm{a}} = P_{l,\mathrm{a}}^{\max}$. Initially, we develop the mathematics for $\gamma = 0$. We do this for clarity, and also because alfalfa, in which we have an experimental interest, has a small effective value of γ, if one judges from the smoothness of light-response curves reported by Travis and Reed (1983). The effects of nonzero γ are addressed in "Results and Discussion."

Photosynthetic rates also respond to temporal fluctuations in irradiance (Gross 1982). These transient responses are significant but are beyond the scope of our discussion and, in fact, beyond the scope of all existing canopy models.

Both $P_{l,\mathrm{a}}^{\max} \equiv p(m)$ and $I_\mathrm{s} = I_\mathrm{s}(m)$ are monotonically increasing functions of m, as shown experimentally at least for $p(m)$ (e.g., Dornhoff and Shibles 1970; Khan and Tsunoda 1970). Field et al. (1983) and deJong and Doyle (1985) showed similar behavior of $P_{l,\mathrm{a}}^{\max}$ as a function of nitrogen content per leaf area, which is closely related to SLM within a species (deJong and Doyle 1985). Both $p(m)$ and $I_\mathrm{s}(m)$ are initially linear in m, saturating ultimately as thick leaves suffer high diffusive resistance for CO_2 transport and also poor light penetration (Gutschick 1984*a*). We choose two alternative models, one purely linear and the other saturating:

$$\begin{aligned} p(m) &= p_0(m - m_\mathrm{c}) \\ I_\mathrm{s}(m) &= I_\mathrm{s}^0(m - m_\mathrm{c}) \end{aligned} \tag{7a}$$

$$\begin{aligned} p(m) &= p_0(1 - e^{-(m - m_\mathrm{c})/m_\mathrm{s}}) \\ I_\mathrm{s}(m) &= I_\mathrm{s}^0(1 - e^{-(m - m_\mathrm{c})/m_\mathrm{s}}). \end{aligned} \tag{7b}$$

The offsets m_c reflect the presence of purely structural, nonphotosynthetic material at a minimal SLM. The parenthetical factors are identical for $p(m)$ and $I_\mathrm{s}(m)$, so that $p(m)/I_\mathrm{s}(m)$ is constant; this reflects the independence from m of the initial quantum yield, $Q = dP_{l,\mathrm{a}}/dI$ as I approaches zero (Ehleringer and Björkman 1977). Typically, we approximated m_c as 5 g m^{-2} and m_s as 60 g m^{-2} to agree with slopes reported earlier. Note that we consider m = SLM averaged over diurnal fluctuations, because we are interested in canopy architecture generated over the longer term.

The canopy photosynthetic rate, P_can, is composed simply as the integral of $P_{l,\mathrm{a}}$ over the canopy depth expressed as L:

$$P_\mathrm{can} = \int_0^{\mathrm{LAI}} dL P_{l,\mathrm{a}} = \int_0^{\mathrm{LAI}} dL p(m) I_l e^{-KL}/\{I_l + I_\mathrm{s}[m(L)]\}. \tag{8}$$

Optimization of $m(L)$ means that no variations in $m(L)$ from $m^{\mathrm{opt}}(L)$ can improve the optimal canopy photosynthetic rate, $P_{\mathrm{can}}^{\mathrm{opt}}$, while meeting the constraint that the biomass per ground area is unchanged:

$$M = \int_0^{\mathrm{LAI}} dL\, m(L) = \text{constant}. \tag{9}$$

Lagrange multipliers can be used to formulate $m^{\mathrm{opt}}(L)$ as the solution of

$$\partial \mathcal{L}/\partial m - (d/dL)\, \partial \mathcal{L}/\partial m' = 0, \tag{10}$$

with suitable boundary conditions (trivial herein). The Lagrangian is

$$\mathcal{L}(m, m'; L) = \mathcal{L}(m; L) = p(m) I_l e^{-KL}/[I_l + I_s(m)] - \lambda m, \tag{11}$$

where λ is the Lagrange multiplier chosen to satisfy equation (9). The analytical solution of equation (10) is

$$f(m) = \{p(m)/[I_l + I_s(m)]\}\, I_l d/dm = \lambda e^{KL}. \tag{12}$$

If $p(m)$ and $I_s(m)$ are linear functions of m as in equations (7a), this reduces to

$$I_l p_0/(I_l + I_s^0 m)^2 = \lambda e^{KL} \tag{13}$$

or

$$m^{\mathrm{opt}}(L) = [(p_0/\lambda)^{1/2} e^{-KL/2} - 1] I_l/I_s^0. \tag{14}$$

Clearly, $m^{\mathrm{opt}}(L)$ is greatest at the top of the canopy ($L = 0$), as expected. The constraint equation (9) is used to set λ:

$$M = [2(p_0/\lambda)^{1/2}(1 - e^{-K*\mathrm{LAI}/2})/K - \mathrm{LAI}] I_l/I_s^0. \tag{15}$$

For exponential $p(m)$ and $I_s(m)$ as in equations (7b), a more complicated transcendental equation can still be written explicitly.

At sufficiently large L, the computed $m(L)$ is very small or even negative. We improve the biological realism by constraining $m \geq m_{\min}$, with $m_{\min} \approx 20$ g dry matter per square meter of leaf. The local optimization relation, equation (10) or (12), is unchanged down to a depth L^*, at which $m(L) \rightarrow m_{\min}$. The equation for M is a bit more complicated:

$$M = [2(p_0/\lambda)^{1/2}(1 - e^{-KL^*/2})/K - L^*]\, I_l/I_s^0 - m_{\min}(\mathrm{LAI} - L^*) \tag{16}$$

and L^* satisfies

$$[(p_0/\lambda)^{1/2} e^{-KL^*/2} - 1]\, I_l/I_s^0 = m_{\min}. \tag{17}$$

Again, numerical solutions are readily achieved.

