

Designing rice for the 21st century: the three laws of maximum yield

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John E. Sheehy and P.L. Mitchell

Abstract

Designing high-yielding rice plants

When trying to design high-yielding rice plants, several questions arise. What sets the limit to the maximum yield of a crop? What are those limits? To what extent does photosynthesis shape yield? What is the importance of canopy architecture in yield formation? Why are high yields achieved in one region not achievable in another? Below, we describe tools that allow us to answer those questions and, using them, we propose that breeders should aim for an advanced type of rice, different from the traditional or semidwarf or new plant type (NPT) varieties currently available. Furthermore, we believe that an advanced type with very erect leaves and a large leaf area index (Vela) would increase the maximum yield of C_3 rice to about 13 t ha^{-1} (at a moisture content of 14%).

The results show that in the tropics a Vela variety would increase maximum yield by 11% (from 11.7 to 13.0 t ha^{-1}). Yields in the subtropics are about 38% higher than in the tropics largely owing to the lower average daily temperatures, which reduce the coefficient of maintenance respiration and increase the quantum yield of C_3 photosynthesis. The C_4 syndrome could increase yields by about 40% above the yields of semidwarf cultivars in the tropics and by about 24% above the predicted yields for C_3 rice in the subtropics.

Tools for designing high-yielding plants: the laws of maximum yield

A major aim of this work is to provide simple tools to obtain a better understanding of how solar energy can be used most efficiently for growth and what sets the limit to the maximum yield of a crop. In the spirit of simplification to describe ideal gases, we set the challenge of deriving three simple expressions linking maximum daily crop photosynthesis (P_{gdmax}) and maximum aboveground biomass and grain yield ($W_{\text{smax}}, W_{\text{gmax}}$) to the driving variables radiation (I_{day}) and temperature (T):

$$P_{\text{gdmax}} = \kappa_T \phi I_{\text{day}} \quad (\text{A1})$$

$$W_{\text{smax}} = c_T P_{\text{gdmax}} \quad (\text{A2})$$

$$W_{\text{gmax}} = H W_{\text{smax}} \quad (\text{A3})$$

The term I_{day} is the photosynthetically active solar radiation (PAR) incident on a crop in a day ($\text{MJ m}^{-2} \text{d}^{-1}$). The term ϕ is the fractional interception of PAR by the crop; in theory, the maximum value of ϕ (ϕ_{max}) is 1 but, in practice, full interception is achieved when $\phi = 0.95$. Solar energy (PAR) is converted into the energy contained in carbohydrate by κ_T , the quantum use efficiency of PAR intercepted by the crop. The term κ_T is temperature dependent for C_3 ($\kappa_{T\text{max}} = 6.6 \text{ g CH}_2\text{O MJ}^{-1}$ at 30°C), but not for C_4 crops ($\kappa_{T\text{max}} = 8.0 \text{ g CH}_2\text{O MJ}^{-1}$). We explore how κ_T is affected by canopy architecture and leaf photosynthesis. Maximum aboveground biomass (W_{smax}) depends on maximum crop photosynthesis and a conversion factor (c_T), which is crop and temperature dependent. We show that c_T depends on major losses of carbohydrate from shoot biomass in respiration and allocation to roots. In addition, it is influenced by the decline in maximum canopy photosynthesis toward final yield owing to nitrogen recycling from vegetative to reproductive sinks. Maximum grain yield (W_{gmax}) is simply the product of harvest index and maximum shoot biomass; we describe the relationship between the fraction of biomass supporting grain yield and harvest index. Our analysis gave us an opportunity to derive a theoretical expression for the radiation use coefficient, ϵ_{rue} :

$$\epsilon_{\text{rue}} = S_r (1 - \sigma) \kappa_T \quad (\text{A4})$$

where S_r is the shoot weight ratio and σ is the fraction of gross photosynthesis lost as respiration. The theoretical estimates for rice and maize were 2.5 and 3.4 g MJ^{-1} (aboveground biomass, intercepted PAR), respectively. We tested the equations for a contrasting crop (forage grass) grown in an environment very different from that of rice (Appendix).

Keywords: photosynthesis, biomass, yield, source-sink, radiation use efficiency, respiration, models.

Introduction

The world population is predicted to reach a plateau of 9.3 billion in 2050, with the population of Asia rising by about 27% to 5.2 billion and that of Africa almost doubling to nearly 2 billion. Asia and Africa are continents where most of the world's existing poverty is concentrated. More than 850 million people are hungry and each day about 25,000 people die from hunger-related causes. Sheehy and Mitchell (2011a, b) discussed these global concerns from the perspective of the research in rice required to prevent potentially catastrophic consequences of rising populations and climate change. Of all the problems facing the human race, food and energy, with many links between them, must be the largest. And, rice, wheat, maize, millet, and sorghum provide 70% of the food energy of the world.

How do we design a very high yielding rice type for the 21st century? Have the semidwarf varieties of the Green Revolution reached a source-sink bottleneck set by their dwarfing genes? What sets the limit to the maximum yield of a crop? What are those limits? To what extent does photosynthesis shape yield? What is the importance of canopy architecture in yield formation? Why are high yields achieved in one region not achievable in another? What is the role of crop management? It is easy to ask such questions, but answering them is always more difficult. In order to do so, we trace the route from solar energy via photosynthesis to crop yield in a simple and quantitative manner. The ultimate aim of that journey is to gain a better understanding of the core characteristics of rice plants capable of delivering substantially higher yields. Each part of the yield puzzle needs a name and a number; in this paper, we attempt to provide tools to supply them. The work described grew out of an attempt to use simple models to describe the relationship between crop photosynthesis and yield. We noticed that predicted daily crop photosynthesis plotted against fractional interception of PAR could be described by a straight line. This suggested that, even in the tropics, the irradiance of leaves inside a canopy was sufficiently low that the relationship between photosynthesis for such leaves and irradiance could, to a good approximation, be described by a straight line. We decided to investigate the consequences of making that assumption and whether such simplifications could be extended to produce a set of simple equations describing maximum crop yield.

Our previous analyses of limitations to rice yields (Sheehy et al 2000a, Mitchell and Sheehy 2000, Sheehy et al 2007b) led to the C_4 Rice Project at IRRI (von Caemmerer et al 2012; and see C_4 Rice

Project at www.irri.org). What has become clear is that the supercharged engine (C_4 photosynthesis) will need a fuel supply (light) to match its capacity, and transmission and suspension (structure and proportions of the rice plant) that use the increased power (more fixed carbon) in the way required (increased grain yield). To this end, we propose that breeders aim for an advanced type of rice, different from traditional or semidwarf or new plant type (NPT) varieties currently available. Furthermore, we believe that an advanced type with very erect leaves and a large leaf area index (Vela) would increase the yield of C_3 rice significantly.

Assumptions

Several assumptions have to be made to achieve the comparative simplicity of equations describing canopy photosynthesis and yield. The principal ones are sketched below. Values for the parameters are given in Table 1.

1. The carbon content of biomass is taken as 40% so that carbohydrate (CH_2O) and dry matter can be used interchangeably (Latshaw and Miller 1924, Jimenez and Ladha 1993).
2. Respiration is divided into two components: one associated with synthesis of new biomass, a cost of 25% of the carbohydrate available, and the other associated with the maintenance of biomass and thus varying with the amount of biomass at any one time and also sensitive to temperature (see Appendix).
3. Roots are taken as 0.15 of total crop biomass (roots and shoots combined), and are accounted for through a parameter so that attention is solely on aboveground biomass.
4. The crop exhibits a logistic growth pattern in which maximum rate of growth occurs halfway through the growth duration and then decreases to zero as maximum biomass is reached at the end of growth duration.
5. The maximum rate of crop photosynthesis is achieved at flowering, about halfway through crop duration.
6. Although the shape of the curve relating leaf photosynthesis to PAR incident on the leaf is hyperbolic, in practice, with erect canopies and the angular distribution of PAR through the day, the leaf is never receiving an amount of PAR that would take it beyond the more or less linear portion of the curve.
7. Canopy photosynthesis when maximum biomass is achieved is less than its maximum value by the fraction f . This allows for changes in the canopy

Table 1. Values for the driving variables (I_{day} , T_{ps} , T_{mean}) and parameters (α_T , ϵ_c , β , m_T , f , τ , k_d , H , p_g) for a well-fertilized and irrigated rice crop. (The driving variables for temperature do not appear in the final equations but control the values for α_T and m_T .) The equations consider 1 m² of ground and use values for a day, averaged over the second half of crop duration. This is the period when the canopy is complete, interception of PAR is maximal, the rate of canopy photosynthesis is near maximum, and biomass is near maximum so that the maximum amount of maintenance respiration is occurring.

Variable or parameter (units)	Meaning	Value, typical	Value, alternative	
I_{day}	Daily total of PAR incident on the crop (MJ m ⁻² d ⁻¹)	Main driving variable: energy source for photosynthesis.	10 for tropics, subtropics, and unusually sunny temperate growth season	
T_{ps}	Temperature during daylight (°C)	Controls quantum yield (α_T) of C ₃ plants: changing it by 0.14 g CH ₂ O MJ ⁻¹ °C ⁻¹ from value of 5.9 g CH ₂ O MJ ⁻¹ at base temperature of 30 °C.	30 °C tropics; 25 °C subtropics and warm temperate	
T_{mean}	Mean daily temperature (°C)	Controls rate of maintenance respiration (m_T): using $Q_{10} = 2$ from a value of 0.007 g g ⁻¹ d ⁻¹ at base temperature of 20 °C.	28 °C tropics; 23 °C subtropics and warm temperate	
α_T	Apparent quantum yield of leaf photosynthesis (g CH ₂ O MJ ⁻¹) at daylight temperature	Maximum amount of photosynthesis for unit increment in PAR incident on crop.	For C ₃ , 5.9 at 30 °C; 6.6 at 25 °C	For C ₄ , 7.2 (invariant with temperature)
ϵ_c	Canopy efficiency factor (dimensionless)	Allows for the effect of the canopy architecture and maximum rate of leaf photosynthesis on the effective quantum yield of a canopy.	For C ₃ , 0.87	For C ₄ , 0.97
τ	Fraction of PAR transmitted by a leaf (dimensionless)	Allows for leaf photosynthesis inside the canopy.	0.1	
k_d	Fraction of dead matter in aboveground dry matter (dimensionless)	Reduces the amount of biomass needing maintenance respiration.	0.15	
m_T	The rate of maintenance respiration (g g ⁻¹ d ⁻¹) at mean daily temperature	Main variable source of losses of fixed carbon, depending on crop biomass and mean daily temperature.	0.012 (at 28 °C); 0.0086 (at 23 °C)	
β	Coefficient representing losses from gross photosynthesis (dimensionless)	Allows for synthetic (growth) respiration, losses as exudates from roots, and in legumes the respiratory cost of nitrogen fixation; also allocation to roots (in perennial grasses, the weight of stubble).	0.59	0.38 (legumes); 0.3 (perennial grasses)
f	Factor representing gross daily canopy photosynthesis as a fraction of its maximum value (dimensionless)	Allows for the decline in photosynthetic activity of the canopy at crop maturity, from its maximum value earlier in crop duration; particularly when nitrogen is transferred from senescing lower leaves to filling grain.	0.7	
H	Harvest index	Fraction of crop biomass (aboveground) for harvest.	0.5	
p_g	Maximum rate of leaf photosynthesis (μmol CO ₂ m ⁻² s ⁻¹)	At 2,000 μmol quanta m ⁻² s ⁻¹ .	32.5 rice (C ₃)	56 maize (C ₄)

and changes in leaf photosynthesis characteristics that occur during the second half of growth duration.

