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# A general model for the light-use efficiency of primary production

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## Summary

1. Net primary production (NPP) by terrestrial ecosystems appears to be proportional to absorbed photosynthetically active radiation (APAR) on a seasonal and annual basis. This observation has been used in 'diagnostic' models that estimate NPP from remotely sensed vegetation indices. In 'prognostic' process-based models carbon fluxes are more commonly integrated with respect to leaf area index assuming invariant leaf photosynthetic parameters. This approach does not lead to a proportional relationship between NPP and APAR. However, leaf nitrogen content and Rubisco activity are known to vary seasonally and with canopy position, and there is evidence that this variation takes place in such a way as to nearly optimize total canopy net photosynthesis.

2. Using standard formulations for the instantaneous response of leaf net photosynthesis to APAR, we show that the *optimized* canopy net photosynthesis is proportional to APAR. This theory leads to reasonable values for the maximum (unstressed) light-use efficiency of gross and net primary production of C<sub>3</sub> plants at current ambient CO<sub>2</sub>, comparable with empirical estimates for agricultural crops and forest plantations.

3. By relating the standard formulations to the Collatz–Farquhar model of photosynthesis, we show that a range of observed physiological responses to temperature and CO<sub>2</sub> can be understood as consequences of the optimization. These responses include the CO<sub>2</sub> fertilization response and stomatal closure in C<sub>3</sub> plants, the increase of leaf N concentration with decreasing growing season temperature, and the downward acclimation of leaf respiration and N content with increasing ambient CO<sub>2</sub>. The theory provides a way to integrate diverse experimental observations into a general framework for modelling terrestrial primary production.

*Key-words:* Climate change, net primary production, photosynthesis

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## Introduction

Evidence for proportionality between net primary production (NPP) and absorbed photosynthetically active radiation (APAR) has been accumulating since the seminal papers by Monteith (1972, 1977). The relationship has been shown to hold for both agricultural crops (Monteith 1977; Russell, Jarvis & Monteith 1989; Monteith 1994) and forests (Jarvis & Leverenz 1983; Linder 1985). The ratio of NPP to APAR is called the PAR utilization efficiency (or light-use efficiency, LUE or  $\epsilon$ ). LUE appears to be roughly constant within ecosystems but to vary with environmental conditions. Environmental stress due to drought, extreme temperatures or nutrient limitations may act to reduce LUE below its unstressed value (Legg *et al.* 1979; Green, Hebblethwaite & Ison 1985; Green 1987; Hughes *et al.* 1987). Such environmental stresses may also influence APAR through reductions in leaf area.

In the class of models known as 'production efficiency models' or 'diagnostic models', remotely sensed vegetation indices are used to estimate NPP on a seasonal basis across a geographic grid. The vegetation index is assumed to be related directly to the fraction of incident PAR absorbed by plants (FPAR) (e.g. Heimann & Keeling 1989; Prince 1991; Potter *et al.* 1993) as supported by theoretical results from Kumar & Monteith (1981), Sellers (1985, 1987), Choudhury (1987) and Sellers *et al.* (1992). A simple approach then is to assume a single universal value for LUE (Heimann & Keeling 1989). More recent models allow LUE to decrease at high and low temperatures, and when soil moisture is limiting (e.g. Potter *et al.* 1993; Runyon *et al.* 1994). This is more realistic for a global analysis (Potter *et al.* 1993) because, although deciduous plant types reduce their leaf area when environmental conditions are unfavourable, there are

other plant types (such as evergreen conifers and Mediterranean-type sclerophyll shrubs) that continue to display foliage during cold or dry seasons when photosynthesis may virtually cease (Mooney, Harrison & Morrow 1975; Waring & Franklin 1979; Running & Nemani 1988; Runyon *et al.* 1994).