A single angle of incidence is unrealistic for comparing the model to field data, especially if we wish to examine the effects of varied leaf angles. Also, the direct solar beam is complemented by diffuse sky irradiance that penetrates differently and has a different statistical distribution on leaves at any depth. Therefore, we generalized the model. For an arbitrary solar-zenith angle θ_s (with azimuth $\phi_s = 0$ by convention) and for any given leaf-angle pair (θ_l, ϕ_l), we may readily compute the angle between the solar beam and the leaf normal, θ_{ls}:

$$x_{ls} = \cos\theta_{ls} = \cos\theta_s \cos\theta_l + \sin\theta_s \sin\theta_l \cos\phi_l . \tag{18}$$

The extinction coefficient K in equation (3) is simply the average of x_{ls} over all leaf azimuthal angles, divided by the factor $x_s = \cos\theta_s$ that converts from vertical path length to angled path length. Analytical expressions exist for the average $\langle x_{ls}\rangle$ but do not aid numerical analysis; therefore, we used 20 discrete leaf azimuths ϕ_l in computing $\langle x_{ls}\rangle$. Each class of leaves specified by its azimuth receives a distinct contribution from the direct solar beam:

$$I_l^{\mathrm{dir}}(\phi_l) = I_{00}x_{ls} . \tag{19}$$

Diffuse skylight comes nearly uniformly from all solid-angle elements of the sky and yields a total horizontally projected irradiance, which we denote by D_{00} at the top of the canopy. Departures from uniformity of the diffuse skylight are well known (Moon and Spencer 1942) but should minimally affect our results. Each solid-angle contribution from zenith angle θ_d (with $\cos\theta_d = x_d$) attenuates probabilistically with depth as in equation (3), with its own coefficient K_d. The average diffuse irradiance, projected on a horizontal surface, that penetrates to depth L is simply

$$D_{00}H(L) = 2D_{00}\int_0^1 dx_d x_d e^{-K_d(x_d)} . \tag{20}$$

However, this is not the average diffuse irradiance intercepted by a leaf. The rate of diffuse-irradiance interception in the layer between depths L and $L + dL$ is simply

$$D_{00}[H(L) - H(L + dL)] \approx D_{00}H'(L)dL , \tag{21}$$

such that the average leaf receives a diffuse irradiance $D_{00}H'(L)$. The distinction between $H(L)$ and $H'(L)$ is important, as we cite in "Results and Discussion." The net contribution of diffuse skylight to leaf-received irradiance, I_l^{diff}, is nearly independent of leaf orientation (Gutschick 1984*b*), approximating $D_{00}H'(L)$. Thus,

$$I_l(\phi_l) = \begin{cases} I_{00}x_{ls}(\phi_l) + D_{00}H'(L), & \text{with probability } e^{-K(\theta_l)L} \\ \quad\text{or} & \\ D_{00}H'(L), & \text{with probability } 1 - e^{-K(\theta_l)L} \end{cases} . \tag{22}$$

The generalized Lagrangian is then, for a number N_ϕ of discrete leaf azimuths of equal probability,

$$\begin{aligned} \mathcal{L} = {} & e^{-KL}p(m)\frac{1}{N_\phi}\sum_i \frac{I_{00}x_{ls}(\phi_{l,i}) + D_{00}H'(L)}{I_{00}x_{ls}(\phi_{l,i}) + D_{00}H'(L) + I_s(m)} \\ & + (1 - e^{-KL})p(m)\frac{D_{00}H'(L)}{D_{00}H'(L) + I_s(m)} - \lambda m . \end{aligned} \tag{23}$$

This can be further generalized to average over different solar elevations, $\theta_l = \theta_{l,I}$, with arbitrary weightings w_I that sum to unity. The numerical solution of the generalized version of equation (10) is still straightforward, if tedious. Equation

(23) can be further generalized to treat the case of nonzero γ in equation (5); we use such a form in our computations.

RESULTS AND DISCUSSION

Consider first the elementary overhead-sun case of equations (8)–(17). Let us choose the model parameters to represent a typical crop such as alfalfa. Let the leaf angle θ_l be 30°; take $m_c = 5$ g m^{-2}, $p(m = 40) = 40$ μmol CO$_2$ m^{-2}s^{-1}, and $Q = 0.05$ mol CO$_2$ (mol photons)$^{-1}$, such that $p_0 = 1.143$ μmol CO$_2$ g^{-1}s^{-1}, $I_s^0 = 22.86$ μmol photons g^{-1}s^{-1}, and $I_s(m = 40) = 800$ μmol m^{-2}s^{-1} (compare this I_s with the irradiance of full sun, about 2000 μmol m^{-2}s^{-1}). Further, take $m_{\min} = 20$ g m^{-2}, and use an irradiance condition appropriate to the average over a sunny day, $I_{00} = 1200$ (we will drop all units from here on, for clarity), but using only overhead irradiation ($x_s = 1$) for simplicity. Table 1 presents the results for two mid-season growth stages, $M = 100$ and $M = 200$ g m^{-2}; alfalfa reaches $M \approx 300$ or 400 by the end of the season. The optimal profiles, $m^{\text{opt}}(L)$, are quite sharp at the top, with $m_0 \equiv m(L = 0)$ attaining large values. (Actual profiles are plotted in later figures, for which we used more-realistic irradiance averaging and exponential $p(m)$.) Actual m_0 values for alfalfa are also high but are typically below 80. With an exponential $p(m)$, the m_0 values are somewhat moderated because high $m(L)$ is not as valuable: for $M = 200$ again, we find a smaller optimal average SLM, $\bar{m}^{\text{opt}} = 58$ (vs. 74 when $p(m)$ is linear in m), and a smaller peak, $m_0 = 116.7$ (vs. 153 when $p(m)$ is linear). The optimization of $m(L)$ is clearly profitable at low values of $\bar{m}$. This advantage is diluted as $\bar{m}$ approaches its own optimum, but even contrasting optimized $m(L)$ with constant $m(L) = \bar{m}$ at their respective optimal values of $\bar{m}$, the gain is over 5% for either growth stage, $M = 100$ or 200. The ecological and agricultural significance of these gains is discussed below.

As expected, at the higher biomass density M, the optimal average specific leaf mass, $\bar{m}^{\text{opt}}$, is larger. Simply, the canopy can afford a greater depth of thick leaves that use photons most efficiently. For complementary reasons, higher irradiances favor higher optimal $\bar{m}^{\text{opt}}$ (table 1). Our results are mildly sensitive to the value of $m_{\min}$. We chose $m_{\min} = 20$ to approximate observed values in alfalfa. Upon relaxing this constraint to $m_{\min} = 0$, we found the results at the end of table 1: for high $\bar{m}$ near or above the optimum, there was no effect, and even for a typical field value of $\bar{m} = 50$, there was a gain of only 1% in canopy photosynthesis.

