

## *Letter to the Editor*

### **Optimization of specific leaf mass, internal CO<sub>2</sub> concentration, and chlorophyll content in crop canopies**

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Four novel routes to improving crop growth, water-use efficiency, or both are indicated by comprehensive physiological models of canopy photosynthesis, growth, and canopy gas exchange. These routes are: (a) Simultaneously optimizing specific leaf mass (SLM) and leaf internal CO<sub>2</sub> concentration, to maximize water-use efficiency, yield, or a combination of both. (b) Decreasing the leaf chlorophyll content and thus leaf absorbance, to improve light distribution in the lower canopy and thus increase canopy total photosynthesis. (c) Optimizing specific leaf mass over the whole season, either as a constant compromise value or as an optimal developmental trend. (d) Optimizing the profile of SLM with depth in the canopy. Two of the routes are being tested experimentally at present. All four studies employ explicitly optimizing models, with detailed submodels of light interception and of the statistical distribution of irradiance on leaves. Several historical, surmountable reasons for persistent nonoptimization in agriculture are identified. Canopies are found to restrict severely the magnitude of potential gains in all four routes, except in route (c).

*Additional key words* — Water-use efficiency, photosynthesis, gas exchange, light distribution.

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**Résumé.** Quatre nouveaux procédés d'amélioration de la croissance ou de l'efficacité de l'utilisation de l'eau (ou des deux) chez les plantes cultivées sont suggérés par des modèles physiologiques élaborés de croissance, de photosynthèse et d'échanges gazeux du feuillage. Ces procédés sont: (a) l'optimisation simultanée de la masse foliaire spécifique et de la concentration interne du CO<sub>2</sub> dans les feuilles afin de maximaliser l'efficacité de l'utilisation de l'eau ou le rendement (ou les deux à la fois); (b) la diminution de la teneur en chlorophylle des feuilles, et ainsi de l'absorption par les feuilles, afin d'améliorer la distribution de l'éclairement dans les parties inférieures du feuillage et d'augmenter ainsi la photosynthèse totale du feuillage, (c) l'optimisation de la masse foliaire spécifique soit sous forme d'une valeur

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moyenne constante soit sous forme d'une évolution optimale du développement du feuillage; (d) l'optimisation du profil de la masse foliaire spécifique en fonction de l'épaisseur du feuillage. Deux de ces procédés sont actuellement testés expérimentalement. Ces quatre études ont explicitement recours à des modèles d'optimisation, comportant des sous-modèles détaillés de l'interception de la lumière et de la distribution statistique de l'éclairement des feuilles. Certaines raisons historiques, mais surmontables, de non-optimisation persistante en agriculture sont identifiées. Le feuillage apparaît comme l'obstacle majeur à l'augmentation de gains potentiels dans les quatre procédés, à l'exception du procédé (c). Mots clés additionnels: efficacité de l'utilisation de l'eau, photosynthèse, échanges gazeux, distribution de l'éclairement.

**Abbreviations.**  $C_i$ , leaf internal  $\text{CO}_2$  concentration; Chl, chlorophyll;  $I_b$ , irradiance on leaf surface;  $L$ , cumulative leaf area index measured from the top of the canopy;  $LAI$ , leaf area index;  $m_{\min}$ , minimal specific leaf mass;  $m(L)$ , specific leaf mass as a function of cumulative leaf area index;  $m^{\text{opt}}(L)$ , optimal profile of  $m(L)$  that maximizes canopy photosynthesis;  $P_{\text{can}}$ , canopy photosynthetic rate per unit ground area;  $P_{l,a}$ , leaf photosynthetic rate per unit area;  $P_{l,m}$ , leaf photosynthetic rate per unit dry mass;  $P_{l,a}^{\text{max}}$ , light-saturated rate of  $P_{l,a}$ ; PAR, photosynthetically active radiation; ppmv, parts per million by volume, in air; Rubisco, ribulose 1,5-bisphosphate carboxylase/oxygenase; WUE, water-use efficiency;  $\theta_b$ , angle of leaf normal as departure from zenith.

## Introduction

Physiological modelling is useful for developing hypotheses about the ecological adaptiveness and agricultural utility of various physiological, morphological, and phenological variations in plants. Modelling also can aid in designing experiments to test the hypotheses and in deciding, according to the magnitude of the projected agricultural gains, if a significant experimental effort is merited.

While individual physiological, phenological, and morphological adaptations of plants to meet resource challenges (drought, mineral stress, etc.) are being researched very actively, there is far less effort to quantify the net effect on yield of adaptations acting singly or in concert. Thus, there is mostly only qualitative or intuitive guidance to the most profitable breeding strategies for optimizing the use of water, fertilizers, land, etc. For example, it remains uncertain if breeding for high values of light-saturated photosynthetic rate is desirable (Gifford and Evans, 1981). Similarly, the economic advantages of extending the ability to fix nitrogen to new crop species may be modest or even negative (Hardy, 1977). To aid in designing crop improvement programs, comprehensive models of plant function should be developed. Used judiciously, such models can hasten both basic research and its breeding applications. In making a model, one is forced to develop a clear objective capable of mathematical statement (in terms of yield, yield per input, monetary value, or the like) and a clear conception of the contributory physiological and phenological processes, the environmental variables, and their quantitative relations. Models that explicitly display ultimate crop performance and its optimization can be used

to develop hypotheses of crop improvements; perhaps the four hypotheses presented below so qualify. The models also suggest profitable forms of analyzing experimental data, such as nonlinear regression relations. A detailed exposition of how one might use models in crop improvement is given in the author's recent book (Gutschick, 1987).