The use of a whole-canopy LUE that either is constant or that can be modelled using simple responses to temperature extremes and drought is a convenient simplification for global modelling, as well as being supported by measurements in a wide variety of ecosystems. However, it is *not* consistent with the more conventional 'prognostic' process modelling approach where whole-canopy photosynthesis is obtained by integrating the response of leaf photosynthesis across the canopy using Beer's law or some more explicit light-extinction model. This approach was introduced by Monsi & Saeki (1953), who provided an analytical expression for integrated photosynthesis, assuming a rectangular hyperbola relationship between leaf photosynthesis and PAR. Monteith (1981) performed a similar analysis assuming a Blackman-type relationship with PAR. The rectangular hyperbola gradually approaches a maximum rate of photosynthesis,  $A_{\max}$ , as PAR increases while the Blackman curve increases linearly at first, then abruptly saturates at  $A_{\max}$ . Gas-exchange measurements on individual leaves generally show a response intermediate between these two curves, which can be more accurately represented by a non-rectangular hyperbola. Johnson & Thornley (1984) provided a general analysis for the case of the non-rectangular hyperbola relationship. The integrated canopy responses obtained analytically are approximately linear over a wider range than the assumed leaf responses but they still saturate at high light intensities. McMurtie & Wang (1993) showed considerable scatter around an approximately linear relationship between canopy photosynthesis and absorbed PAR as simulated by a detailed physiologically based model.

A key to this problem has already been noticed and has been discussed in general terms by Farquhar (1989) and Field (1983, 1991). It depends on the fact that both maximum rate of gross photosynthesis ( $A_{\max}$ ) and 'dark' respiration rate ( $R$ ) in leaves increase with the activity of photosynthetic enzymes (most importantly Rubisco) in the chloroplasts. This results in a trade-off: a high net photosynthesis rate at high PAR can be achieved by having a high Rubisco activity, but this also implies a low, or negative, net photosynthesis rate at low PAR. Thus, for any PAR level there is an optimal photosynthetic enzyme activity that produces maximum net photosynthesis. This optimal activity should also be reflected in leaf nitrogen (N) content, because of the observed strong linear correlation between  $A_{\max}$  and leaf N content (Field & Mooney 1986; Hirose & Werger 1987a; Field 1988, 1991). In the general

case, when total N availability may or may not be sufficient to support optimal photosynthesis throughout the canopy, the optimal allocation of N might be expected to maximize the marginal rate of return on N investment (i.e. would minimize  $dA/dA_{\max}$ ). Field (1991) noted (without proof) that total net photosynthesis by a vegetation canopy conforming to this ecological optimization principle would tend to have a linear, as opposed to saturating, response to absorbed PAR.

## Background

Several lines of evidence support the hypothesis that leaves within canopies adjust their N content and Rubisco activity both seasonally and with canopy position in such a way as to maximize net photosynthesis:

1. In forests the lower leaves ('shade leaves') have a lower  $A_{\max}$  and lower compensation points than the upper leaves ('sun leaves'). This has been known for a long time and applies within as well as between species (Böhning & Burnside 1956; Hozumi & Kirita 1970; Boardman 1977; Larcher 1983; Ellsworth & Reich 1993).
2. The vertical distribution of N in both forest and herbaceous canopies follows a similar pattern to  $A_{\max}$ . In several species, leaf N content per unit leaf area has been observed to vary with irradiance within the canopy (Evans 1989a; Werger & Hirose 1991). When grown in controlled environments, leaf N contents have also been found to vary in response to the irradiance received during leaf development (Evans 1989a).
3. Total canopy net photosynthesis is greater than would be achieved with a uniform distribution of N and is close to a calculated theoretical optimum distribution of N (Field 1983; Hirose & Werger 1987a,b; Hirose *et al.* 1988; Pons *et al.* 1989; Werger & Hirose 1991; Schieving *et al.* 1992). For example, Hirose & Werger (1987b) found that for a canopy of *Solidago altissima* daily carbon gain simulated using the observed gradient in leaf N was 20% greater than that simulated for a canopy with a uniform distribution of N and only 4.7% less than that simulated for an optimal distribution of N.
4. As individual leaves in the lower part of a plant canopy become shaded during canopy growth N is redistributed from these leaves to leaves higher in the canopy, and there is evidence that this redistribution acts to maintain a more nearly optimal distribution of N within the canopy (Field 1983; Werger & Hirose 1991). Chen *et al.* (1993) discuss a possible mechanism by which a near-optimal N distribution could be maintained.

Note that the time scale of adjustment of leaf N content and photosynthetic characteristics is apparently days to weeks (Reich, Walters & Ellsworth 1991), sufficiently fast to track the seasonal cycle and canopy development but presumably not short-term weather variations or the diurnal cycle.