Now consider the generalized case with arbitrary angles of solar incidence and a weighted mixture of sky conditions. We studied the case $\theta_l = 20°$, a closer approximation to alfalfa, under a mix of three different sky conditions weighted by probability of occurrence w to approximate the time course of a sunny day: (1) $I_{00} = 800$, $x_s = 0.25$, $D_{00} = 200$, $w = 0.35$; (2) $I_{00} = 1000$, $x_s = 0.7$, $D_{00} = 250$, $w = 0.35$; (3) $I_{00} = 1200$, $x_s = 1.0$, $D_{00} = 300$, $w = 0.3$. (Using larger numbers of distinct sky conditions in order to sample the sun's daily trajectory more finely altered the computed results negligibly, adding only computation time.) As for the simpler case of a single irradiance condition, optimizing $m(L)$ gives large gains (even above 20%) at low $\bar{m}$ and modest gains (about 5%) at optimally high $\bar{m}$. Profiles of $m^{\text{opt}}(L)$ are likewise strong (fig. 1) and are broadly comparable with

TABLE 1

PHOTOSYNTHETIC IMPROVEMENT WITH OVERHEAD ILLUMINATION BY OPTIMAL DISTRIBUTION OF SPECIFIC LEAF MASS

$\bar{m}$	P_{can}	$P_{\text{can}}(\bar{m})$	m_{top}	m_{bottom}	L^*
A. Base case: $M = 100$					
30	23.68	20.10	71.5	20	1.44
40	25.56	23.10	86.2	20	1.72
50	26.02	24.56	94.3	20	1.86
55	26.03	24.92	97.2	22.4	—
60	25.96	25.09	100.4	28.2	—
65	25.80	25.13	103.8	33.9	—
70	25.60	25.06	107.4	39.5	—
B. Base case: $M = 200$					
30	29.42	21.22	99.2	20	1.96
40	32.69	25.76	123.2	20	2.32
50	34.04	28.91	136.7	20	2.50
60	34.63	31.02	145.2	20	2.60
70	34.83	32.33	151.5	20	2.68
75	34.85	32.76	153.9	21.0	—
80	34.82	33.07	156.5	26.4	—
C. Exponential $p(m)$ and $I_s(m)$					
45	30.17	26.94	106.8	20	2.97
50	30.40	27.84	110.9	20	3.08
55	30.52	28.49	114.2	20	3.15
60	30.54	28.96	116.9	20	3.21
65	30.50	29.25	119.3	23.4	—
70	30.40	29.42	121.9	29.0	—
75	30.25	29.47	124.8	34.6	—
D. Low irradiance: $I_{00} = 400$					
30	14.52	12.41	82.5	20	2.61
40	15.23	13.77	102.9	20	3.07
50	15.42	14.49	114.6	20	3.30
55	15.43	14.69	118.7	20	3.37
60	15.39	14.80	122.2	21.2	—
65	15.33	14.86	125.6	25.8	—
E. $m_{\text{min}} = 0$; otherwise as in case A					
50	34.52	28.91	148.7	0	3.58
60	34.70	31.02	149.0	4.4	—
70	34.83	32.33	151.8	15.5	—

NOTE.—In all calculations, the leaf angle θ_l is 30° from horizontal; the direct-beam irradiance is $I_{00} = 1200$ μmol m^{-2}s^{-1} (except in case D), incident from the zenith; diffuse irradiance is absent; and the leaf photosynthetic parameters are as in the text. The columns present, in order, the average specific leaf mass, $\bar{m}$, in g m^{-2}; the canopy photosynthetic rate (in μmol m^{-2}s^{-1}) for the optimized profile $m^{\text{opt}}(L)$; the canopy photosynthetic rate for constant $m(L) = \bar{m}$; the value of $m^{\text{opt}}(L)$ at the top of the canopy, $L = 0$; the value of $m^{\text{opt}}(L)$ at the bottom, $L = M/\bar{m}$; and the cumulative-leaf-area index beyond which $m^{\text{opt}}(L) = m_{\text{min}}$. In all but case E, $m_{\text{min}} = 20$. In all but case C, the leaf photosynthetic parameters $p(m)$ and $I_s(m)$ are linear in m (eq. 7a); in case C, saturating exponentials are used (eq. 7b).

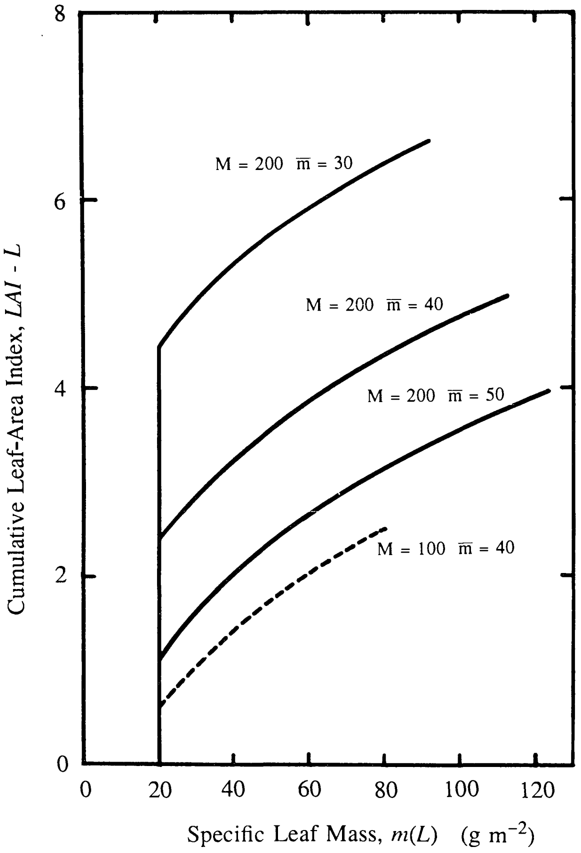

Fig. 1.—Profiles of $m^{\mathrm{opt}}(L)$, the optimized distribution of specific leaf mass according to depth in the canopy, for a leaf angle of 20° and a mix of three irradiance conditions. To emphasize differences in the total leaf-area index and therefore in plant height, the cumulative leaf-area index is plotted from the bottom of the canopy as LAI $-$ L.