A common expectation currently is that fundamental yield limitations are being approached in improved crop cultivars, even in some cases the absolute limits set by quantum conversion efficiency of sunlight. How much room for improvement is left, and how might we get it? Modelling can help to answer both questions. Consider a cultivar noted for its high yield potential. Even though crop genotypes have been bred for millenia, crops still retain many, and unsuspected, responses to the environment that are adaptive for wild growth but maladaptive in agriculture. Wild plants have been naturally selected to survive in the long term, while agricultural goals such as high yield are both narrower and more ambitious. Wild and agricultural "goals" conflict for several reasons: (a) Maximal reproductive yield and survival capacity can conflict. For example, a high harvest index derives in large part from lowered investment in stems in dwarf plants; dwarf plants grow well in even-aged stands of uniform height, but are severely disadvantaged in the competition for light in a heterogeneous population in the wild. (b) Risks from adverse weather, resource shortages, pests, and diseases are often handled more conservatively in wild growth (at a yield sacrifice) than in managed agricultural growth. Taproots may be useful for insuring late-season water availability in wild growth, but represent an unneeded

diversion of growth substrates in intensive agriculture. (c) Crop genotypes are an admixture of genes which are adaptive in their individual, diverse environments but not necessarily all adaptive in the final environment of use. Because of such conflicts, crops have several maladaptive traits, e.g. maturation is inhibited and stems elongate excessively when soil N levels are high late in the season (analysis by Gutschick, 1981); this behavior has had to be bred out of specific cultivars such as "Green Revolution" grains (Loomis *et al.*, 1976). Other examples are carryover of wild-growth competitive strategies of water use (Passioura, 1972, 1976) and of inappropriate photoperiodic controls (Vince-Prue and Cockshull, 1981). Explicit recognition of potential conflicts can suggest routes to improve crops.

Four potential routes to crop improvement will now be presented in terms of the basic hypotheses, some details of modelling, some key supporting experimental evidence (where available), and notes on the author's own experimental programs (where in progress).

### Route 1

*Simultaneously optimizing the choice of specific leaf mass (SLM) and leaf internal CO<sub>2</sub> concentration (C<sub>i</sub>) may maximize water-use efficiency (WUE), yield, or a combination of both.*

The ecological idea (e.g. Givnish, 1979) that higher SLM correlates with higher WUE provided the initial impetus for the full modelling effort. The author examined the biophysical basis of the idea and combined the concept with several others to devise a selection strategy for SLM and C<sub>i</sub> that could give higher WUE with no change in yield, or an even greater WUE improvement with a very modest penalty in yield. The four component concepts are:

(A) Higher SLM → higher WUE: Higher SLM correlates with higher carboxylation capacity (Bowes *et al.*, 1972; Hesketh *et al.*, 1981). In turn, higher photosynthetic capacity is generally accompanied by higher stomatal conductance (Wong *et al.*, 1979), hence by higher transpiration rates at high irradiances. Thus, leaves with high SLM are cooler under a given radiative load and have a lower water-vapor pressure deficit and a lower (better) transpiration ratio.

(B) Lower C<sub>i</sub> → Higher WUE: Lower C<sub>i</sub> means a greater fractional contribution of stomatal resistance to total resistance in photosynthesis, and a greater relative decrease in transpiration than in photosynthesis (Jones, 1983; Nobel, 1983). This

gain is independent of the photosynthetic pathway, involving only initial gas exchange.

Items (A) and (B) can be summarized in the biophysical formula:

$$WUE \approx \frac{C_a - C_i}{(e^{sat}(T_l) - e_a) 0.7}, \quad (1)$$

where C<sub>a</sub> = ambient CO<sub>2</sub> concentration (mol m<sup>-3</sup>), e<sup>sat</sup>(T<sub>l</sub>) = saturated water vapor concentration (mol m<sup>-3</sup>) at the leaf temperature T<sub>l</sub>, e<sub>a</sub> = water vapor concentration in ambient air. Leaf temperature depends upon solar radiation load, transpiration, and several other physiological and environmental factors. This is where the complexity in modelling enters.

(C) Lower C<sub>i</sub> → Lower P<sub>l,a</sub> (photosynthesis per unit leaf area): at values of C<sub>i</sub> typical of C<sub>3</sub> plants, about 230 ppmv or 0.70 of C<sub>a</sub>, a given fractional change in C<sub>i</sub> generates about the same fractional change in P<sub>l,a</sub> (many experimental references, such as Badger *et al.* (1984), can be derived from the kinetic analysis of Farquhar *et al.* (1980)). How might the photosynthetic penalty from decreased C<sub>i</sub> be compensated if the C<sub>i</sub> is decreased by breeding?

(D) Higher SLM → Higher P<sub>l,a</sub><sup>max</sup> = light saturated photosynthetic rate: the increase in P<sub>l,a</sub><sup>max</sup> is almost linear, only saturating at high SLM (see (A) above). However, neither light-saturated photosynthesis nor photosynthesis of a leaf at a reference irradiance level is a measure of yield. Two considerations clarify this: (a) In a closed canopy, almost all the incident sunlight is intercepted and used at an average quantum efficiency that improves as P<sub>l,a</sub><sup>max</sup> increases. Behavior in a closed canopy at high irradiance therefore favors high SLM. (b) In early growth: consider a fixed mass of leaves, m<sub>p</sub>, which may be deployed at any particular SLM. Two plant attributes vary with SLM: L<sub>p</sub> = leaf area per plant = m<sub>p</sub>/SLM; clearly, this declines linearly as SLM increases. P<sub>l,a</sub> = average leaf photosynthetic rate over all leaves and over the day: this increases with increasing SLM, but more slowly than linearly, for two reasons: (a) Increased SLM brings an increased rate of photosynthesis at light saturation, P<sub>l,a</sub><sup>max</sup>, almost linearly, as noted earlier, but has progressively less effect at lower irradiances. In fact, at low irradiances, the slope of photosynthetic rate with irradiance, dP<sub>l,a</sub>/dI, which is the initial quantum yield, is almost independent of leaf attributes, even of species (Ehleringer and Björkman 1977; Ehleringer and Pearcy 1983); (b) Thick leaves of high SLM have relatively high

diffusive resistances to  $\text{CO}_2$  transport in the mesophyll liquid phase, which depress  $C_i$  and carboxylation rate. Gutschick (1984b) and Parkhurst (1986) have so interpreted experimental data of limited resolution.

The net effect upon relative growth rate can be estimated:  $\text{RGR} = (\text{total plant photosynthesis}) \times (\text{conversion rate from photosynthate to dry matter}) / (\text{total plant mass})$

$$\text{RGR} = (\overline{P_{l,a}} \cdot LAI) (\beta) / m_{\text{plant}} = \overline{P_{l,a}} \beta \cdot \alpha / \text{SLM} \quad (2)$$

where  $\alpha = m_l / m_{\text{plant}}$  is the fraction of the shoot dry matter in leaves. The relative growth rate declines with increasing SLM, because the negative effect of SLM in the denominator is greater than the positive effect on  $\overline{P_{l,a}}$  in the numerator.