- The driving variables of PAR and temperature are each supplied as a single average value for the second half of growth duration. This assumption is reasonable in the tropics and subtropics where variations in solar angle and in temperature are relatively small across a period of 2 or 3 months. In temperate regions where solar angle and temperature change greatly during the growing

season, this assumption—of linear averaging across a period of months—works less well.

Canopy architecture and the distribution of solar irradiance

Photosynthetically active radiation (PAR, wavelengths 400–700 nm) at Earth's surface is about 50% of the total shortwave incident solar radiation, with the other 50% being shortwave

infrared radiation. On a clear day, the amount of PAR incident on a horizontal surface varies in an approximately sinusoidal manner with a typical maximum daily irradiance in the tropics of about $10 \text{ MJ m}^{-2} \text{ d}^{-1}$, giving $1,673 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at midday. Erect leaves do not experience full midday solar irradiance. To illustrate the principle, contrast the PAR incident on a horizontal leaf at midday with the sun overhead with the irradiance of a leaf inclined at 80° to the horizontal. The horizontal leaf would receive $1,673 \mu\text{mol m}^{-2} \text{ s}^{-1}$, whereas the inclined leaf would receive $334 \mu\text{mol m}^{-2} \text{ s}^{-1}$. In order to intercept the entire energy incident on its horizontal counterpart, the area of the erect leaf would have to be five times that of the horizontal leaf. Many leaves within the canopy receive PAR after transmission through other leaves. Monsi and Saeki (1953) demonstrated that the decline in solar irradiance inside a canopy can be described by the Bouguer-Lambert Law:

$$I_L = I_0 \exp(-kL) \quad (1)$$

where I_L is the irradiance (on a horizontal surface) beneath leaf area index L of a canopy, I_0 is the irradiance incident on the canopy, and k is the extinction coefficient for PAR ($\text{m}^2 \text{ ground m}^{-2} \text{ leaf}$). Canopies with erect leaves have values of $k \approx 0.2-0.3$ and canopies with more prostrate leaves have values of $k \approx 0.6-0.8$. The fraction of incident PAR that is intercepted by the canopy, ϕ , can be written as

$$\phi = [1 - \exp(-kL)] \quad (2)$$

At a given value of L , the PAR incident on a leaf (I_L) is given by

$$I_L = kI_0 \exp(-kL)/(1 - \tau) \quad (3)$$

where τ is the fractional transmission of PAR through a leaf. The fractional distribution of irradiance incident on leaves of a prostrate canopy ($k = 0.6$) and an erect canopy ($k = 0.2$) is shown in Figure 1. At the top of the canopy (less than 3 LAI units downward), it can be seen that the leaves of the erect canopy receive lower irradiance than the leaves of a prostrate canopy. Overall, the erect canopy distributes the irradiance more uniformly through the canopy than the prostrate canopy.

From the perspective of nitrogen recycling from leaves during reproductive growth, it is sometimes convenient to divide the leaf area into different categories. In this respect, a model of light distribution derived by Monteith (1965) is valuable. The interception and distribution of irradiance in a

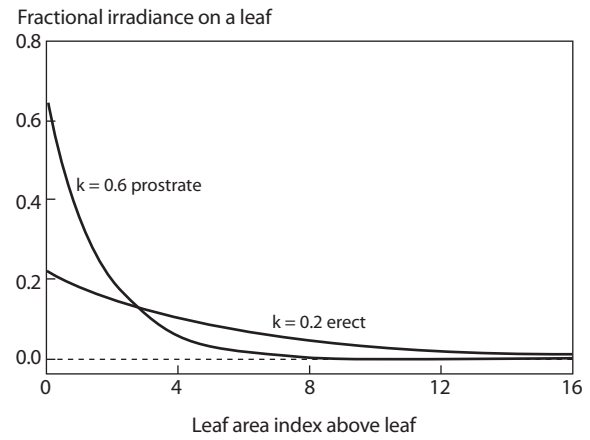


Fig. 1. Fractional irradiance on a leaf in a canopy as a function of leaf area index above the leaf, for prostrate leaves ($k = 0.6$) and erect leaves ($k = 0.2$). Fractional irradiance is computed as I_L/I_0 from equation 3; it is the amount of PAR received by a leaf as a fraction of what is available at the top of the canopy.

Monteithian canopy are defined by a parameter, s , where s defines the fraction of irradiance that passes through unit LAI without interception. The model divides the LAI according to the irradiance received by leaves: there are sunlit, once-shaded, and twice-shaded categories of LAI. Twice-shaded leaves exist just above the light compensation point and are unimportant photosynthetically, but important as a nitrogen store (Sinclair and Sheehy 1999). The sunlit, once-shaded, and twice-shaded fractions of the LAI approach an asymptotic value of $(1 - s)^{-1}$.

The values of k , s , mean leaf angle, sunlit leaf area index, and the LAI required to intercept 95% of the PAR incident on the canopy are shown in Table 2. The smaller the extinction coefficient, the more erect are the leaves and the greater the LAI required for full interception of PAR. Improvements in the erectness of leaves must be accompanied by increases in LAI to ensure the full interception of PAR. Such high LAIs are probably key to nitrogen reservoirs and high rates of canopy photosynthesis at crop maturity.

Leaf photosynthesis, leaf angle, and solar irradiance

The simplest model of leaf photosynthesis is defined in terms of limiting factors (Fig. 2A) and goes back to Blackman (1905). At first, photosynthesis is limited by light and then, at high irradiance, by other factors such as CO_2 , temperature, and intrinsic anatomical and biochemical factors (Farquhar et al 1980). The relationship between leaf photosynthesis (p_g) and irradiance (I_L) incident on a leaf (Fig. 2B) is often described using a simple rectangular hyperbola:

Table 2. Properties of rice canopies for different architectures. The four canopy types are defined by approximate extinction coefficients and values of Monteith's parameter s , which was computed using $s = (\exp(-k) - \tau)/(1 - \tau)$ (Sheehy and Johnson 1988), with $\tau = 0.1$. Using the extinction coefficient (two significant figures as tabulated), the LAI for 95% interception of PAR was derived. In turn, the s value was used to calculate the sunlit LAI with the formula $(1 - s^4)/(1 - s)$ from Monteith (1965); the leaf angle was also estimated using the approach described in that paper. The advanced canopy architecture described by very erect leaves and large LAI is called Vela.

Item	Canopy type			
	Traditional	Semidwarf	Erect	Vela
Monteith's parameter, s	0.5	0.6	0.7	0.8
Extinction coefficient, k	0.60	0.45	0.31	0.20
LAI for 95% interception, LAI_{95}	5.0	6.7	9.7	15.0
Sunlit LAI	1.9	2.4	3.2	5.2
Leaf angle (degrees from horizontal)	60	66	73	79

$$p_g = \alpha_T I_l p_{\max} / (\alpha_T I_l + p_{\max}) \quad (4)$$

where α_T is the quantum yield, T is temperature, and p_{\max} is the theoretical rate of leaf photosynthesis as $I \rightarrow \infty$. The practical maximum rate of leaf photosynthesis ($32.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for rice and $52.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for maize at an irradiance of $2,000 \mu\text{mol m}^{-2} \text{ s}^{-1}$) depends linearly on the nitrogen content of the leaf as described by Peng (2000) and Evans and von Caemmerer (2000). It should be noted that the greater the maximum rate of leaf photosynthesis, the greater the range of irradiance values over which photosynthesis can be described in terms of the light-limited portion of the relationship. This can be seen in Figure 2B, where noticeable curvature occurs at lower values of incident PAR looking from the uppermost curve downward.