those seen (fig. 2) in field data on alfalfa (Gutschick et al., unpubl. data) and potatoes (Tooming and Tammets 1984). (Caldwell et al. [1986] found significant gradients in SLM and photosynthetic capacity in a tree canopy, and Meister et al. [1987] showed by numerical searches that these distributions were nearly optimal.) The gains in canopy photosynthesis from optimizing $m(L)$ are not strongly sensitive to the peak value attained in SLM, m_0: we perturbed $m(L)$ while preserving M and found that gains in P_{can} were broadly parabolic in m_0.

The peak value, m_0, and especially its ratio to m_{min} are both higher than observed in plants so far. A large part of the discrepancy is surely caused by deficiencies in our description of light interception. First, the foliage in many canopies is clumped rather than randomly distributed in space. Consequently, light penetrates more deeply into the canopy than predicted by equation (3) or its generalization to off-zenith sunlight (P. Miller 1969; Baldocchi et al. 1985). Formulas that can treat clumping were given by Nilson (1971), Ross (1981), and Oker-

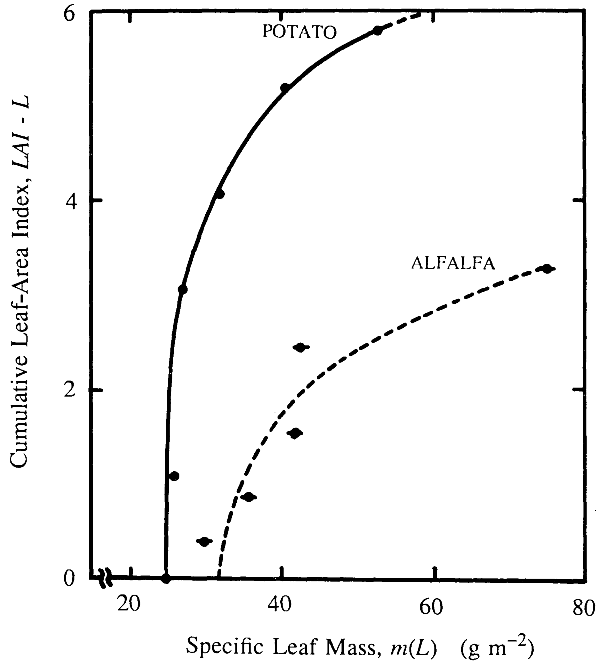

FIG. 2.—Profiles of $m(L)$ in potato (redrawn from data in Tooming and Tammets 1984) and in alfalfa (Gutschick et al., unpubl. data). Cumulative leaf-area index is plotted from the bottom of the canopy as LAI − L.

Blom and Kellomäki (1983), but they apply only to the average, plane-projected irradiance. No one has worked out formulas for the statistical distribution of irradiance on clumped leaves themselves. We hope to pursue this task later. Second, the leaf-angle distribution may vary with depth in the canopy. With more-erect leaves at the top and more-horizontal leaves toward the bottom, light penetration is enhanced (Duncan et al. 1967). A few crop species tend to display this distribution (Ross 1981).

The results above were obtained with the simple light-response curve of equation (6). We repeated the calculations using equation (5) with $\gamma = 0.9$ and with $P_{l,a}^{max}$ chosen to give the same value of $P_{l,a}$ as with $\gamma = 0$ at the maximum irradiance used (1500 μmol $m^{-2}s^{-1}$). With nonzero γ, leaves photosynthesize more at intermediate values of irradiance. Therefore, 10% to 15% more photosynthesis occurs in canopies (fig. 3*B*). However, the qualitative trends of photosynthesis with leaf angle and $\bar{m}$ remain unchanged. The optimal profiles $m(L)$ are almost identical to those obtained in the case $\gamma = 0$. The relative gains from optimizing $m(L)$ are very similar at both values of γ; the gain in canopy photosynthesis with increasing $\bar{m}$ is steeper and the optimal $\bar{m}$ is somewhat larger when γ is 0.9.

To reiterate, both crops and wild plants show strong $m(L)$ profiles that are broadly near the predicted optimum. However, they typically exhibit average SLM values, $\bar{m}$, well below optimal according to our calculations. Agriculturally,