Thus, extremes of SLM, both low and high, are disadvantageous if maintained over the growing season. For a given value of  $C_i$  and other traits, there is an optimal SLM in the middle range. Presumably, one may breed any choice of  $C_i$  and SLM, within a broad range, in order to optimize a chosen performance criterion. Both traits are quite stable, e.g. Wong *et al.* (1985 a, b and c) for  $C_i$ , and heritable, e.g. Hubick *et al.* (1986) for  $C_i$  in peanut and Song and Walton (1975) for SLM in alfalfa.

A detailed model of canopy photosynthesis, transpiration, and growth is used to evaluate the yield and WUE for given values of SLM and  $C_i$ . The model proceeds as follows: (a) A stage of growth is described by the shoot biomass per unit ground area,  $M$ . Given the planting density, this determines the shoot dry mass of the average individual plant. Given in turn the (measured or estimated) allometric growth relations, this specifies the leaf mass per plant,  $m_l$ . The leaf area per plant,  $L_p$ , then equals  $m_l / \text{SLM}$  for any chosen value of SLM, and the canopy leaf area index equals  $L_p$  times the planting density. One must then describe the canopy architecture, particularly the leaf angle distribution. (b) the statistical penetration of direct and diffuse sunlight is calculated as a function of depth in the canopy, described by the cumulative leaf area index from the top,  $L$ . Exact attenuation coefficients for the particular leaf angle distribution are used, assuming leaves are placed randomly (that is, the location of any one leaf does not affect the probability of finding any other leaf; this assumption is not completely accurate and is only partly remediable as a simplification). (c) The penetration of wind as a function of  $L$  is approximated by the formulae of Cowan

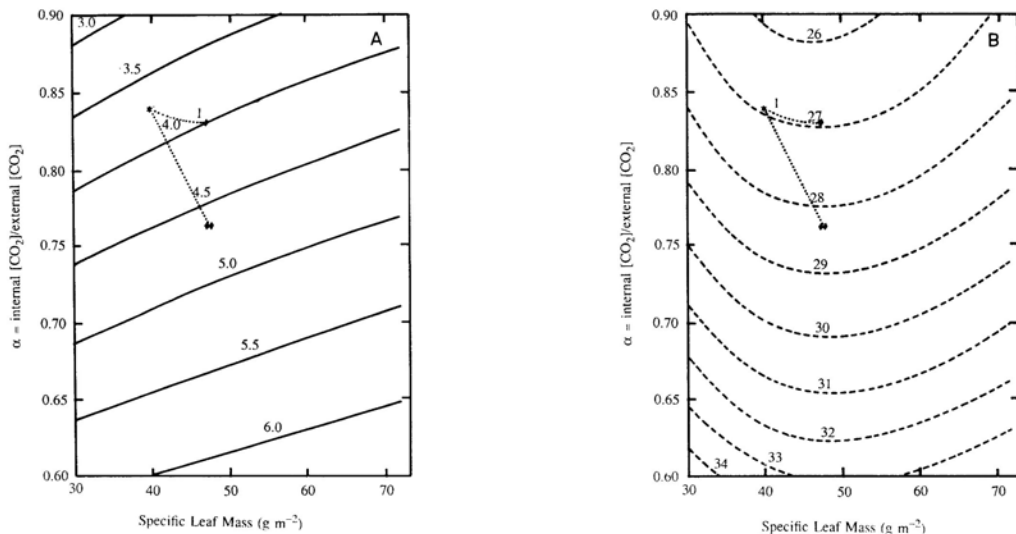
(1968). This allows computation of convective-conductive heat-transfer coefficients for individual leaves and of the eddy diffusivity of water vapor,  $\text{CO}_2$ , and heat vertically in the canopy. (d) For each of 10 to 20 discrete leaf angle classes (zenith and azimuth angles), for each of 21 discrete depths  $L$ , and for sunlit and shaded leaves separately, the total irradiance  $I_t$  on the leaf is calculated. The contribution of secondary radiation scattered from other leaves is approximated. The contribution of diffuse skylight to  $I_t$  has a complete statistical distribution but the model uses only the mean value (justified by Gutschick, 1984c). One must be careful to calculate the mean in a way that does not double-count photons (Gutschick and Wiegand, 1968). Given  $I_t$ , the leaf photosynthetic rate per unit area,  $P_{l,a}$ , is calculated with the equation of Johnson and Thornley (1984) for the irradiance response; parameter values are chosen to approximate measured alfalfa performance. In connection with the chosen value of  $C_i$  (choice of a genotype),  $P_{l,a}$  determines the stomatal conductances to water vapor and to  $\text{CO}_2$ . (e) The heat balance for a leaf of each given angle, depth, and sunlit or shaded status is calculated. Heat inputs come from photosynthetically active radiation (PAR), near-infrared radiation, and thermal infrared radiation. Transpirational losses of latent heat, thermal infrared emission, and conductive-convective heat transfer to air are heat outputs. This calculation yields leaf temperature  $T_l$  and transpiration rate (not immediately and explicitly, but as partial coefficients dependent on the  $\text{CO}_2$  concentration and air temperature at depth  $L$ , which are yet unsolved). (f) The profiles of  $\text{CO}_2$ , water vapor, and heat as functions of depth  $L$ , as determined by leaf sources and sinks and by eddy diffusion, are calculated as polynomial series. This yields the total canopy rates of photosynthesis and transpiration, respectively  $P_{\text{can}}$  and  $E_{\text{can}}$ , as functions of the chosen growth stage and environmental conditions (diffuse and direct solar irradiance values, solar elevation angle, air temperature, relative humidity, and windspeed at the top of the canopy). Subsequently,  $P_{\text{can}}$  and  $E_{\text{can}}$  are averaged, with weightings, over a variety of environmental conditions. For each set of environmental conditions the calculations of steps a through f are repeated. (g) Seasonal totals of canopy photosynthesis and transpiration are calculated by analytically integrating polynomial approximations to  $P_{\text{can}}$  and  $E_{\text{can}}$  as functions of 21 discrete growth stages,  $M$ ; a mathematical transformation converts time increments  $dt$  to growth increments  $dM$ .

In the original version of the model, the effects of maintenance energy costs and of the diversion of photosynthate to root growth were accounted on a *post hoc* basis. The model ignored effects of the atmospheric boundary layer above the canopy, which tend to suppress WUE differences between plant genotypes (of different SLM and  $C_i$ ) within extensive plant stands (Jarvis and McNaughton, 1985). Boundary-layer effects are limited in relatively small-scale plantings in irrigated agriculture of the American Southwest.