The quantum yield, α_T , is the initial slope of the hyperbola fitted to leaf photosynthesis plotted against PAR incident on the leaf and it represents the maximum amount of carbon dioxide fixed by unit amount of PAR. It is sometimes called photochemical efficiency and general values for C_3 and C_4 photosynthesis can be estimated from measurements. Ehleringer and Pearcy (1983) found that measured quantum yields (at 30°C leaf temperature and 330 ppm carbon dioxide concentration) varied little among C_3 species and averaged $0.053 \text{ mol CO}_2 \text{ mol}^{-1}$ quanta, absorbed PAR. In C_4 plants with the NADP-ME pathway, which is the group including maize and sorghum, the measured quantum yield was $0.065 \text{ mol CO}_2 \text{ mol}^{-1}$ quanta, absorbed PAR. Converting units (1 mol CO_2 produces $1 \text{ mol CH}_2\text{O}$; $30 \text{ g CH}_2\text{O mol}^{-1}$; $4.6 \text{ mol quanta MJ}^{-1}$ PAR) gives 7.314 and $8.970 \text{ g CH}_2\text{O MJ}^{-1}$, absorbed PAR, for C_3 and C_4 plants, respectively. To adjust the basis of expression from absorbed PAR to PAR incident on

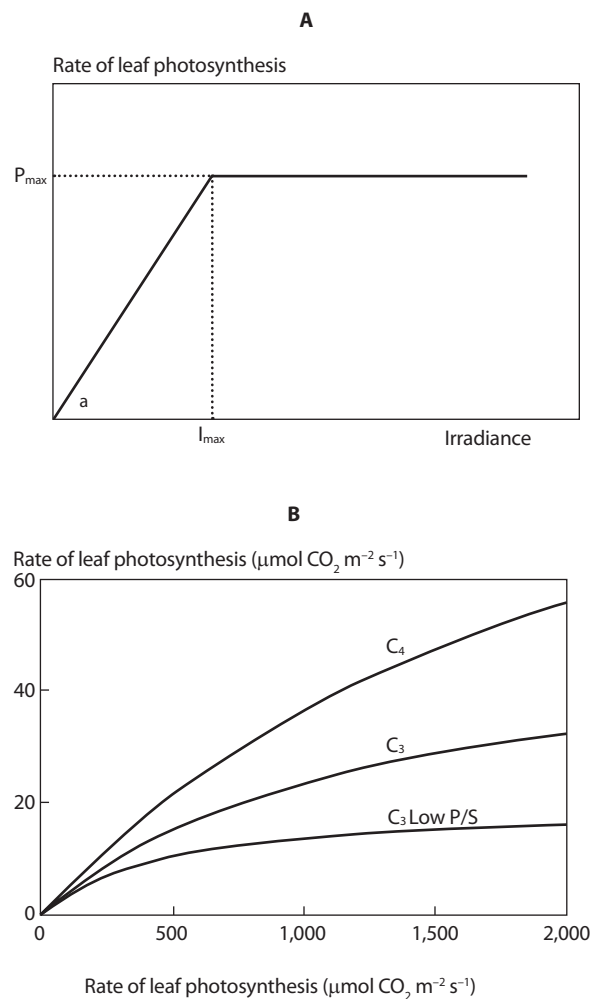


Fig. 2. (A) Diagram of the Blackman (1905) representation of leaf photosynthesis as a function of irradiance. The quantum yield (α) is the slope of the line given by P_{\max} divided by I_{\max} (which is the tangent of angle a). (B) Leaf photosynthesis as a function of irradiance represented by simple hyperbolic curves for C_4 and C_3 photosynthesis (quantum yields 0.042 and $0.052 \text{ mol CO}_2 \text{ mol}^{-1}$ quanta, respectively, where quanta are incident PAR). The curves are calculated to provide rates of photosynthesis at $2,000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR of 56 , 32.5 , and $16.25 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for C_4 , C_3 , and C_3 with low photosynthesis, respectively. The asymptotes for the curves are 121.3 , 53.0 , and $20.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in the order used above.

the leaf, we take general values for the fractions of incident PAR that are reflected or transmitted (τ in the equations above) each as 0.1, averaged across the PAR waveband and across all angles of incidence (Monteith and Unsworth 1990, p 86). Then measured quantum yields for one unit of absorbed PAR are for $1/0.8 = 1.25$ units of incident PAR so they must be divided by 1.25 to express them on the incident basis, producing 5.8512 and 7.176, rounding to 5.9 and 7.2 g CH₂O MJ⁻¹, incident PAR, for C₃ and C₄ plants, respectively. Quantum yield for C₄ plants does not vary with temperature but for C₃ plants the amount of photorespiration increases with temperature and changes the quantum yield by -0.0013 mol CO₂ mol⁻¹ quanta, absorbed PAR, for each 1 °C increase in leaf temperature (measurements in the range of 16–38 °C; Ehleringer and Pearcy 1983). Converting units and adjusting the basis gives a temperature coefficient of 0.14 g CH₂O MJ⁻¹ °C⁻¹, incident PAR. This can be summarized as

$$\alpha_T = \alpha_{30} - 0.14(T_{PS} - 30) \quad (5)$$

where α_T is the quantum yield at temperature T_{PS} (°C), which is the mean leaf temperature during photosynthesis, that is, during daylight, taken for convenience as sunrise to sunset; α_{30} is the quantum yield at 30 °C (leaf temperature during daylight); 0.14 g CH₂O MJ⁻¹ °C⁻¹ is the temperature coefficient; and 30 °C is the base temperature of the leaf during daylight.

For crops with sufficient water for maximal photosynthesis, as considered here, transpiration will be sufficient to maintain leaf temperature close to that of the air. The mean air temperature during daylight can be taken as the mean of maximum and mean daily temperatures, where mean daily temperature is the mean of maximum and minimum temperatures. This can be calculated from these temperatures as

$$T_{PS} = (3 T_{max} + T_{min})/4 \quad (6)$$

If only mean temperature is available, then an alternative approach is to estimate the span between minimum and maximum temperatures, T_{span} , and use

$$T_{PS} = T_{mean} + 0.25 T_{span} \quad (7)$$

In the tropics, T_{span} can be as low as 5 °C so that T_{PS} is only about 1 °C higher than mean daily temperature; in temperate climates, where T_{span} could be 10 °C, then T_{PS} would be 2–3 °C higher than T_{mean} .

Canopy architecture and canopy photosynthesis

Models of canopy photosynthesis are the result of combining models of the distribution of irradiance with a model of leaf photosynthesis as a function of irradiance (Thornley and Johnson 1990). The diurnal pattern of incident solar irradiance is assumed to vary sinusoidally (Monteith 1965). The classical equation for canopy photosynthesis is the outcome of combining the rectangular hyperbolic function of leaf photosynthesis and irradiance with the Bouguer–Lambert Law description of PAR distribution in the canopy. This equation linking canopy photosynthesis and irradiance (Verhagen et al 1963, Sheehy and Johnson 1988) can be written as

$$P_g(I) = (p_{max}/k) \ln \{[\alpha_T k I + p_{max}(1 - \tau)] / [\alpha_T k I \exp(-kL) + p_{max}(1 - \tau)]\} \quad (8)$$

where $P_g(I)$ is gross canopy photosynthesis (g CH₂O m⁻² ground) at irradiance I , which is the irradiance incident on the canopy (PAR, MJ m⁻² ground), τ is the fraction of PAR transmitted by a leaf, and L is the leaf area index (m² leaf m⁻² ground).

We used this equation to make a series of predictions of daily canopy photosynthesis for clear conditions (PAR = 10 MJ m⁻² d⁻¹). We observed that, for high rates of individual leaf photosynthesis and erect canopies, the relationship between predicted canopy photosynthesis and fractional light interception was to a good approximation linear. The predictions for erect C₄ ($y = 80.8x$, $r^2 = 0.99$) and C₃ ($y = 61.5x$, $r^2 = 0.99$) canopies are shown in Figure 3A. To ensure that the result was not a quirk of equation 8, we used the Monteith model to confirm this observation.

The leaf irradiance data shown above suggest that the photosynthetic rate of leaves in a canopy could, to a good approximation, be represented by the light-limited linear portion of the leaf photosynthesis irradiance relationship. Consequently, we assumed that the constant of proportionality linking leaf photosynthesis and irradiance was $\epsilon_c \alpha_T$, where ϵ_c is a canopy efficiency factor representing the effect of canopy architecture and maximum leaf photosynthesis on the effective quantum yield of a leaf over the range of irradiances experienced by leaves in a canopy during the day.

The linear approximation to the relationship between leaf photosynthesis (Fig. 3B) and irradiance (instantaneous rate of receipt of PAR) can be written as

$$p_g = \epsilon_c \alpha_T I \quad (9)$$

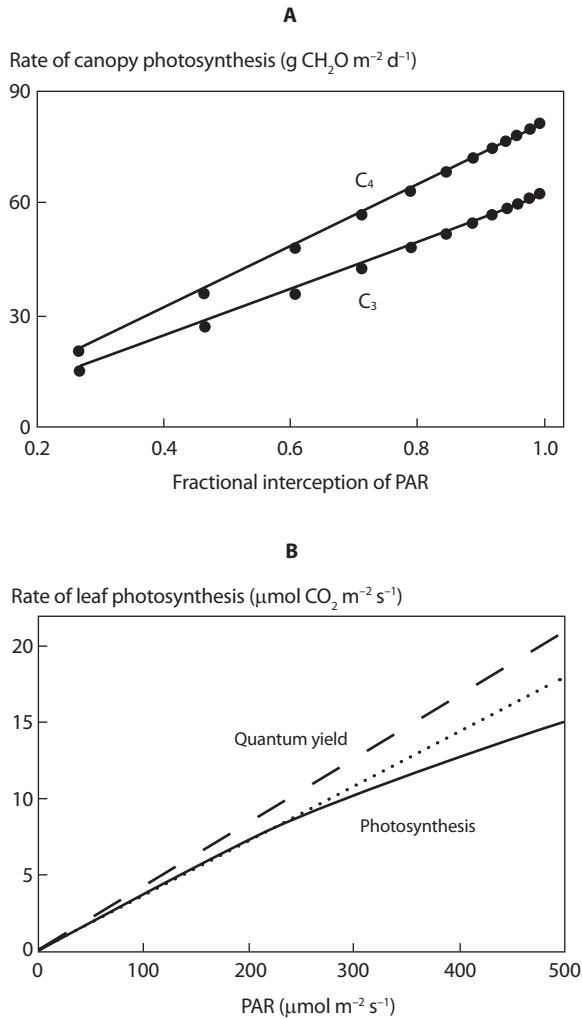


Fig. 3. (A) The relationship between canopy photosynthesis predicted by equation 8 and fractional interception of PAR when PAR (variable I) is set at 10 MJ m⁻² d⁻¹. The points come from calculation with various values of leaf area index (variable L) to cover a range of fractional interception of PAR. Values of parameters are in Table 1. The equations of the fitted lines are $y = 61.5x$ ($r^2 = 0.99$) for C₃ rice and $y = 80.8x$ ($r^2 = 0.99$) for C₄ maize.