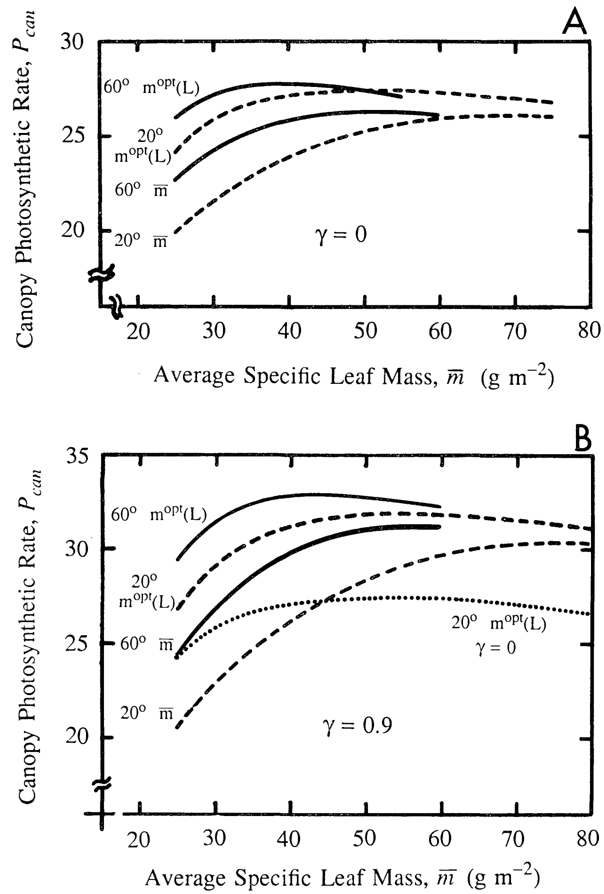

FIG. 3.—Canopy photosynthetic rate (μmol $m^{-2}s^{-1}$) as a function of average specific leaf mass, $\bar{m}$ (g m^{-2}) for a total leaf biomass per ground area, $M = 200$. The gain in P_{can} from optimizing $m(L)$ is apparent, as is the reduction of sensitivity to $\bar{m}$. With steeper leaf inclination ($\theta_l = 60°$), the maximum in P_{can} is reached at lower $\bar{m}$ but differs little from the maximum attained with other leaf angles. *A*, With parameter $\gamma = 0$ in the leaf photosynthetic response to irradiance, equation (5). *B*, With parameter $\gamma = 0.9$. *Dotted line*, One case with $\gamma = 0$, for comparison. Clearly, the trends of P_{can} with leaf angle and with $\bar{m}$ are largely unaffected by the choice of γ, which primarily shifts all the curves up or down.

the trend has often been to increase $\bar{m}$ in more-modern cultivars. This trend is apparent for soybeans in the data of Dornhoff and Shibles (1970). Ecologically one can rationalize why $\bar{m}$ is below the value that optimizes photosynthesis alone. Simply, a plant with lower $\bar{m}$ but optimized $m(L)$ sacrifices a little of potential P_{can} but has a larger leaf-area index and corresponding ability to shade competitors. If a plant retains $m(L)$ optimization, forgoing $\bar{m}$ optimization in favor of shading ability, the sacrifice in P_{can} can be smaller yet (fig. 3). In fact, a canopy with optimized $m(L)$ needs only about half as large an $\bar{m}$ to match the highest ($\bar{m}$-optimized) photosynthetic rate of a canopy with constant $m(L)$. Thus, a canopy

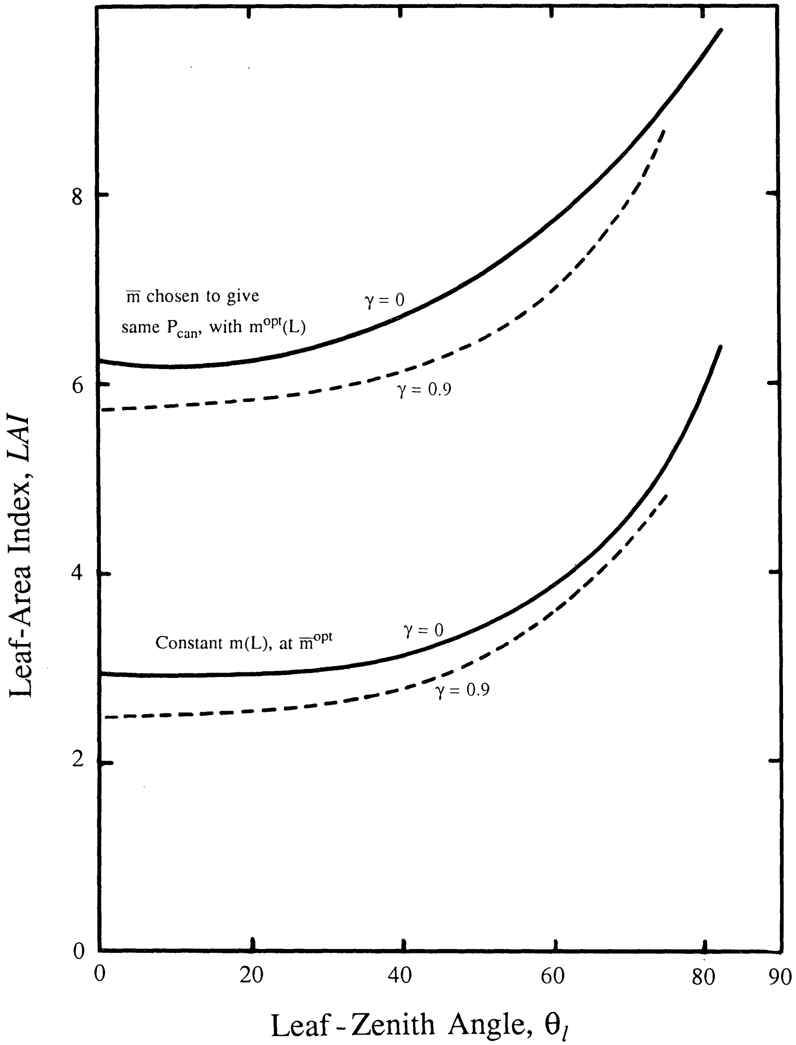

FIG. 4.—The large advantage in leaf-area index, LAI, and thus in competitor-shading capability, for a canopy with optimized $m(L)$ (*top curve*) that achieves the same photosynthetic rate as a canopy with constant $m(L) = \overline{m}$ (*bottom curve*). The advantage occurs at all leaf angles, θ_l. The constant-m canopy is optimized in $\overline{m}$. For both canopies, $M = 200$ and a standard mix of three irradiance conditions was used. *Solid curves*, For parameter $\gamma = 0$ in the leaf photosynthetic response to irradiance, equation (5). *Dashed lines*, $\gamma = 0.9$. Clearly, $m(L)$ optimization is of primary importance and γ is secondary.

with optimized $m(L)$ can have almost twice the LAI as a canopy with constant $m(L)$ for the same P_{can} (fig. 4). We propose that strong profiles of $m(L)$ near the predicted optima are deployed not for the modest gain (as little as 4%) in P_{can} relative to a constant $m(L)$. Rather, optimizing $m(L)$ gives a plant a nonphotosynthetic advantage in competitor shading with negligible photosynthetic penalty. By comparing figures 3*A* and 3*B* or by comparing the solid and dashed curves in figure 4, one can see that this proposal is unaffected by the kind of light-response curve (the value of γ). We cannot quantify the fitness contribution of shading ability within our model; we leave this for other investigators.