The results of the calculations are seasonally averaged WUE and yield (with yield expressed indirectly as a growth time between cuttings for alfalfa, a forage crop) for a given mixture of environmental conditions (temperature, irradiance, solar elevation, relative humidity, wind velocity). Figure 1A and B presents these calculations as contour plots. The asterisk indicates the average values of SLM and of  $C_i$  (as  $\alpha = C_i/C_a$ ) for a currently used cultivar in New Mexico, Mesilla. The diamond indicates a new target for SLM and  $C_i$  that should give the same growth time (which

is a constant along the dotted curve denoted as "1") and 8% greater WUE. The double diamond indicates a second breeder's target that should give a 5% longer growth time but 27% greater WUE.

Experimental support exists only for individual hypotheses (A), (B), and (D), and will be detailed in a publication in preparation. The concept of a strategy of "walking" to new combinations of SLM and  $C_i$  to get more desirable combinations of WUE and yield is new and has limited support from the experiments of the author with J. Pushnik and B. Swanton (in prep.). The experiments are being carried out in four growth chambers modified for high-irradiance use (up to  $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) while averting problems of air-temperature control, excessive leaf temperatures from the great thermal infrared output of the lamps, water stress, etc. (Pushnik *et al.*, 1988). Realistic field growth rates are obtained for alfalfa, comparable to record field yields. On each of 40 individual plants of two cultivars each, the following are measured: SLM, destructively;  $C_i$  (and  $P_{L, a}$ , etc.),



**Figure 1.** Computed contours of (A) season-long water-use efficiency ( $\text{mmol CO}_2 \text{ mol}^{-1} \text{ water}$ ; solid lines) and (B) growth time ( $t^*$ ; days; dashed lines) for alfalfa between stages of 60 and  $600 \text{ g m}^{-2}$  biomass density. The independent variables controlling WUE and growth time are taken as the average specific leaf mass (SLM) and internal  $\text{CO}_2$  concentration in leaves ( $C_i$ ), assumed as stable and breedable. A mix of four common environmental conditions was used in the modelling. All the conditions had equal weights corresponding to 1/8 of the day each. Their respective values of direct-beam irradiance normal to the propagation direction are 800, 1000, 1200, and  $0 \mu\text{E m}^{-2} \text{s}^{-1}$ . The respective angles of solar elevation above the horizon were 14.5, 44.4, 90, and  $90^\circ$ . The diffuse sky irradiances were 200, 250, 300, and  $250 \mu\text{E m}^{-2} \text{s}^{-1}$ . The wind velocities were all  $1 \text{ m s}^{-1}$ . The respective ambient air temperatures were 21, 26, 30 and  $24^\circ\text{C}$ , and the relative humidities were 60, 50, 40, and 60%. The values of  $t^*$  require an additional scaling factor of about 1.5 to account for diversion of photosynthate to root growth and to maintenance processes, which processes have been incorporated explicitly into newer model versions.) The asterisk is an estimate of average SLM and  $C_i$  for the currently popular Mesilla cultivar. The diamond indicates a new target for choices of SLM and  $C_i$  that should give the same growth time (which is constant along the dotted contour denoted as "1") and 8% higher WUE. The double diamond indicates a second target that should give only 5% longer growth time but 27% higher WUE.



nondestructively with a LI-COR portable photosynthesis system; yield, destructively at harvest; and water use per plant, by the difference between known excess applications and runoff recovered from freely-draining soil columns.

Results to date on 17 plants of the cultivar Wilson 9D11A support the hypotheses in three of four pairwise linear correlations of yield or WUE against  $C_i$  or SLM. Let  $C_i$  be represented as  $C_i/C_a = \alpha$ . One may characterize an individual plant (which is an individual genotype, as alfalfa is an outcrossing tetraploid) by the value of  $\alpha$  of top leaves at the time of harvest ( $\alpha_{late}$ ) or by the average over mid-growth and harvest times and over top and mid-canopy leaves ( $\alpha_{avg}$ ). In terms of these variables, the correlations are:

$$(1a) \quad \text{WUE} = -23.5 \alpha_{avg} + 20.2 \\ r = -0.72 \quad (N=10 \text{ plants})$$

$$(1b) \quad \text{WUE} = -7.9 \alpha_{late} + 7.9 \\ r = -0.56 \quad (N=17)$$

$$(2) \quad \text{WUE} = 0.03 \text{ SLM} + 1.18 \\ r = 0.23 \quad (N=17)$$

$$(3a) \quad Y = -19.1 \alpha_{avg} + 19.4 \\ r = -0.43 \quad (N=10)$$

$$(3b) \quad Y = -3.3 \alpha_{late} + 7.4 \\ r = -0.15 \quad (N=17)$$

$$(4) \quad Y = 0.14 \text{ SLM} + 0.35 \\ r = 0.66 \quad (N=17)$$

All the above correlations except (3a and b) have approximately the slope and  $r$ -value expected from the model. The anomalies (3a and b) do not reflect poor correlation of leaf photosynthetic rates with SLM ( $r=0.66$ ,  $N=17$  even in late growth). Rather, the correlation of  $P_{l,a}$  with  $C_i$ , which is fair at mid-growth ( $r=0.58$ ,  $N=10$ ) is lost at maturity ( $r=-0.10$ ,  $N=18$ ). A hypothesis to explain the change is that  $C_i$  in late growth no longer reflects rate limitation of photosynthesis because Rubisco is no longer the most-limiting factor.

## Route 2

*Decreasing the leaf chlorophyll content may improve canopy photosynthesis in sunny climates.*