(B) The rate of leaf photosynthesis (solid curve) calculated with equation 4 up to 500 μmol m⁻² s⁻¹ PAR, the range of values experienced inside the rice canopy. The straight lines are the quantum yield (dashed line; the initial slope of the curve, 0.042 mol CO₂ mol⁻¹ quanta) and the linear approximation (dotted line; slope 0.036 mol CO₂ mol⁻¹ quanta). The linear approximation is within ±10% of photosynthesis given by the curve for the range 0–350 μmol m⁻² s⁻¹ PAR.

and, if we substitute for I₁ from equation 3 and integrate it over the leaf area index L, canopy photosynthesis is given by

$$P_g(I) = \epsilon_c \alpha_T I [1 - \exp(-kL)] / (1 - \tau) \quad (10)$$

Canopy photosynthesis over a day can be obtained by integrating irradiance over a day to give

$$P_{gd} = \epsilon_c \alpha_T I_{\text{day}} [1 - \exp(-kL)] / (1 - \tau) \quad (11)$$

where I_{day} is the total photosynthetically active solar radiation (PAR) incident on a crop in a day

(MJ m⁻² d⁻¹). It is convenient to write the quantum yield of the canopy as $\kappa_T = \epsilon_c \alpha_T / (1 - \tau)$, and canopy photosynthesis as the product of the fraction of daily PAR intercepted by the canopy, ϕ , multiplied by the quantum yield of the canopy:

$$P_{gd} = \kappa_T \phi I_{\text{day}} \quad (12)$$

where $\phi = [1 - \exp(-kL)]$ and it is the fractional interception of PAR by the crop. Mathematically, the maximum value of ϕ is 1, but, in practice, full interception is achieved when $\phi = 0.95$. The maximum rate of canopy photosynthesis is

$$P_{gd\text{max}} = 0.95 \kappa_T I_{\text{day}} \quad (13)$$

The quantum yield of the canopy $\kappa_T = \epsilon_c \alpha_T / (1 - \tau)$ has as units g CH₂O MJ⁻¹, and ϵ_c is a canopy efficiency factor (dimensionless) governing the effect of the canopy architecture and maximum rate of leaf photosynthesis on the effective quantum yield of leaves in a canopy. The fractional transmission of PAR by a leaf, τ , is assumed to be 0.1. The magnitude of ϵ_c was calculated by comparing the predictions of canopy photosynthesis models using the hyperbolic and linear descriptions of leaf photosynthesis as a function of irradiance (Table 3). The value of ϵ_c for C₃ crops increases with canopy erectness from 0.83 to 0.98. For a C₄ crop, $\epsilon_c = 1.0$. At the other extreme, the lowest value of ϵ_c , 0.75, was obtained for the assumption that the maximum rate of leaf photosynthesis was limited to 50% of its normal value. The values of canopy photosynthesis for the scenarios considered in this paper are shown in Table 3, with semidwarf canopies having a rate of 55.2 g CH₂O m⁻² d⁻¹, which rises to 61.5 g CH₂O m⁻² d⁻¹ for a Vela canopy.

Canopy photosynthesis is rarely measured in a direct way but, when data have been obtained, they support the assertion above that canopy photosynthesis is linearly related to intercepted PAR. For example, the relationship between measured canopy photosynthesis (y) and fractional interception of PAR (x) for data obtained for lucerne and sainfoin by Sheehy and Popple (1981) is $y = 38.1x$, $r^2 = 0.93$ (Fig. 4). The daily total of PAR close to harvest was 7.3 MJ m⁻² d⁻¹, the average daylight temperature, T_{psf}, was 18.6 °C, and the mean daily temperature was 16.1 °C. From equation 5, we estimate the quantum yield to be 7.5 g CH₂O MJ⁻¹; both lucerne and sainfoin have prostrate canopies and, by comparing equation 12 and the regression equation, we estimated the mean value of their canopy factor, ϵ_c , as 0.63.

Canopy photosynthesis increases as LAI increases but at a decreasing rate and so approaches

Table 3. The effect of extinction coefficient (k) and maximum rate of leaf photosynthesis (at 2,000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PAR and 390 ppm CO_2) on the canopy efficiency factor and maximum daily canopy photosynthesis. The four canopy types of rice were defined in Table 2. The extra subtypes of erect canopy are for a C_4 rice and for C_3 with low photosynthesis (half the usual maximum rate of leaf photosynthesis of $32.5 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$). Note the different units for leaf and canopy photosynthesis, including that leaf photosynthesis is for unit leaf area and canopy photosynthesis is for unit ground area.

Item	Canopy type			
	Traditional	Semidwarf	Erect	Vela
Extinction coefficient, k	0.60	0.45	0.31	0.20
Leaf photosynthesis, $P_{g\text{max}}$ ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)	32.5	32.5	32.5 (C_4 , 56.0) (low, 16.3)	32.5
Canopy efficiency factor, ϵ_c	0.83	0.88	0.93 (C_4 , 1.00) (low, 0.75)	0.98
Canopy photosynthesis, $P_{g\text{dmax}}$ ($\text{g CH}_2\text{O m}^{-2} \text{d}^{-1}$)	52.1	55.2	58.3 (C_4 , 76.0) (low, 47.0)	61.5

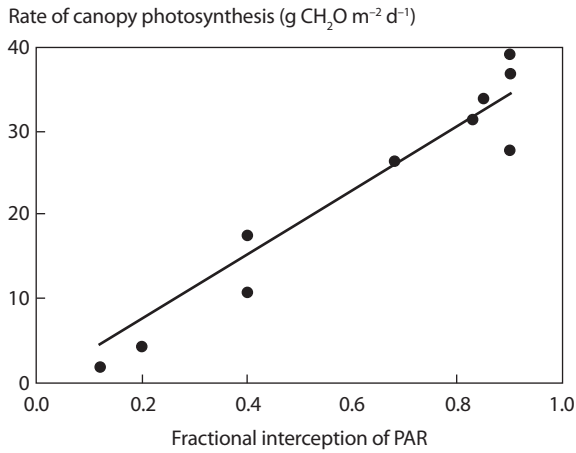


Fig. 4. The relationship between canopy photosynthesis and fractional interception of PAR using experimental data for lucerne and sainfoin (Sheehy and Popple 1981). The equation of the fitted line is $y = 38.1x$ ($r^2 = 0.93$).

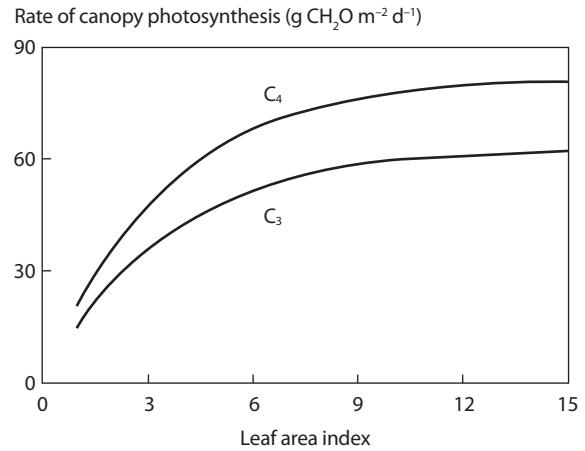


Fig. 5. The relationship between canopy photosynthesis and leaf area index as predicted by equation 8 using values for variables and parameters from Table 1.

an asymptote (Fig. 5) at full PAR interception. In rice, the maximum value of LAI is achieved near flowering, thus imposing a maximum rate of canopy photosynthesis. Usually, the live LAI declines toward maturity as nitrogen is withdrawn from leaves and they become senescent. It is interesting to note that the loss of the once-shaded leaves results in a decline of only 22–27% in canopy photosynthesis (Sheehy 2000). This emphasizes the point that, in a mature canopy, nitrogen and carbohydrates can be recycled from approximately 70% of the leaves without a proportionate loss in canopy photosynthesis. Growth and leaf area data for a high-yielding rice crop of IR72 (Sheehy et al 2000b) are shown in Table 4.

Mass conservation: the link between photosynthesis and yield for the ideal crop

The mass balance of the whole crop (shoots plus roots) at time t can be written as

$$dW/dt = F_{ci}(t) + F_{mi}(t) - F_{co}(t) - F_{eo}(t) - F_{do}(t) \quad (14)$$

where W is the total weight of the crop (shoots plus roots), $F_{ci}(t)$ is the input of carbon-based matter associated with the instantaneous rate of canopy gross photosynthesis, $F_{mi}(t)$ is the rate of input of mineral elements, $F_{co}(t)$ represents the losses from the system as respiration in the same

Table 4. Measurements of a high-yielding crop of indica rice (Sheehy et al 2000b) at different stages of growth. Components of shoot weight and of LAI are offset in the table. Stem is culm (the true stem) plus leaf sheaths surrounding it. Photosynthetic LAI is defined as the sunlit and once-shaded fractions of LAI, given here as a percentage of total LAI. Useful LAI is defined as the sunlit, once-shaded, and twice-shaded fractions of LAI, given here as a percentage of total LAI; these leaves are alive and, if not photosynthetic (twice-shaded), acting as a store of nitrogen, which can be moved later to the maturing grain. At final harvest, live leaves are present only at the top of the canopy and hence all are sunlit. This crop yielded 11.6 t ha⁻¹ (14% moisture content).

Measurement	Stage of growth (days after transplanting)			
	Panicle initiation (43)	Flowering (61)	Maximum LAI (67)	Final harvest (102)
Shoot dry weight (t ha ⁻¹)	3.9	9.2	11.8	21.8
Leaf dry weight (t ha ⁻¹)	1.7	3.2	4.0	1.9
Stem dry weight (t ha ⁻¹)	2.1	4.5	5.2	4.5
Panicle dry weight (t ha ⁻¹)	0	1.2	2.2	12.2
Dead dry weight (t ha ⁻¹)	0.1	0.3	0.4	3.2
Leaf area index	3.0	5.9	7.0	2.8
Sunlit area index	2.2	2.9	3.1	2.8
Once-shaded area index	0.7	1.9	2.2	–
Twice-shaded area index	0.1	0.9	1.2	–
More than twice-shaded	0	0.2	0.5	–
Photosynthetic LAI (%)	97	81	76	–
Useful LAI (%)	100	97	93	–
Intercepted PAR (%)	61	84	89	–
Canopy photosynthesis (g CH ₂ O m ⁻² d ⁻¹)	40	56	59	–

units as photosynthesis, $F_{eo}(t)$ is the rate of loss of carbohydrate through root exudation, and $F_{do}(t)$ is the rate of loss of dead matter by detachment. It is recognized that age and crop composition will affect the variables used in evaluating equation 14. However, to fully represent the crop throughout its life would require a complex model and our aim is to keep things simple and to evaluate the consequences of this approach later.