Adaptive arguments can also be advanced for the retention of m_{min} at significant levels. First, $m_{\text{min}} = 20$ does not substantially penalize the potential P_{can}, as noted earlier. Allowing $m_{\text{min}} = 0$, in contrast, is equivalent to letting LAI be self-limited, avoiding "excess" LAI that only minimally increases light interception for photosynthesis while bearing significant costs of leaf growth. However, excess LAI does help to shade competitors, such that leaves of some nominally minimal SLM are useful. Furthermore, lower leaves with significant photosynthetic capacity (modest m_{min}) can regenerate the canopy's photosynthetic capacity after herbivory damage, which is a constant hazard to vegetation.

Leaf angle as a heritable trait affecting photosynthesis is of inherent interest. Because leaf angle also affects the depth of light penetration into a canopy, it couples with $m(L)$ optimization. More-erect leaves allow deeper light penetration when the sun is overhead or nearly so. At moderate to high LAI, erect-leaved canopies intercept almost all the light, as do planophile canopies ($\theta_l \approx 0°$), but do so at lower average leaf irradiances and hence with greater quantum efficiency in photosynthesis (less saturation). For example, two leaves at 60° cover the same horizontally projected area as does one leaf at 0°. When the sun is overhead, the 60° leaves that are receiving I_l half as large as that on the 0° leaves may do ⅔ as much photosynthesis per leaf area as the 0° leaves. Thus, together they do 1⅓ times as much photosynthesis as 0° leaves, with the same amount of light. The photosynthetic value of leaf erectness was hypothesized by Boysen Jensen in 1932 and much later was brought to fruition in a few crops such as maize (review in Trenbath and Angus 1975). (It should be noted that significant gains were not expected in maize, which is a C_4 plant showing only a modest degree of photosynthetic-rate saturation at full solar-irradiance levels.)

We have examined varied θ_l, to see how $m(L)$ optimization varies in degree and in benefit as θ_l varies. We verified (fig. 5) that pronounced erectness ($\theta_l^{\text{opt}} \approx 60°$ to 75°) is advantageous for P_{can} but only slightly so. Although the advantage of erectness is great when the sun is nearly overhead, it declines for a solar-zenith angle greater than zero and even becomes negative at low solar elevations above the horizon. Thus, averaged over a whole day's course of solar angles, P_{can} is fairly insensitive to leaf angle. This insensitivity is independent of the light-curve parameter γ, as one can surmise from figure 3*B*. The insensitivity of P_{can} to leaf angle is fully apparent when one accounts, as we did, for the role of diffuse skylight. A precise accounting for diffuse skylight is prohibitively difficult in numerical calculations. Although one can estimate the average irradiance projected onto a horizontal surface at any depth L (e.g., Norman and Welles 1983),

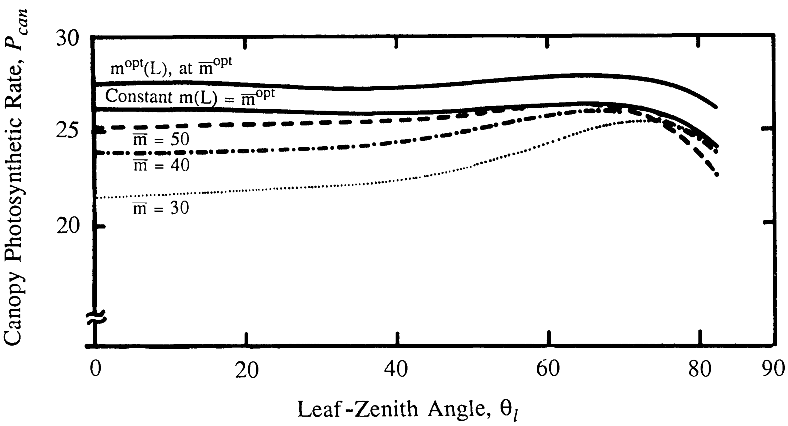

FIG. 5.—Dependence of canopy photosynthetic rate (μmol m^{-2}s^{-1}) on leaf angle θ_l, for optimized $m(L)$ and optimized $\bar{m}$ (*top solid curve*); constant $m(L)$ = optimized $\bar{m}$ (*second solid curve*); three different values of constant $m(L)$ (*lowest three curves*). In all cases, $M = 200$, $\gamma = 0$ in equation (5), and a standard mix of three irradiance conditions was used.

calculating the statistical distribution of irradiance on a leaf of arbitrary orientation, or even calculating the coefficient of variance, is prohibitively complex. We therefore used the set of approximations noted after equation (20): (1) leaves of all orientations receive the same diffuse-irradiance level; (2) the absolute variance in irradiance is small; (3) the irradiance received is $D_{00}H'(L)$. Such an accounting was not developed in the earlier canopy modeling reviewed by Trenbath and Angus (1975). If one follows the spirit of these earlier models and approximates that all the solar irradiance arrives in the direct beam, one estimates that canopies with leaf-zenith angles of 60° to 75° have over 20% greater P_{can} than canopies with θ_l near zero. This misleadingly great estimate of the advantage of erect leaves persists even if we (incorrectly but plausibly) account for diffuse irradiance as attenuating with the correct $H(L)$ factor of equation (20) but use $D_{00}H(L)$ rather than $D_{00}H'(L)$ as the diffuse irradiance on the average leaf (table 2). Of course, such an accounting violates the conservation of flux. The great importance of correctly accounting for diffuse flux surprised us and has not been reported previously by canopy modelers.

Interestingly, optimizing $m(L)$ gives an almost invariant relative gain near 5% at all leaf angles (fig. 5). That is, P_{can} with optimal $m(L)$ at its optimal $\bar{m}$ is about 1.05 as large as P_{can} for $m(L)$ = constant at its respective $\bar{m}^{\text{opt}}$. Again, it is evident that optimization of $m(L)$ is more beneficial to P_{can} than is optimization of $\bar{m}$ (see also fig. 3). Also, one can see in figure 5 that optimization of $\bar{m}$ is most important for planophile leaves. At low θ_l, a high $\bar{m}$ is optimal, while at large θ_l, a low $\bar{m}$ is optimal (fig. 6). Figure 7 demonstrates that the optimal $m(L)$ profile scales to the depth of effective light penetration; the profile extends to greater depth when θ_l is large.