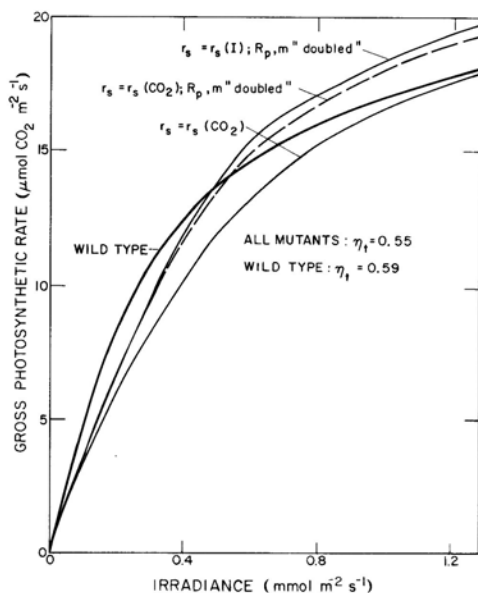
Mutants of soybean (Keck *et al.*, 1970 *a* and *b*), pea (Highkin *et al.*, 1969), and tobacco (Schmid and Gaffron, 1967 *a* and *b*) with reduced chlorophyll (Chl) content per leaf area show normal or slightly elevated rates of leaf photosynthesis per

area in full sunlight. One may say that the light-gathering ability of normal leaves exceeds their photo- and dark-reaction capabilities. This imbalance is apparent from the existence of light saturation in photosynthesis and its attribution to limited Rubisco activity (review by Sharkey, 1985). The low-Chl mutants also have greater reflectance and transmittance of photosynthetically active radiation (PAR). Consequently, one may expect that in a moderately dense canopy of mutants, the top leaves might pass more light to the mid-canopy and enhance the contributions of both the top and mid-canopy to canopy-total photosynthesis,  $P_{can}$ . While the growth of the mutants has been observed cursorily in the field and appears near normal, no one has studied their growth and yield in detail in pure stands, in which light-sharing is most effective. Likewise, no studies have attempted to find the optimal planting density, the optimal degree of chlorophyll reduction, or other trait changes. In order to assess the agronomic potential of the mutants, Gutschick (1984 *a* and *b*) first modelled the canopy performance—both to see if gains might be significant and thus experiments would be worth pursuing, and to get approximate answers to the questions above. The modelling had two principal parts: (a) Estimating light curves, reflectances, and transmittances of leaves of arbitrary Chl content per area. (b) Estimating the light distribution within canopies of leaves with any given values of reflectance and transmittance (and LAI, incident solar irradiance, etc.). In the latter task, there was an emphasis on accuracy in calculating the diffuse light generated by sunlight striking leaves and subsequently intercepted by other leaves.

The leaf model (Gutschick, 1984 *a* and *b*) incorporated: (a) The basic biochemistry of photo- and dark reactions in  $C_3$  leaves, as presented by Farquhar *et al.* (1980). (b) The distribution of light absorption by depth in a leaf. Irradiance varies considerably with depth (Terashima and Saeki, 1985; and refs. therein). Consequently, one could expect more uniform light absorption in paler leaves, hence more efficient use of Rubisco and other photosynthetic enzymes throughout the leaf thickness. (c) The kinetics of diffusion of  $\text{CO}_2$  within the leaf. The finite thickness of leaves may limit  $\text{CO}_2$  availability moderately in the middle of leaves' thickness (Parkhurst, 1986) and tends to damp out gains in photosynthetic capacity from better light distribution.

The canopy light interception model (Gutschick and Wiegel, 1984) was built on concepts of earlier investigators but added: (a) An exact accounting for diffuse light to all orders of scattering (done

initially for a special but realistic distribution of leaf inclination angles, and subsequently generalized (Myneni *et al.*, 1988 *a, b, c* and *d*). (b) A nearly exact accounting of the statistical distribution of light on leaves. Even in the simplest of illumination geometries and canopy structures, leaves of different orientations receive direct sunlight at different angles, hence at different projected irradiances. The interception of diffuse skylight is much more complex; the many independent directions of skylight have a complex probability of jointly arriving at a leaf surface (Gutschick, 1984 *c*).



**Figure 2.** Photosynthetic light-response curves of wild-type and low-chlorophyll mutant soybean leaves, computed with the model of Gutschick (1984 *a* and *b*). Three different assumptions were explored for the mutants regarding physiological parameters not yet measured for the mutants. The curve labelled " $r_s = r_s(\text{CO}_2)$ " uses the same model of stomatal control by absolute  $\text{CO}_2$  concentration in the leaves as was used for the wild-type leaves. The curve labelled similarly but with  $R_{p,m}$  doubled adds a doubling of two photochemical capacities on a per-chlorophyll basis (which means constancy on a per-leaf-area basis when chlorophyll is halved). The curve labelled " $r_s = r_s(I)$ ;  $R_{p,m}$  doubled" assumes that stomatal resistance is controlled not by  $\text{CO}_2$  concentration in the leaf but follows the same irradiance-dependence as do wild-type leaves. In all cases, the efficiency ( $\eta_i$ ) of excitation transfer from all pigments to photosynthetic reaction centers was considered to be reduced in the mutants (0.55 vs. 0.59 in the wild type). These curves agree qualitatively with experimental observations, as noted in the text.

Figure 2 presents the calculated light-response curves for leaves of wild-type and mutant soybeans. The slight superiority of mutants at high

irradiances and slight inferiority at low irradiances are apparent, and agree qualitatively with experimental observations. (The inferiority at low irradiances arises from reduced light capture, the limiting step at such irradiance levels.) Table 1 presents the calculated whole-canopy photosynthesis rates for six different conditions of solar irradiance (temperature effects are ignored as minor, for the moment), for a canopy with a leaf area index of 4. The greatest gain for a canopy of mutants over one of the wild type is 8% in high light, while there is a loss of 7% in low light. Over a normal seasonal mix of sky conditions and LAI trends, one might expect a gain of perhaps 5% in sunny climates. This would translate to a 5% gain in either yield or earliness.

The conclusions are: (a) There is a modest agronomic potential for these pale mutants. It might be amplified by additional selection for optimal SLM or canopy architecture. The gain is estimated to be fairly independent of solar elevation, unlike the gain from leaf erectness (Boysen Jensen, 1932; Duncan *et al.*, 1967; Trenbath and Angus, 1975). Gutschick and Wiegel (1988) have recently re-evaluated the effect of leaf angle on canopy photosynthesis over the day. They used an improved accounting for diffuse skylight. Their model predicts that 60 or 70° leaf angles improve canopy photosynthesis up to 30% relative to a 20° leaf angle, for  $C_3$  plants of low to modest photosynthetic capacity [ $P_{l,a}^{\max}$ ] such as wheat or rice. This prediction agrees with field results reviewed by Trenbath and Angus (1975). Surprisingly, the predicted gains from erect leaves are insignificant for  $C_3$  plants of high photosynthetic competence, such as alfalfa, even though such leaves still show substantial light-saturation in full sunlight. Gains of about 5% are predicted for  $C_4$  plants, as indeed seen in maize, although such gains are difficult to rationalize simply. (b) Despite apparent large imbalances between light-gathering and enzymatic capacities in individual leaves,  $P_{can}$  is remarkably resistant to breedable improvements meant to redress the imbalance. The modest (5%) improvement potential with lower Chl contents was probably traded off early in evolution for the greater shading ability of high-Chl leaves that aids the plants' competition with neighbors, especially understory plants.