The units throughout are g m⁻² for the time interval being considered, typically 1 day. The carbon content of crop plants is approximately 40% so that calculating the mass balance of a plant in terms of carbohydrates gives an acceptable prediction of weight change. This occurs because the proportion of dry matter that is mineral elements more or less compensates for the higher proportion of carbon in lipids and other substances than in carbohydrates. If greater precision is required, the fraction of carbon in the dry weight, f_c , needs to be known for each organ and the amount of carbohydrate is multiplied by $0.4/f_c$ to obtain dry matter.

Using daily time steps, equation 14 can now be written in units of carbohydrate (g m⁻²) as

$$dW/dt = (1 - \Omega)P_g(t) - R_s(t) - R_m(t) - D(t) \quad (15)$$

where P_g is gross photosynthesis (shoot net photosynthesis plus shoot respiration for the daylight hours), Ω is the fraction of gross photosynthesis exuded through the roots and lost through nodule respiration in legumes, R_s is the crop synthetic respiration (shoots plus roots), R_m is the crop maintenance respiration, and D is the daily loss of matter through detachment.

If it is assumed that synthetic respiration is equivalent to $0.25 P_g$ and maintenance respiration (see below and Appendix) can be written as the product of a maintenance coefficient and live crop weight (McCree 1970, Penning deVries et al 1983, Thornley and Johnson 1990, Amthor 2000), $k_d(t)$ is the fraction of dead matter in total aboveground dry matter, and, if root exudates account for 5% of daily photosynthesis (Marschner 1995) and nodule respiration is zero, equation 15 can be rewritten as

$$dW/dt = 0.70 P_g(t) - m_T W(t) (1 - k_d(t)) - D(t) \quad (16)$$

where m_T is the maintenance respiration coefficient (g carbohydrate g^{-1} DM d^{-1} ; Table 1) assumed to have a Q_{10} of 2 from a base temperature of 20 °C (Ryle et al 1976). The value of m_T at any time is calculated from a value at the base temperature and the temperature at the time, $T(t)$, as

$$m_T = m_{20} 2^{(T(t)-20)/10} \quad (17)$$

where m_{20} (g g^{-1} d^{-1}) is the maintenance respiration coefficient at 20 °C and $T(t)$ is the mean daily temperature (°C).

Maintenance respiration declines with age (Loomis and Connor 1992, Liu et al 2011) and published values for m_T vary (McCree 1970, Thornley and Hesketh 1972, Ryle et al 1976, Thornley and Johnson 1990). In the absence of data for rice, we have used a base value of 0.007 g g^{-1} d^{-1} estimated using the approach described in the Appendix.

Roots account for a comparatively small fraction of crop dry matter (measured as root weight ratio) for most of crop duration, typically declining at harvest to 0.1 in irrigated rice (Sheehy et al 2000b) or 0.3 in wheat (Siddique et al 1990). To make progress, we assume a general value of 0.15 for root weight ratio so that total crop dry matter is $1/0.85 = 1.18$ times larger than aboveground dry matter (Sheehy 2000). Substituting in equation 16 and assuming proportional detachment of dead material, we obtain

$$1.18 \frac{dW_s}{dt} = 0.70 P_g(t) - 1.18 m_T(t)W_s(t) (1 - k_d(t)) - 1.18 D_s(t) \quad (18)$$

where W_s is aboveground dry matter and $D_s(t)$ is detached dead aboveground dry matter. Dividing throughout by 1.18 and assuming that $D_s(t)$ is negligibly small in a rapidly growing crop gives

$$\frac{dW_s}{dt} = 0.59 P_g(t) - m_T(t)W_s(t) (1 - k_d(t)) \quad (19)$$

More generally, the relationship between crop growth rate and crop photosynthesis can be written as

$$\frac{dW_s}{dt} = \beta P_{gd}(t) - m_T W_s(t)(1 - k_d(t)) \quad (20)$$

where β is a coefficient whose value is derived as shown in the Appendix (0.59 in general). When respiration is defined as a biphasic process (see Appendix), maintenance respiration (m_T) is defined as the second phase associated with the maintenance of metabolic activity (Ryle et al 1976).

Maximum yield of biomass

To fully understand the dynamics of internal transfers of nitrogen between vegetative and reproductive structures, Sheehy et al (2007a) described the growth of rice in terms of three phases. For simplification, we assume here that aboveground dry matter accumulation follows the classical logistic pattern (Williams 1964) as shown in Figure 6. At maturity, we can write $dW_s/dt \rightarrow 0$, as $W_s \rightarrow W_{smax}$ and $P_{gd} \rightarrow f P_{gdmax}$, largely owing to a recycling of nitrogen associated with senescence (the loss of leaves shaded once or twice), and, associated with that process, $k_d(t) \rightarrow k_{dmax}$. Setting dW_s/dt to zero in equation 20 gives

$$W_{smax} = f \beta P_{gdmax} / (m_T(1 - k_{dmax})) \quad (21)$$

where W_{smax} is the maximum crop aboveground dry matter (g m^{-2}) and f is P_{gd} as a fraction of its maximum value, P_{gdmax} . As described by Sheehy (2000) in a canopy with a high LAI, leaves that are shaded once or twice can become senescent for a loss of less than 30% of canopy photosynthesis ($f \approx 0.7$). For convenience, we rewrite equation 21 as

$$W_{smax} = c_T P_{gdmax} \quad (22)$$

where

$$c_T = f \beta / (m_T(1 - k_{dmax})) \quad (23)$$

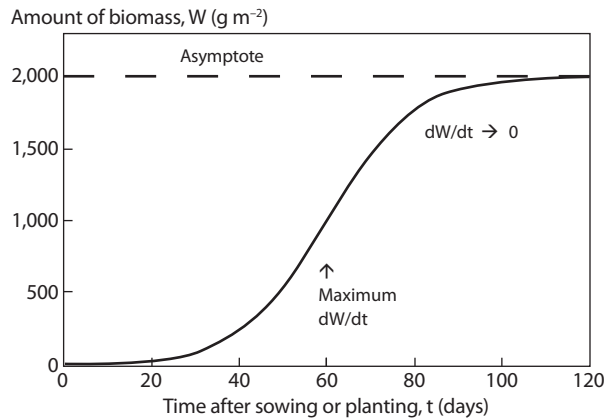


Fig. 6. The classical S-shaped curve for accumulation of crop biomass (aboveground dry matter) with time for an annual crop (Williams 1964). It is represented here using a logistic equation; the numbers are plausible values for illustration and do not relate to any particular crop. Maximum growth rate occurs at the steepest point on the curve, the point of inflection, which is taken to be the time of maximum rate of canopy photosynthesis. As biomass approaches the asymptote (W_{max}), the growth rate (dW/dt) approaches zero.

so that c_T is a temperature-dependent parameter governing the conversion of photosynthate into aboveground biomass.

We can now combine equations 13 and 22 to obtain maximum crop biomass (aboveground dry matter) from the main driving variable, I_{day} , and several parameters. Canopy quantum efficiency, κ_T , is a combination of the parameters ϵ , α_T and τ . Parameter c_T accounts for major losses of carbohydrate from shoot biomass in growth respiration, maintenance respiration (m_T), and allocation to root growth. Parameter f largely represents the consequences for canopy photosynthesis of nitrogen transfer from leaves to panicles. Temperature is also a driving variable because during daylight it acts through the values for α_T (equation 5), and the mean daily temperature acts throughout 24 hours on m_T (equation 17).

For a semidwarf crop that recycles nitrogen from once-shaded and twice-shaded leaves, but retains nitrogen in sunlit photosynthetically active leaves, $f \approx 0.7$ (Sheehy 2000). The value of f will be strongly influenced by nitrogen management and the demand for nitrogen from the reproductive organs. The data in Table 4 give the value of k_{dmax} as 0.15 and we assume that this value remains constant in the calculations made in this paper. It is likely that f and $(1 - k_{\text{dmax}})$ are related although we do not explore that here. The maintenance respiration coefficient (see Appendix) for rice in the tropics is $0.012 \text{ (g g}^{-1} \text{ d}^{-1}, T = 28 \text{ }^\circ\text{C)}$ and for subtropical or temperate rice ($T = 23 \text{ }^\circ\text{C}$) it is $0.0086 \text{ (g g}^{-1} \text{ d}^{-1})$ when the applicable temperatures are for the period of flowering to maturity (Sheehy et al 1998). We discuss the factors influencing the value of the conversion factor c_T below. Using the data in Tables 1 and 4, we calculated values of c_T for a range of values of f (Table 5): for $f = 0.7$, then c_T is 40.5 for the tropics and 56.5 for the subtropics (units $\text{g DW g}^{-1} \text{ CH}_2\text{O d}$, i.e., the inverse of the units for m_T).

Table 5. Values of the photoassimilate conversion parameter c_T ($c_T = f\beta/(m_T(1 - k_{\text{dmax}}))$) for tropics and subtropics for various values of the factor f governing the decline from maximum canopy photosynthesis by crop maturity, assuming m_T for the tropics = $0.012 \text{ g g}^{-1} \text{ d}^{-1}$ and $0.0086 \text{ g g}^{-1} \text{ d}^{-1}$ for the subtropics; β is assumed to be 0.59 and $k_{\text{dmax}} = 0.15$.

f	c_T tropics ($\text{g g}^{-1} \text{ d}$)	c_T subtropics ($\text{g g}^{-1} \text{ d}$)
0.8	46.3	64.6
0.7	40.5	56.5
0.6	34.7	48.4

The law of maximum grain yield

The maximum grain yield is obtained by multiplying equation 22 by the harvest index to give

$$W_{\text{gmax}} = Hc_T P_{\text{gdmax}} \quad (24)$$

where H is the harvest index defined as the harvested part of the crop, which is grain, as a fraction of crop aboveground dry matter (Hay 1995). Substituting for P_{gdmax} from equation 13 in equation 24 gives

$$W_{\text{gmax}} = 0.95 H \kappa_T c_T I_{\text{day}} \quad (25)$$

Harvest index

The analysis of canopy structure in relation to the interception of PAR suggests that, as canopies become more erect, a larger LAI is required for full interception. It follows that leaf weight and stem weight must both increase and this also has the consequence of increasing the size of the nitrogen reservoir and the amount of structural biomass available to support increased yield. The balance between the investment of resources in grain and support structures can be examined by considering the equation for calculating harvest index. Harvest index (H) can be written as

$$H = Y/(W_{\text{sst}} + \rho Y) \quad (26)$$

where Y is grain dry weight, W_{sst} is the weight of the leaves and stems, which for convenience we call support structure, ρ describes the weight of the panicle relative to grain weight, and, from the data in Table 4, we can write $\rho \approx 1.25$.