Erect leaves are not common, and we may hypothesize that it is for the same reason that $\bar{m}$ optimization is unsatisfied: the gain in P_{can} is nearly insignificant,

TABLE 2

PROPER AND IMPROPER ACCOUNTINGS FOR DIFFUSE SKYLIGHT

	Best Approximation, $D_{00}H'(L)$			Simple Approximation, $D_{00}H(L)$		
θ_l	$\bar{m}$	P_{can}	$P_{can}(\bar{m})$	$\bar{m}$	P_{can}	$P_{can}(\bar{m})$
20°	30	25.92	21.60	30	26.22	21.87
	50	27.47	25.30	50	27.78	25.59
	70	27.04	26.12	70	27.33	26.40
60°	30	27.24	24.23	30	30.70	27.53
	50	27.49	26.29	50	30.71	29.41

NOTE.—The values in the left half of the table were generated using equation (21) to estimate the interception of diffuse skylight by leaves. The values in the right half were generated using the simpler approximation noted, which does not conserve photon flux. Here, $\bar{m}$ is the average specific leaf mass in the canopy; P_{can} is the canopy photosynthetic rate for optimized specific leaf mass, $m(L)$; and $P_{can}(\bar{m})$ is the rate for constant $m(L) = \bar{m}$. Note how the absolute error from using the second approximation is largest for more-erect leaves ($\theta_l = 60°$), making them appear significantly advantageous. All the entries were generated for canopy mass $M = 200$ g m^{-2}, using the same exponential forms (eq. 7b) of $p(m)$ and $I_s(m)$, the same weighted mix of three sky conditions, and the same value of $m_{min} = 20$ g m^{-2} used previously to generate table 1.

especially when averaged over a season (at low LAI, erectness is a clear disadvantage), whereas the forfeiture of the ability to shade competitors may be fairly large. Some shading of competitors is sacrificed even though the optimal $\bar{m}$ is smaller (hence, LAI is larger at a given canopy mass M) for highly erect leaves than for planophile leaves. In order to integrate the effects of leaf angle over a season, vegetative growth times have been simulated between specified limits of shoot-biomass density for C$_3$ and C$_4$ plants (Gutschick, MS). At $\bar{m}$ values near 40 g m^{-2} typical of alfalfa and other photosynthetically robust plants, the time needed to grow from 50 to 500 g m^{-2} in shoot-biomass density is virtually unchanged between leaf angles of 20° and 60° in a C$_3$ plant, yet counterintuitively decreased about 5% in a C$_4$ plant. However, at a low $\bar{m}$ of 20 g m^{-2}, a C$_3$ plant with 60° leaves is predicted to grow in 80% the time required by a plant with 20° leaves. These results agree broadly with field results reviewed by Trenbath and Angus (1975).

In addition to foliage clumping, the importance of light scattered by other leaves, and possible variations in leaf-angle distribution with depth, we leave for future research four significant aspects of canopy performance. First, it is known that leaf angles vary by time of day in some plant species. Alfalfa leaves in particular track the sun to maximize light interception when the sun is at low elevations above the horizon, but they become nearly horizontal for the bulk of the photoperiod (Scott and Wells 1969; Travis and Reed 1983). Other species track the sun to maximize the leaf-received irradiance when the plant's water potential is adequate, but alter their tracking to minimize I_l when leaves are water-stressed (Berg and Hsiao 1986). Such tracking clearly affects P_{can} and the optimal $m(L)$ profile.

Second, there is the related consideration of water-use efficiency (WUE). Leaf erectness and solar tracking for minimal I_l both reduce the leaves' heat load, and

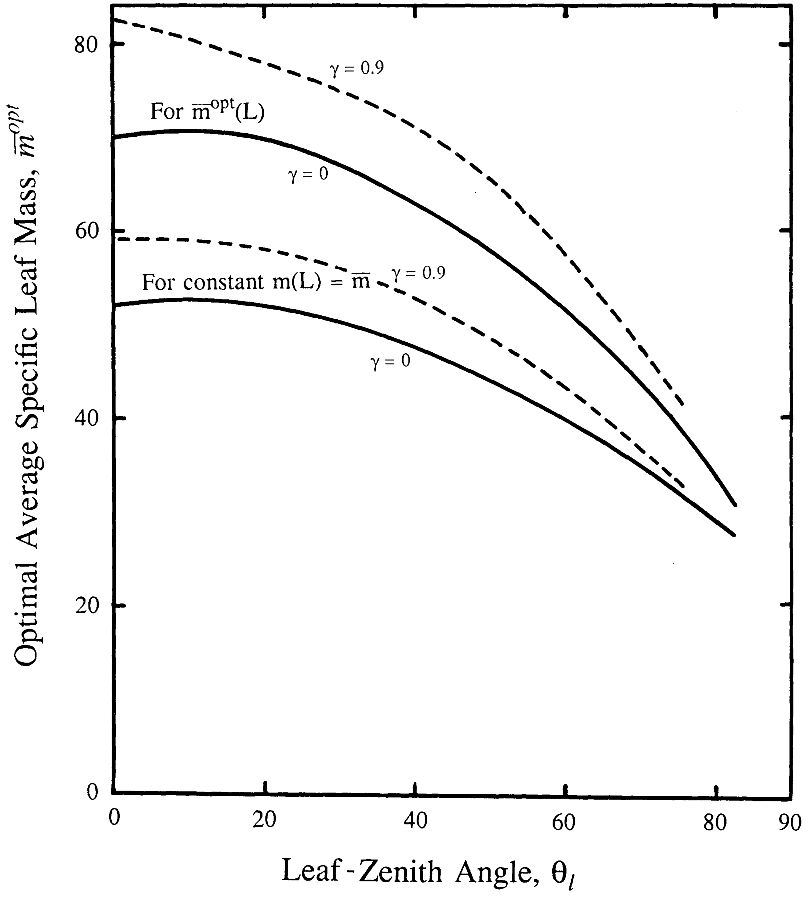

FIG. 6.—Dependence of optimal average specific leaf mass, $\overline{m}^{opt}$ (g m^{-2}) on leaf angle θ_l and on optimization of $m(L)$ (*top curve*) or lack of it (constant $m(L) = \overline{m}$; *bottom curve*). *Solid curves*, Parameter $\gamma = 0$ in the leaf photosynthetic response to irradiance, equation (5). *Dashed lines*, $\gamma = 0.9$. Again, the choice of γ does not affect qualitative trends of $\overline{m}^{opt}$ with leaf angle or the differences between performance with and without $m(L)$ optimization.