No full experimental program is in progress to test the agronomic potential of pale mutants. However, a novel system has been built to measure light interception throughout the canopy, on 32 individual leaves (Gutschick *et al.*, 1985).

**Table 1.** Calculated whole-canopy photosynthesis,  $P_{can}$ , by wild-type and chlorophyll-deficient soybeans. The varied sky conditions are described by (1)  $I_0$  = direct-beam solar irradiance on a horizontal surface, in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; (2)  $D_0$  = diffuse irradiance on a horizontal surface, same units; (3)  $\theta_s$  = solar elevation above the horizon. For comparison, full sunlight with the sun overhead in a clear sky corresponds approximately to  $I_0 = 1600$ ,  $D_0 = 400$  in the given units. The canopy temperature is assumed to be  $25^\circ\text{C}$  and the leaf area index is 4. Leaf angles are uniformly distributed statistically. Soil reflectivity is 5%.  $F_{abs}$  = fraction of incident irradiance absorbed by canopy.

Sky condition: $I_0$ ( $\theta_s$ ); $D_0$	Canopy photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )				Relative gain by mutant
	Wild Type		Mutant		
	$F_{abs}$	$P_{can}$	$F_{abs}$	$P_{can}$	
Clear sky: 800 (60°); 400	0.870	29.72	0.807	32.08	+7.9%
Clear sky, low sun: 500 (30°); 250	0.916	20.59	0.847	21.95	+6.6%
Hazy day: 400 (60°); 400	0.875	24.60	0.812	25.03	+1.8%
Low sun: 300 (30°); 150	0.916	14.94	0.847	15.13	+1.3%
Partial overcast: 400 (60°); 200	0.870	19.49	0.807	19.57	+0.4%
Full light overcast: 0; 400	0.871	15.53	0.825	14.49	-6.7%

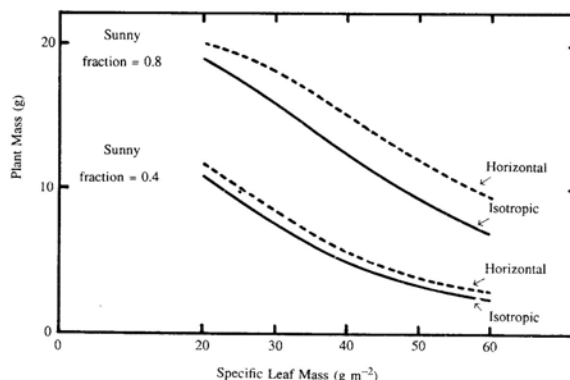
### Route 3

*Optimizing specific leaf mass over a whole season may increase yield.*

The discussion of Route 1 includes simplified arguments that, for the best growth of a stand, SLM of leaves in the upper canopy should be low in early growth before canopy closure and high in later growth. Such a pattern is observed in wheat (Aggarwal and Sinha, 1984) but has not been related to optimization of photosynthesis. To estimate optimal SLM patterns and their effect on yield, one may use a simple comprehensive model of light penetration into canopies, light distribution on leaves, and light responses of leaf photosynthesis as dependent upon SLM (steps *a*, *b* and *d* of the model described in Route 1) with a simple integration over depth  $L$  to calculate canopy-total photosynthesis.

Figures 3 and 4 present the results. It is apparent that the optimal SLM is very low in early growth, in fact, lower than limits set by structural demands on leaves. This lowness is, admittedly, partly an artifact of my form for representing the dependence of maximal  $P_{l,a}$  upon SLM. In late growth, the optimal SLM is larger (fig. 4). The peak still lies at moderate to slightly low values because the model assumed a fixed value of SLM over the entire season. In late growth in dense canopies, the peak value of instantaneous canopy photosynthesis occurs at much higher SLM (not shown).

Tentative conclusions are: (a) Phenological trends in SLM to optimize  $P_{can}$  over a whole season are rather striking. Perhaps the SLM trend in current agricultural cultivars is suboptimal and improvable, for up to 10% greater yield. Reasons



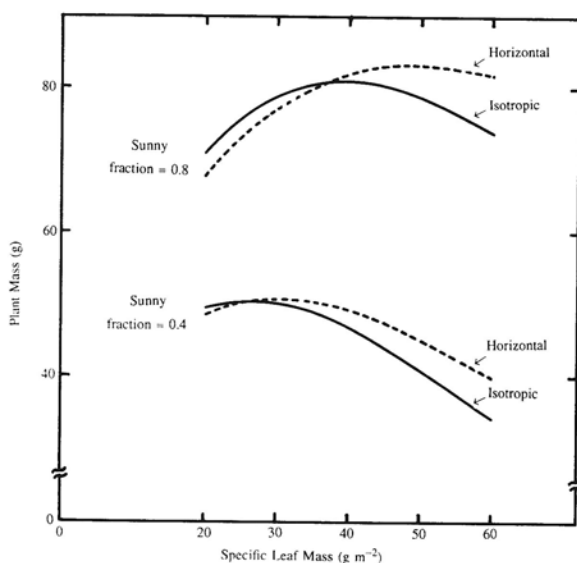
**Figure 3.** Modelled growth (final mass) of individual plants in a canopy, as dependent upon a fixed specific leaf mass, at age 40 days, when the canopy is not dense. The calculations were done for two choices of crop leaf angle distribution (all leaves horizontal, or leaves distributed at random in the cosine of the zenith angle) and for two choices of irradiance histories (80% or 40% sunny days, the rest overcast).

that optimal SLM is not achieved and that nonoptimization does not have much quantitative significance for canopy photosynthesis are hypothesized in the discussion of Route 4 below. (b) Again, gains in growth within the range of physiologically attainable SLM values are modest, not spectacular. Despite strong effects of SLM variations on leaf photosynthetic rates per area, there are contrary effects on leaf area per plant and on photosynthesis per unit mass of leaves, which is a closer determinant of growth rate. To understand the last claim, rewrite Eq. (2) for relative growth rate, RGR:

$$RGR = \beta \alpha \overline{P_{l,a}} / \overline{SLM} = \beta \alpha \overline{P_{l,m}} \quad (3)$$

where  $\overline{P_{l,m}}$  is photosynthesis per leaf mass,  $P_{l,m}$  averaged over the day and over all the leaves.