We can make another useful simplification by assuming $W_{\text{sst}} = \eta Y$ so that

$$H = Y/(\eta Y + \rho Y) \quad (27)$$

where η describes the weight of the biomass (leaves, stems, and dead matter) invested in support of grain production relative to grain weight. By rearranging equation 27, we get

$$\eta = (1/H) - 1.25 \quad (28)$$

Figure 7 shows the relationship between η and H and it can be seen that, when $H = 0.5$, the weight of the support structures is 75% of the weight of the grain; when $H = 0.45$, the weight of the support

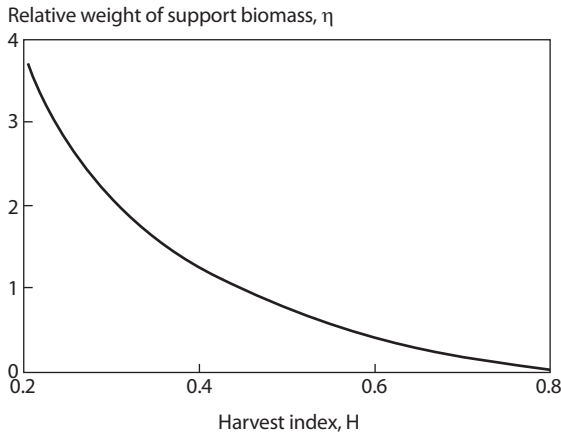


Fig. 7. The weight of the biomass (leaves, stems, and dead matter) invested in support of grain production relative to grain weight (η) decreases nonlinearly as the harvest index (H) increases (from the equation $\eta = (1/H) - 1.25$).

structures and grain is equal; and, when $H = 0.4$, the weight of the support structures is equal to the weight of the panicle. Equation 28 shows, as has long been known, that, for a given biomass, a higher grain yield is obtained by reducing the amount of support structures. There are limits: thus, $H = 0.8$ gives the mathematically correct, but biologically ridiculous, conclusion of unsupported grain weight.

Predicting yield

Grain yields of rice are stated at a nominal moisture content (fresh weight basis) of 14% (for wheat, it is 15%). To convert yield as dry matter in g m^{-2} to t ha^{-1} , divide by 100; then divide by 0.86 to allow for moisture content.

Table 2 shows that a Vela variety would have to increase LAI by 50% to 100% above that of a semidwarf variety to intercept the available PAR. At constant specific leaf area, this means that leaf weight and stem weight would have to increase proportionally. The ratio of weight to LAI at maximum LAI ($W_{\text{sst}}/\text{LAI} = 1.37$) from the data in Table 4 combined with the predicted LAIs in Table 2 suggest that, for an erect NPT-like canopy, $W_{\text{sst}} \approx 13.3$ and, for the Vela canopy, $W_{\text{sst}} \approx 20.6$. It is clear that erect canopies achieve higher rates of canopy photosynthesis than the more semidwarf canopies. In order to do so, they have to invest heavily in the support structures that the dwarfing genes limit, suggesting that H may decrease in the more erect canopies. One consequence of this extra investment would be an increase in the size of the nitrogen reservoir available for grain growth and the fractional decline in canopy photosynthesis toward maturity might be reduced, for example, $f \rightarrow 0.8$. The effect of increasing f to 0.8 and reducing H to

0.4 increases the biomass of the Vela type to 28.4 t ha^{-1} , the grain yield to 13.2 t ha^{-1} (14% m.c.), and the support biomass (stem, leaves, and dead matter) to 14.2 t ha^{-1} . At the moment, uncertainty exists about the values of f and H for a Vela type; however, the changes in f and H affect the predicted support weight but not the grain yield.

Values for the driving variables ($I_{\text{day}}, T_{\text{PS}}, T_{\text{mean}}$) and parameters ($\alpha_r, \epsilon_c, \beta, m_r, f, \tau, H, p_g$) are listed in Table 1 for a well-fertilized and irrigated rice crop. Achievable values of ϵ_c and canopy photosynthesis for various combinations of leaf architecture and leaf photosynthesis are given in Table 3, and values of c_T are shown in Table 5. We used the above equations to predict maximum yield as shown in Table 6.

The results show that, in the tropics, a Vela variety would increase maximum yield by 11% (from 11.7 to 13.0 t ha^{-1}). Yields in the subtropics are about 40% higher than in the tropics owing to the lower average daily temperatures, which reduce the coefficient of maintenance respiration (m_r). The C_4 syndrome in the erect canopy type could increase yields by about 38% in the tropics or subtropics compared with the semidwarf type.

Radiation use efficiency

Although radiation use efficiency is a valuable agronomic parameter, it is not an ideal trait for use in breeding. It requires careful measurement throughout the growing season and, because of its low precision, small differences between breeding lines cannot be reliably distinguished. Here, we provide a theoretical derivation of the coefficient that provides insight into the factors shaping its value.

If we assume that, over the growing period, respiration is some fraction (σ) of gross photosynthesis, the accumulated crop biomass (including roots), W_{cum} , can be written as

$$W_{\text{cum}} = (1 - \sigma) \int P_{\text{gd}} \quad (29)$$

Substituting for P_{gd} from equation 12 and integrating equation 29 over the growing season gives

$$W_{\text{cum}} = (1 - \sigma) \epsilon_c \alpha_r R_{\text{cum}} / (1 - \tau) \quad (30)$$

where R_{cum} is the total PAR intercepted over the growing period, that is, $\int \phi I_{\text{day}}$. The constant of proportionality between accumulated biomass and accumulated intercepted PAR ($W_{\text{cum}}/R_{\text{cum}}$) was defined by Monteith (1977) to be the radiation use efficiency (ϵ_r). Thus, equation 30 defines radiation use efficiency for total crop biomass as

Table 6. The calculated grain yields (14% moisture content) of rice in the tropics and subtropics for the four canopy types of rice as defined in Table 2. The extra subtypes of erect canopy are for a C_4 rice and for C_3 with low photosynthesis (half the usual maximum rate of leaf photosynthesis of $32.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Canopy photosynthesis is calculated for 95% interception of PAR; values of c_T are 40.5 for the tropics and 56.5 for the subtropics (units $\text{g DW g}^{-1} \text{ CH}_2\text{O d}$); biomass yields are dry weights; and the harvest index is 0.45.

Item	Canopy type			
	Traditional	Semidwarf	Erect	Vela
Extinction coefficient, k	0.60	0.45	0.31	0.20
Canopy photosynthesis, P_{gdmmax} ($\text{g CH}_2\text{O m}^{-2} \text{ d}^{-1}$)	52.1	55.2	58.3 (C_4 , 76.0) (low, 47.0)	61.5
Tropics, grain yield (t ha^{-1} , 14% m.c.)	11.0	11.7	12.3 (C_4 , 16.1) (low, 9.9)	13.0
Tropics, biomass (t ha^{-1})	21.1	22.3	23.6 (C_4 , 30.8) (low, 19.0)	24.9
Subtropics, grain yield (t ha^{-1} , 14% m.c.)	15.4	16.2	17.3 (C_4 , 22.5) (low, 13.9)	18.1
Subtropics, biomass (t ha^{-1})	29.4	31.1	33.0 (C_4 , 42.9) (low, 26.6)	34.7

$$\varepsilon_r = (1 - \sigma) \varepsilon_c \alpha_T / (1 - \tau) \quad (31)$$

which can be written as

$$\varepsilon_r = (1 - \sigma) \kappa_T \quad (32)$$

The more usual form of the coefficient (ε_{rue}) is calculated for shoot biomass and, if we define the shoot weight ratio as S_r , it can be written as

$$\varepsilon_{\text{rue}} = S_r (1 - \sigma) \kappa_T \quad (33)$$

Ryle et al (1976) suggested that total respiration could amount to 50% of gross photosynthesis, that is, $\sigma = 0.5$. Several of the terms in equation 33 could be influenced by temperature, but possibly in opposite directions, giving an expression that is often regarded as describing a conservative entity and one independent of location (Russell et al 1989, Mitchell et al 1998). Using Ryle's suggestion ($\sigma = 0.5$), $\tau = 0.1$, and the parameters for semidwarf rice ($\varepsilon_c = 0.88$, $\alpha_T = 5.9 \text{ g CH}_2\text{O MJ}^{-1}$) and maize ($\varepsilon_c = 1.0$, $\alpha_T = 7.2 \text{ g CH}_2\text{O MJ}^{-1}$) at a daytime temperature of 30°C , the ε_r of rice and maize computed using equation 33 would be 2.9 and $4.0 \text{ g total biomass MJ}^{-1}$ intercepted PAR, respectively. Converting to the more familiar basis of aboveground biomass, by multiplying by shoot weight ratio, for example, 0.85 for a cereal crop, we obtain values for ε_{rue} of 2.5 and 3.4 g MJ^{-1} (aboveground biomass, intercepted PAR),

in moderate (rice) or good (maize) agreement with general values of RUE for these crops (Mitchell et al 1998).