hence the leaf temperature and the water-vapor-pressure deficit from leaf interior to external air; this increases the water-use efficiency. Unfortunately, experimental tests of WUE changes with leaf erectness have not been adequately tested (Trenbath and Angus 1975). (In view of our above results showing insignificant photosynthetic gain from leaf erectness, we hypothesize that yield gains with erect leaves may result from changes in WUE.) High SLM also contributes positively to WUE. At high SLM, both photosynthetic and transpirational rates are high; the consequent transpirational cooling lowers the leaf temperature. Water-use efficiency is as significant as P_{can} both ecologically and agriculturally; even in humid climates, water supplies are exhausted episodically, such that water husbandry in plants is adaptive (for a longer discussion, see Gutschick

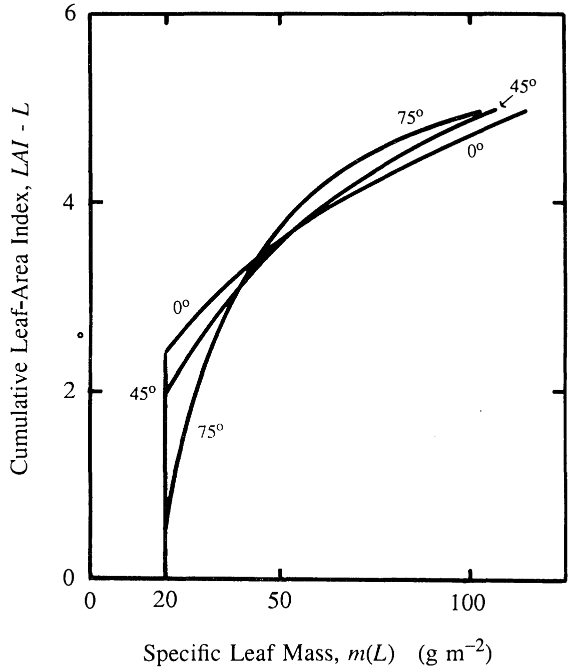

FIG. 7.—Increased depth of the $m(L)$ profile (g m^{-2}) with increasing steepness of leaf inclination. Cumulative leaf-area index is plotted from the bottom of the canopy as LAI $-$ L for ease in visualization.

1987). It should be instructive to see how optimal $m(L)$ profiles are altered when the value of WUE is accounted for in a generalized model.

Water-use efficiency and photosynthesis (hence, growth) are also strongly affected by the internal CO_2 concentration, C_i, maintained in the leaf (numerous references, e.g., Cowan 1986 and references therein). Variation in C_i with depth in a canopy has been inferred from isotopic-fractionation data (Schleser and Jayasekera 1985; Ehleringer et al. 1986). We have observed that C_i measured instantaneously by gas exchange is greater for lower leaves in an alfalfa canopy, even when all leaves are measured at the same irradiance. The pattern of C_i variation with depth should be subject to optimization, though only when photosynthesis and WUE are considered simultaneously in some weighted measure of performance.

Third, we have not addressed here the issue of nitrogen-use efficiency, NUE. We have considered what we may term carbon-use efficiency, or CUE, that is, how photosynthetically gained carbon (dry matter) should be apportioned to maximize its continued rate of gain. We have assumed that local investment in SLM is paralleled by investment in nitrogen as nitrogen content per area, N_a (deJong and Doyle 1985). However, nitrogen availability is often limited by external and internal factors having time scales and physiological responses quite different from the factors limiting carbon availability. NUE can become a separate, important consideration. Deploying thick leaves at the top of the canopy can maximize CUE but may not maximize NUE. Using the simplest definition of NUE as $P_{l,\mathrm{a}}/N_{\mathrm{a}}$, Field et al. (1983) found that it correlated negatively with WUE between species. They did not analyze CUE for leaves or for canopies. Before pursuing NUE, one must resolve the problem of defining it in the most ecologically relevant form (Gutschick 1987).

Fourth, we have not discussed here how an optimal or nearly optimal canopy at one growth stage (one M value) can develop into an optimal canopy of larger M. For simplicity of argument, let us compare canopies for parts A and B of table 1, assuming that $\bar{m}$ is unchanged between M stages and has the value 50. Leaves that were on top at $M = 100$ had an optimal $m(L) = m(0) = 94.3$. When the canopy has grown to $M = 200$, these leaves have been overtopped and now reside at $L = 2$; their new optimal $m(L)$ is 34.1, much lower than before. In reality, overtopped leaves do decline in SLM, at least as they senesce (see, e.g., Lugg and Sinclair 1980; Jurik 1986), and the energetic value of the lost biomass is partly recovered. We must develop hypotheses to examine how nearly optimal is the schedule of SLM readjustment in overtopped leaves.

SUMMARY

Given the total leaf mass per ground area in a laterally homogeneous vegetative canopy (of a crop, even-aged stand, or clonal plant), how should this mass be distributed with depth to maximize the canopy's photosynthetic rate? That is, how should the specific leaf mass, m (mass per unit of leaf area), vary with cumulative-leaf-area index, L? We present a formal solution using the calculus of variations, an analytical solution for simple cases, and general numerical methods. The predicted optimal gradients in $m(L)$ are large but broadly comparable with those seen in field crops. Optimizing $m(L)$ gives typically 5% greater photosynthesis than the best possible choice of a constant $m(L)$. More significantly for competitive growth, optimizing $m(L)$ upholds canopy photosynthesis down to very low average m; hence, it allows a high leaf-area index and attendant capacity to shade competitors. Photosynthetic gains from $m(L)$ optimization are remarkably insensitive to leaf angle. Equally surprisingly, daily average canopy photosynthesis is also predicted to be insensitive to leaf angle, contrary to the predictions of earlier models. The accuracy of accounting for diffuse skylight interception appears crucial. We further analyze the ecological and agricultural significance of leaf angle, and we outline research needs for related problems of light interception, canopy developmental patterns, water-use efficiency, and nitrogen-use efficiency.

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