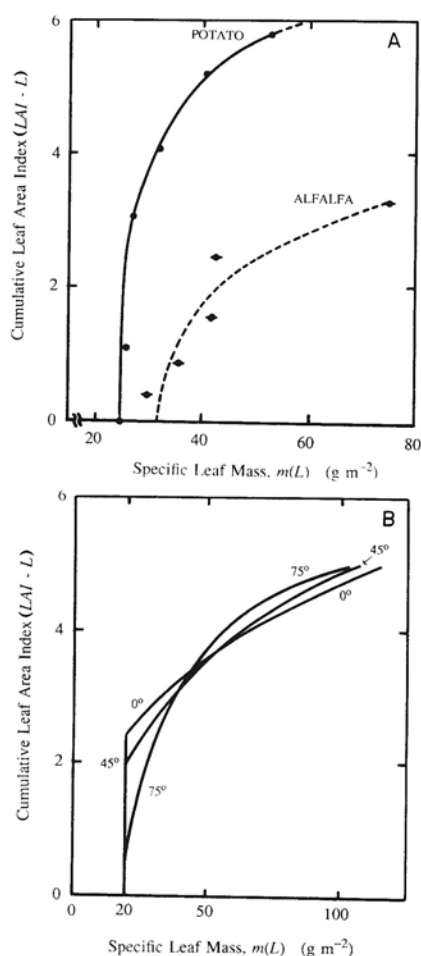
**Figure 4.** Modelled growth (final mass) of individual plants in a canopy, as dependent upon a fixed specific leaf mass, at age 100 days, when the canopy is dense. Other descriptors are as for figure 3.

#### Route 4

Canopy photosynthesis is optimized by a marked variation of specific leaf mass with depth in the canopy, with very thick leaves on top.

Leaves at the top of a laterally uniform canopy receive the most light of all leaves, both on a daily-integral basis and on a peak-value basis. Thus, they have the greatest potential for photosynthesis. Clearly, a plant should invest the most carbon or growth substrate here in the top leaves, where the ratio of potential payback (carbon fixed over leaf lifetime) to investment (carbon used for initial leaf growth) is highest. One expects, and observes, that SLM is highest at the top and drops off with depth (fig. 5A). Several questions arise: (a) How nearly optimal are observed profiles of  $m = \text{SLM}$  with canopy depth  $L = \text{cumulative leaf area index from the top}$ ? That is, how much gain is possible going from the current  $m(L)$  profile to the optimal one? Evaluating this requires a formalism to predict the optimal  $m(L)$ . (b) If cultivars or wild genotypes and species do not attain the optimal form of  $m(L)$ , what are the reasons? Do the reasons apply in agriculture or can they be safely circumvented for yield gains?

To answer these questions, Gutschick and Wiegand (1988) employed the calculus of variations, familiar in physics but not in plant physiology. Consider a potential shift of leaf mass  $\delta m(L)$  from one depth in the canopy to another depth. If the



**Figure 5.** Variation of specific leaf mass with depth in the canopy. (A), observed variation. The depth is described by  $L = \text{cumulative leaf area index from the bottom of the canopy}$ . Data for potato are from Tooming and Tammets (1984); data for alfalfa are from the author's laboratory. (B), modelled variations of specific leaf mass with depth that should maximize canopy-total photosynthesis. All results are for a simulation of mid-season growth, in which the canopy mass per ground area is  $200 \text{ g m}^{-2}$  ( $2 \text{ t ha}^{-1}$ ), and the average specific leaf mass over the whole canopy depth is  $40 \text{ g m}^{-2}$  (hence, the leaf area index is 5). The leaf photosynthetic parameters and the solar irradiance conditions are described in Gutschick and Wiegand (1988). Results are presented for three different leaf inclination angles.

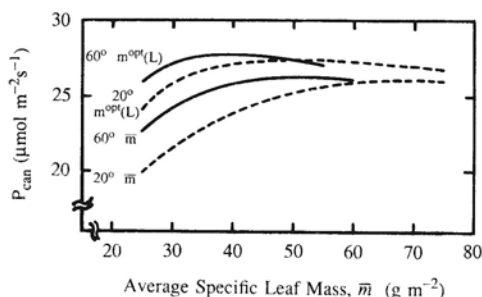
original distribution  $m(L)$  is optimal, no potential shift can improve  $P_{\text{can}}$ . In calculus notation,

$$\frac{\delta P_{\text{can}}}{\delta m(L)} = 0 \quad (4)$$

with the constraint that we have not changed the total mass of the canopy per area of ground,

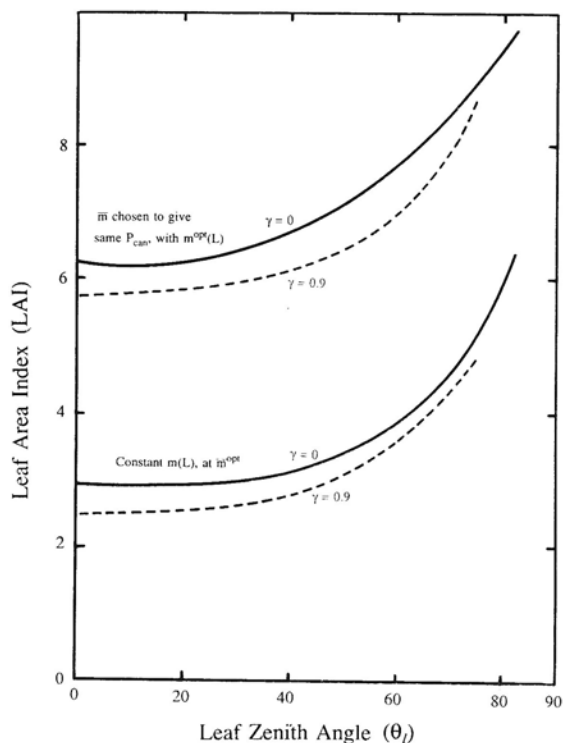
$M = \int dL m(L)$ , that is,  $\delta M = 0$ . The calculus of variations gives explicit mathematical formulae that can always be solved numerically in our case. The authors chose the best simple submodels of (a) Leaf photosynthetic responses to light, as dependent on the value of SLM. (They also addressed the questions of the relation of SLM to nitrogen content per area as a better or allied measure of photosynthetic capacity.) (b) Light penetration into the canopy. Diffuse light generated by sunlight striking leaves was ignored as unimportant for the trends they wished to see, but diffuse sunlight was accounted as accurately as possible; see earlier. (c) The statistical distribution of irradiance on individual leaves.