Given that PAR is about half of solar radiation, and the peak growth rate above would be attained by a crop intercepting 95% of incident PAR, then the maximum growth rate for rice in the tropics is given by $I_{\text{day}} \phi \varepsilon_{\text{rue}}$, which would be $10 \times 0.95 \times 2.5 = 23.8 \text{ g d}^{-1}$ (for C_4 rice, it would be 32.3 g d^{-1}). A crude estimation of crop duration can be obtained by dividing total biomass by the radiation use coefficient and dividing that by the average daily incident PAR. The ratio of W_{smax} and ε_{rue} gives the total radiation intercepted, which, if used with the energy balance equation (see Appendix), can be used to calculate the total amount of water transpired by the crop.

Discussion

As canopies become increasingly erect, the LAI required for full light interception increases (Table 2). Maximum rice yields in irrigated systems are obtained in the clear sunny conditions of the dry seasons in the tropics and subtropics. The relationship between daily total canopy photosynthesis and irradiance was calculated using a model based on the Bouguer–Lambert Law of PAR distribution in a canopy and a hyperbolic description of the relationship between leaf photosynthesis and PAR. For erect

canopies, the total daily rate of canopy photosynthesis was shown to be linearly related to fractional interception of PAR (Fig. 3). The leaves of modern erect varieties receive only a fraction of full sunlight, so, to a good approximation, their photosynthesis can also be described by the linear part of the leaf photosynthesis versus irradiance curve. Consequently, a model of daily canopy photosynthesis was derived assuming that the relationship between leaf photosynthesis and PAR was linear, with a slope proportional to the quantum yield of photosynthesis. The model described the relationship between daily canopy photosynthesis and daily irradiance as being proportional to the fraction of the irradiance intercepted (ϕ) and the quantum yield of the canopy (κ_T), which was shown to be the product of leaf quantum yield (α_T) and a canopy efficiency factor, $\epsilon_c/(1 - \tau)$. The factor ϵ_c is a measure of the effective quantum yield of leaves in a crop, which approaches unity for erect canopies with high maximum rates of leaf photosynthesis. Thus, daily canopy photosynthesis can be described as the product of the interception of daily PAR and canopy quantum yield ($\kappa_T \phi I_{\text{day}}$) and at full interception of PAR for modern crop canopies with erect leaves and when $\tau = 0.1$ is approximately $0.95 \alpha_T I_{\text{day}}$. Consequently, for modern canopies with erect leaves, the only way to improve canopy photosynthesis is by increasing the quantum yield (α_T) and removing its temperature sensitivity by introducing the C_4 syndrome into rice.

A simple growth analysis based on the mass balance of a crop showed that maximum grain yield depends on canopy photosynthesis, the ability to convert photoassimilate into biomass (c_T), and the harvest index (H). The conversion factor c_T (which is the group of parameters $f \beta / (m_T (1 - k_{\text{dmax}}))$ collected together) is inversely related to the coefficient of maintenance respiration. Carbon fixed by photosynthesis that did not contribute to crop aboveground biomass was used in allocation to roots, in synthetic respiration, and by exudation from roots. All of those factors were combined into a dimensionless parameter, β . For cereals in general, β is about 0.59 but will vary between crops; for example, in legumes it is likely to be less because of additional expenditure of carbon in symbiotic nitrogen fixation. The parameter f allows for canopy photosynthesis declining from its maximum value toward maturity. Maintaining canopy photosynthesis close to its maximum value by good fertilizer and crop management (Table 5) as the crop approaches maturity is important for maximizing biomass and yield (equations 22–25).

The grand simplification of crop growth that we sought is represented by equations 22 and 25.

We tested our equations for a contrasting crop in a contrasting environment, forage grasses growing in the autumn of a temperate climate, and we found them to work well (see Appendix). It may be fortuitous that plausible figures for rice biomass and yield can be calculated from equations 22 and 25—unrealistic results can easily be obtained using other values for the parameters—but we believe that the general principles represented in the equations are sound.

The largest uncertainties are in the base rates for maintenance respiration and quantum yield, and the effects of temperature on respiration and quantum yield. Good data for rice, for example, are largely absent from the literature. Work by Hogewoning et al (2012) suggests that the spectral composition of the high-pressure sodium lamps used by Ehleringer and Pearcy (1983) may have led to an incorrect estimate of the value of quantum yield in daylight. When more quantitative information concerning such spectral effects becomes available, it will be a simple matter to estimate their impact on the calculation of photosynthesis and yield. A further uncertainty is that values for all driving variables and parameters are being averaged over crop duration or over the period of closed canopy and maximum photosynthesis. These values are hard to obtain exactly even if linearity does hold over the relevant period so that an average value can be meaningful.

Equations 22 and 25 highlight the importance of both photosynthesis and maintenance respiration. (The coefficient of maintenance respiration, m_T , occurs within c_T in equations 22 and 25 and is sensitive to temperature—see Figure 8.) We hope that the prominent effect of maintenance respiration in determining yield differences between climatic zones will encourage more research aimed at answering the various questions about respiration raised by Amthor (2000), especially for rice. Meanwhile, the conclusion must be that photosynthesis (through quantum yield) and maintenance respiration are the prime drivers of crop biomass and yield. Improvements in photosynthesis will be essential for productive and sustainable agriculture.

Both theory (Table 2) and practice (Table 4) give a maximum LAI of around 7 for semidwarf indicas. The predictions for erect and Vela canopy architectures (Table 2) show that leaf area would have to increase by 50–100% to intercept all of the available PAR. The changed canopy architecture has two effects: (1) it improves canopy photosynthesis and (2) it probably increases the size of the vegetative reservoir of nitrogen, which is required for increased grain yield. In the tropics, a Vela variety would increase maximum yield by 11% (from 11.7 to 13.0 t

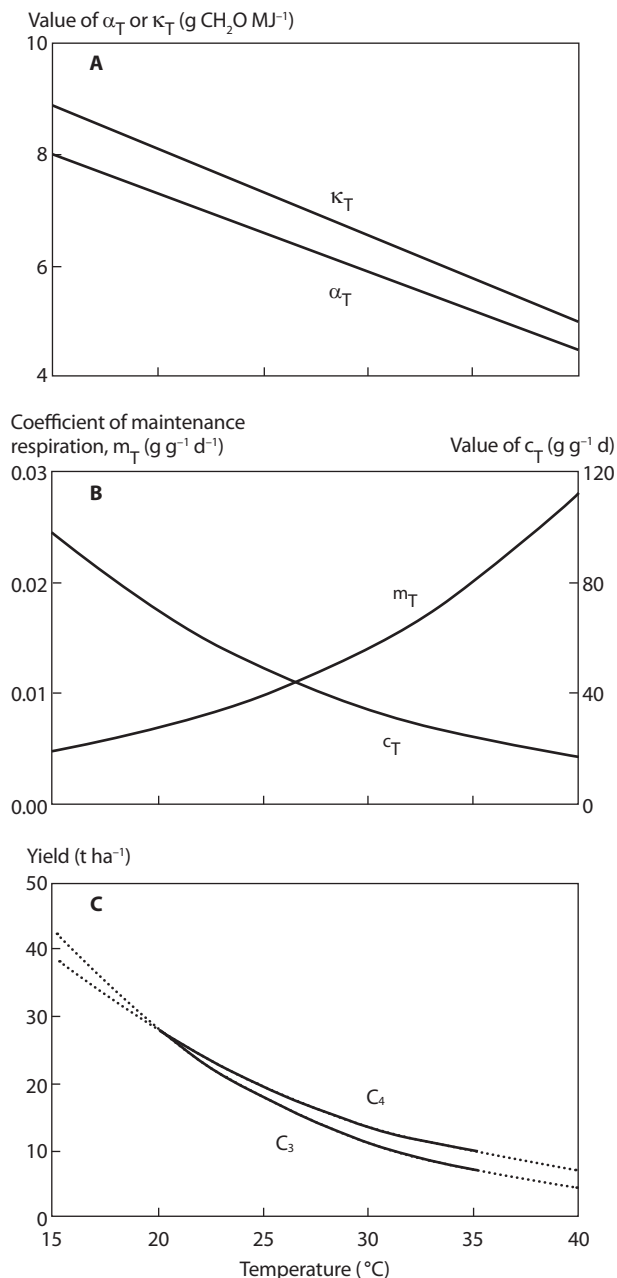


Fig. 8. The effect of temperature (considered constant across 24 h) on the model parameters (graphs A and B) and predicted grain yields (graph C). Yields (14% moisture content) were calculated with harvest index of 0.45, PAR of 10 MJ m⁻² d⁻¹. For C₃ crops, the value of leaf quantum yield (α_T) varies as shown in (A); for C₄ crops, the value of leaf quantum yield is constant at 7.2 g CH₂O MJ⁻¹. The value of ϵ_c for calculating κ_T was taken as 1.0. The lines for yield of C₃ and C₄ crops cross over at about 20 °C and 28 t ha⁻¹. The dotted portions of the lines indicate temperature ranges (below 20 °C and above 35 °C) where harvest index for rice tends toward zero.

ha⁻¹). Yields in the subtropics are about 40% higher than in the tropics owing to the lower average daily temperatures, which reduce the coefficient of maintenance respiration (m_T). (The simplification used here removes crop growth duration as a factor influencing maximum yield, which we have used in other analyses (Mitchell and Sheehy 2000) to explain the differences between yields in the tropics

and elsewhere.) The C₄ syndrome could increase rice yields to 16.1 t ha⁻¹ in the tropics and to 22.5 t ha⁻¹ in the subtropics, about 38% above the yields of semidwarf cultivars (Table 6).

Links between photosynthesis and crop yield were discussed by Long et al (2006) and in Sheehy et al (2000b). From the results above, we suggest that yield increases of 50% resulting from improvements in photosynthesis wanted by Long et al (2006) could be achieved, in rice, only by increasing the quantum yield to the value achieved by the C₄ syndrome and improving canopy architecture and sink capacity during vegetative growth. The possibility of converting rice from a C₃ pathway to a C₄ pathway was discussed in Sheehy et al (2007b) and in von Caemmerer et al (2012) and research is in progress (see www.irri.org/c4rice).