The potential profiles  $m^{opt}(L)$  were calculated for varied canopy masses  $M$  and varied leaf inclination angles from horizontal to highly erect. Figure 5B shows that strong profiles of  $m(L)$  are optimal. (The limiting low value,  $m_{min} = 20 \text{ g m}^{-2}$  was chosen arbitrarily to represent structural limitations on leaves; the results are quite insensitive to the value chosen.) The effect upon  $P_{can}$  of optimizing the profile  $m(L)$  is very significant at low



**Figure 6.** Computed canopy photosynthetic rate as a function of three traits. The rate is given in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The three traits are: (1) average specific leaf mass,  $\bar{m}$ , ( $\text{g m}^{-2}$ ) (horizontal graph axis); (2) inclination angle of leaves (20 or 60°; two curves for each choice); and (3) optimization of specific leaf mass with canopy depth ( $m^{opt}(L)$ ) or constancy of same ( $\bar{m}$ ). See the text for interpretation. The calculations were done with the parameter  $\theta = 0$  in the curve describing the angularity of the leaf photosynthetic response to irradiance (Johnson and Thornley, 1984). The results are quite insensitive to the value of  $\theta$ .

average SLM over the canopy,  $\bar{m}$ . Figure 6 shows that at  $\bar{m} = 30$  and leaf angle  $\theta_l = 20^\circ$ , the gain in  $P_{can}$  from optimizing  $m(L)$  (second curve from top) over having a constant  $m(L) = \bar{m}$  at all depths (lowest curve) is substantial—about a 20% gain. The gain is similar for more erect leaves,  $\theta_l = 60^\circ$ . At larger  $\bar{m}$ , say, 40, which is more typical of crops, the relative gain is less but still significant.



**Figure 7.** The large advantage in leaf area index, LAI, possible for a canopy with optimized variation of SLM with depth. The optimized canopies have a low average specific leaf mass that yet allows them to just match the photosynthetic rate of a canopy of the same biomass density but a depth-invariant specific leaf mass. The leaf area index of the optimized canopies (top two curves) much exceeds that of the unoptimized canopies (bottom two curves). In all cases, a canopy biomass density of  $200 \text{ g m}^{-2}$  was assumed and a standard mix of three environmental conditions was used. The solid curves and dashed curves differ in the assumed shape of the light response of leaf photosynthesis (the value of the parameter  $\theta$  in the equation of Johnson and Thornley (1984); called  $\gamma$  here to avoid confusion with leaf angle).

However, this optimization is already an evolutionary fact—even if crops are not optimal, they do have pronounced profiles of  $m(L)$ . What might improved profiles bring in improved yield? We can compare figures 5A and 5B to see that crops have lower contrasts between top and bottom  $m(L)$  than is predicted to be optimal. There are three reasons: (a) The model does not describe the clumping of leaves in real canopies that allows more light deep in the canopy. This deeper light penetration favors a less-pronounced  $m(L)$  profile. (b) Rather substantial lessening of the profile affect  $P_{can}$  only modestly; the principal gains from having a profile with thick leaves on top come from the initial trend to top-heaviness. (c) Plants

probably retain an evolutionarily selected conservatism in their  $m(L)$  profiles. Successful individual plants that overtop their competitors get a more even light distribution over their height and need a less-pronounced profile of  $m(L)$ . Plants have not been selected for growth in even-aged stands, where a sharper profile is advantageous. Only item (c) could be exploited for agricultural improvement, but items (a) and (b) indicate that the gains would be modest, 3 or 4% perhaps. This affirms empirical results (Elmore, 1980; Gifford and Evans, 1981; Khan and Tsunoda, 1970) that in canopies the gains in performance one may posit for individual leaves are greatly reduced.

It is of ecological and evolutionary interest as well that, over a broad range in average specific leaf mass,  $\bar{m}$ , the change in  $P_{can}$  is very modest, for any leaf angle. Thus, breeding crops for the optimal value of  $\bar{m}$  has very low potential; cultivars are already on the plateau in  $P_{can}$  as a function of  $\bar{m}$ . The author proposes that the plateau in  $P_{can}$  has ecological and evolutionary significance: a cultivar may depart radically in  $\bar{m}$  from the optimum but incur very little penalty in photosynthesis. However, in so doing, the plant gains much in leaf area, hence in ability to shade competitors (fig. 7).

## Conclusion

The general conclusions drawn from the above studies are that: (a) Canopy photosynthesis is rather refractory to improvement from manipulation of some physiological and morphological traits that are important for leaf photosynthesis. (b) There is modest room for improvement of crops, but the effort involved is substantial. (c) Greater promise lies in improving growth and yield per unit resource use, such as WUE, than in improving yield itself.

As an adjunct to this discussion on photosynthesis *per se*, two comments on processes related to the disposition of photosynthate are relevant: (a) One might entertain the prospect of maximizing the scavenging (remobilization) of carbon and nitrogen in leaf tissues to support seed filling. Current crop cultivars vary widely in the percentage of N scavenged (Cregan, 1983). The percentage is only about 15 to 50% in grain legumes (Israel, 1981), well below that for cereals. The author proposes that a major limitation is kinetic—that seed filling also demands balanced amounts of other elements, but many of these are not scavengable from leaf tissue because they cannot be

transported in phloem sap. To provide such phloem-immobile elements in adequate amounts to make greater N scavenging productive, a high rate of uptake from soil is needed. High uptake rates might be possible to breed into crops, and the corequisite application of fertilizer late in the season may also be practical in agriculture. The poor late-season availability of phloem-immobile elements in soil may have provided selection pressure that prevented evolution of the capacity. (b) The timing of anthesis might be improved in a few crops. Much work, primarily in ecology (reviewed in Gutschick, 1987), has addressed the question of when a determinately reproducing plant should shift from vegetative to reproductive growth. An early switch leaves a long time for seed fill but limits the vegetative plant size for feeding seed fill, and *vice versa*. Agricultural selection has implicitly approached optimization of the timing of anthesis (Paltridge and Denholm, 1974), mostly in relation to potential water stress (Derera *et al.*, 1969; Gutschick, 1987). Nonetheless, significant room for improvement may be left in some crop species and cultivars.

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