We hypothesize that semidwarf indica materials may not be suitable platforms for further improvements in C₃ or C₄ rice owing to insufficient sink capacity (leaves and stems) in the vegetative phase of development. Culm length declined from about 128 cm in the rice types before the Green Revolution to about 53 cm afterward. This change prevented lodging in crops receiving large amounts of fertilizer nitrogen. However, the importance of the vegetative component of the crop acting as a reservoir for nitrogen in support of reproductive growth also needs to be borne in mind when designing high-yielding crops. In contrast to the vegetative stage of growth, the reproductive stage of rice has unused sink capacity—there are many more spikelets (florets) initiated than finally develop as grains at harvest (Sheehy et al 2001)—thus enabling observed increases in yield in response to elevated CO₂ up to about 500 ppm although not at higher concentrations (Rowland-Bamford et al 1990, 1991). It is worth noting that rice varieties adapted to deep water can produce elongation growth up to about 25 cm per day, and successful cultivars for those environments have been developed from submergence-tolerant landraces (Catling 1992, Bailey-Serres and Voesenek 2008, Sheehy and Mitchell 2011b). It would seem that there is a limit to the amount of CO₂ that the semidwarf indica types of rice can use and it may be set by the strength of vegetative sinks.

The large amounts of mineral nutrients required in high-yielding crops far exceed the capacity of the soil to supply them without the application of fertilizers (Table 7). The proportion of an applied fertilizer nutrient that appears in the crop (fertilizer use efficiency for each nutrient) is highly variable depending on soil type and other environmental factors. Thus, site-specific nutrient management

Table 7. The mineral element content (kg ha⁻¹) of a rice crop yielding 12 t ha⁻¹ grain (14% moisture content) with a harvest index of 0.43 and total aboveground biomass of 24.2 t ha⁻¹ (after Sheehy et al 2000b). Latshaw and Miller (1924) showed that carbon, oxygen, and hydrogen made up about 95% of the dry weight of corn (maize). The carbon content of rice plants is approximately 40%; rice straw = 38% (Jimenez and Ladha 1993), rice grain = 39.8% (Ladha pers. comm., IRRI 2000), and mineral elements comprise about 8%.

N	P	K	Ca	Mg	S	Cl	Si	Fe	Mn	B	Zn	Cu
234	56	377	33.3	42.5	18	119	1,086	6	1.6	0.8	0.43	0.04

is recommended for increasing yield (Cassman et al 1996, Olk et al 1999, Dobermann et al 2004). Retaining canopy photosynthesis close to its maximum value ($f \approx 0.7$ to $f \approx 0.8$) through good crop management (Greenwood et al 1990, Sheehy et al 1998) while enabling nitrogen to be transferred to the grain as the crop matures is important (Sheehy et al 2004). Shaded leaf areas contribute about 25% of total canopy photosynthesis (Sheehy 2000) and their influence is partly governed by the parameter f . The equations in this paper suggest that improvements in the quantum yield of photosynthesis of the same order as the change that occurs in the change from the C_3 to C_4 syndrome of photosynthesis would probably take yields to their upper limit achievable with current biological technologies (Allen et al 2003).

Our work in this paper was not designed to deal with the problems surrounding climate change, water, or high temperature (Prasad et al 2006), but rather the immediate consequences for crop yield of improving the photosynthetic system under conditions that might exist in the first half of this century. Nonetheless, the equations derived can be used to examine the consequences of changes in temperature. The effects of temperature are implemented in equation 17 for m_T and equation 5 for α_T ; each works in the same direction to decrease biomass and yield as temperature rises (Fig. 8). It is clear that changes in c_T dominate yield responses to temperature in both C_3 and C_4 crops. Below 30 °C, predicted C_3 yields increase more rapidly than those predicted for C_4 crops and above 30 °C they fall more rapidly. Cooler, high-radiation conditions favor high yields but temperature and irradiance tend to be inversely related. Moreover, rice yields approach zero outside the temperature range of 20 to 35 °C. A rising concentration of CO_2 could increase the apparent quantum yield of rice up to a concentration of about 500 ppm, although the work on high- CO_2 effects on rice suggests that rice cultivars capable of being more responsive to CO_2 than the semidwarf indicas would be needed to fully exploit such increases.

Concluding remarks

The overall conclusions in this paper are that (1) improvements in yield can be made with improvements in canopy photosynthesis, (2) those improvements need to focus on improving canopy architecture and the quantum yield of photosynthesis, (3) improvements in canopy architecture should focus on Vela plants with sufficient vegetative and productive sink capacity to realize the benefits of improved carbon capture, and (4) crop management cannot be ignored in the drive for enhanced crop yields.

The negative aspects of the law of unintended consequences should not inhibit research aimed at increasing yield in all rice ecosystems nor should it, like history, be ignored. Good research is about ideas and the testing of hypotheses, with empiricism becoming increasingly important as the products of research are measured against theoretical predictions.

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Appendix

Defining maintenance respiration

Ryle et al (1976), using labeled CO_2 , showed that the respiratory flux of CO_2 from plants could be defined in terms of two phases. The first phase was an intense efflux having a half-life of 4–8 h and was associated with biosynthesis in meristems. The second phase was less intense, with a half-life of 26–120 h and associated with the maintenance of metabolic activity. The first phase amounted to 25% to 35% of the labeled assimilate; the second phase totaled from 12% to 27% of the labeled assimilate. The maintenance efflux showed a temperature

response with a $Q_{10} \approx 2$, and is defined in this paper as the cumulative second phase of respiration divided by the weight of the crop. Given that every unit of carbon assimilated is associated with a biphasic loss of carbon in respiration, associating the cumulative second phase of respiration with weight gives a convenient method of describing maintenance respiration. Sheehy et al (1979, 1980) used the concept of two phases of respiration to model the growth of a grass crop; crop weight was defined in terms of the fraction of carbon captured during photosynthesis that remained in the crop after respiration. We use their approach and define a weight-related maintenance coefficient of respiration as the ratio of the cumulative second phase of respiration divided by the weight of the crop, written here for day d as

$$m_T(d) = \sum_1^{d-1} P(d-t) \Gamma(t) / \sum_0^{d-1} P(d-t) f(t) \quad (1a)$$

where Γ is the fractional amount of previously acquired photoassimilate $P(d-t)$ respired on day d and $f(t)$ is the fraction of $P(d-t)$ remaining after respiration. This approach gives estimates of m_T broadly consistent with published values.

Testing the equations for a contrasting crop

The various equations can be compared with the mean data for eight forage grass species covering a range of canopy structures growing in the field in September to October (Sheehy and Peacock 1975). The average radiation use efficiency of the grasses, ϵ_{true} for the growth rate data is calculated to be 2.2 g DM MJ⁻¹, the same value as the general one for rice (Mitchell et al 1998). The average temperature for daylight was 12.25 °C, just outside the temperature range of equation 5, which predicts α_T to be 8.4 g CH₂O MJ⁻¹ if extrapolated. Agreement was good between the predicted maximum daily rate of canopy photosynthesis from equation 12, 36.7 g CH₂O m⁻² d⁻¹, and the average of the measured values, 33.5 g CH₂O m⁻² d⁻¹, so that $\epsilon_c = 0.91$. There was a large mass of roots relative to shoots (137%; root weight ratio 0.58), which might be expected of a perennial crop measured in autumn when large amounts of stubble were left after the harvest of shoots, so that β was estimated to be 0.3. Equation 20 can be used with the data to calculate m_T as 0.0048 g g⁻¹ d⁻¹ at the mean temperature of 10.5 °C. Using a Q_{10} of 2, this gives a value at 20 °C of 0.0093 g g⁻¹ d⁻¹, a value in good agreement with values reported by McCree (1970) and others above. The value of f for forage grass canopies is likely to approach 0.5 because canopy photosynthesis declines once full light interception is approached owing to the decline

in the maximum rate of photosynthesis of successive leaves (Sheehy 1977).

Solar energy use by crops

Ultimately, the bioenergetics of crops are driven by solar radiation and it is useful to set this out quantitatively. The energy balance of a crop, considering 1 m² of ground for a period of time such as a day, can be written as

$$aR_s = R_l + H + LE + P_e \quad (2a)$$

where a is the fraction of solar radiation absorbed by the crop; R_s is solar (shortwave, wavelengths 300–3,000 nm) radiation received (MJ m⁻²); R_l is the net longwave (thermal, over 3,000 nm wavelength) radiation (MJ m⁻²); H is the exchange of sensible heat (MJ m⁻²); LE is the loss of latent heat (MJ m⁻²), from multiplying the latent heat of vaporization of water (L , MJ kg⁻¹) by the amount of water lost by evapotranspiration (E , kg m⁻²); and P_e is the energy stored in photosynthesis (MJ m⁻²).

On a sunny day, a typical total of solar radiation received would be 20 MJ m⁻². Allowing for longwave radiation exchanges, the net absorption of radiant energy would be about 13.3 MJ m⁻² d⁻¹ (Woodward and Sheehy 1983). The sensible heat loss is zero when crop and air temperatures are the same. The latent heat of vaporization of water is 2.43 MJ kg⁻¹ (at 30 °C) so the daily solar radiation absorbed is equivalent to evaporation of about 5.5 kg H₂O m⁻² or 55 t H₂O ha⁻¹ or 5.5 mm of water, a value often observed for the evapotranspiration of irrigated rice in the tropics. The energy content of biomass is about 15.5 MJ kg⁻¹; therefore, the daily net energy receipt (13.3 MJ m⁻²) is equivalent to about 8.6 t DM ha⁻¹ (DM is oven-dry matter of biomass), far higher than ever observed for crops. As an example of solar energy conversion into biomass, the maximum growth rate of a rice crop in a day was estimated to be about 24 g DM m⁻² (0.24 t DM ha⁻¹), thus equivalent to 0.37 MJ m⁻² d⁻¹ (Sheehy et al 2007a). Relative to incident solar radiation (20 MJ m⁻² d⁻¹), this is a maximum daily efficiency of 1.9%; relative to 10 MJ m⁻² d⁻¹ PAR, it is 3.7%, which is more realistic since photosynthesis cannot use wavelengths longer than 700 nm.

We have two conclusions from this brief analysis. First, much of the solar energy absorbed by crops is used for transpiration, an unavoidable loss of water if stomata are open for photosynthesis to occur. Second, the efficiencies of energy use in photosynthesis and the synthesis of crop biomass are low so there is much scope for improvement, albeit those improvements may be beyond current technologies.

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