## Theoretical analysis

Based on the evidence outlined above, we now derive a model for LUE assuming that N distribution through the canopy is such as to be optimal for photosynthesis. Our analysis considers the special case in which N supply to the canopy is not limiting. Implying that canopy leaf area is not N limited. Vegetation might be expected to optimize leaf area and foliage N concentration simultaneously. However, for this special case we consider the optimization of foliage N concentration independently of the optimization of leaf area. The optimization relies on the fact that leaf respiration costs increase with photosynthetic capacity. The resulting model has the important property that it predicts LUE values that are independent of PAR.

The analysis proceeds in three stages. First we consider an empirical photosynthesis model, applied at the leaf level. Second, the analysis is extended to the whole canopy. Finally, we relate the parameters of the empirical model to a more mechanistic model of photosynthesis.

CASE 1: NON-RECTANGULAR HYPERBOLA —  
DIURNAL CYCLE OF ILLUMINATION

The standard empirical formula relating instantaneous measurements of net photosynthesis and PAR is a non-rectangular hyperbola given by the smaller root of the quadratic:

$$\theta A^2 - (\phi I + A_{\max}) A + \phi I A_{\max} = 0 \quad \text{eqn 1}$$

with

$$A_n = A - R \quad \text{eqn 2}$$

where  $\theta$  is a shape parameter,  $0 \leq \theta \leq 1$ ;  $A$  is gross photosynthesis per unit leaf area;  $\phi$  is the quantum efficiency of photosynthesis;  $I$  is the absorbed PAR per unit leaf area;  $A_{\max}$  is the maximum rate of gross photosynthesis per unit leaf area;  $A_n$  is net photosynthesis per unit leaf area;  $R$  is respiration per unit leaf area (by processes other than photorespiration). We use the observation that  $R$  is approximately proportional to  $A_{\max}$  (Hirose & Werger 1987; Field 1988, Givnish 1988):

$$R = a A_{\max} \quad \text{eqn 3}$$

where  $a$  is an empirical parameter.

We assume that leaf photosynthetic characteristics do not change between day and night. A Taylor expansion to first order for  $A_n$  gives:

$$A_n = A_n(I_a) + (I - I_a) (\partial A_n / \partial I)_{I_a} \quad \text{eqn 4}$$

where  $I_a$  is the mean daytime value for absorbed PAR and  $A_n(I_a)$  is  $A_n$  as a function of  $I_a$ . Integrating this expression separately over the hours of daylight and darkness (for which we assume  $A_n = -R$ ) gives:

$$A_{\text{nd}} = A_n(I_a) t_d - a(24 - t_d) A_{\max} \quad \text{eqn 5}$$

where  $A_{\text{nd}}$  is the total daily net photosynthesis and  $t_d$

is day length. To optimize daily net photosynthesis we use  $\partial A_{\text{nd}} / \partial A_{\max} = 0$ , giving:

$$A_d = \phi I_d [1 - \sigma_b] \quad \text{eqn 6}$$

$$A_{\text{nd}} = \phi I_d [1 - (2\theta - 1)s - 2(1 - \theta s)\sigma_b] \quad \text{eqn 7}$$

$$A_{\max} = \phi I_d (1/a) [(2\theta - 1)s - 2(1 - \theta s)\sigma_b] \quad \text{eqn 8}$$

where

$$\sigma_b = [1 - (1 - s)/(1 - \theta s)]^{1/2} \quad \text{eqn 9}$$

$s = (24/t_d)a$ , and  $I_d$  is the total daily integral of absorbed PAR.

Equations 6 and 7 predict that the optimal LUE (obtained by having optimal  $A_{\max}$ ) is independent of  $I_d$ . This property contrasts with equation 1 which (with fixed  $A_{\max}$ ) predicts that LUE should decrease with increasing  $I_d$ . The same property stands (except for very low daily irradiances) in the more realistic case where the second-order terms are included in equation 4 and irradiance is expressed as a sinusoidal function of time (Appendix A).

From equation 7, the optimal daily LUE for net photosynthesis ( $\epsilon_{\text{nd}}$ ) may be calculated as:

$$\epsilon_{\text{nd}} = \phi [1 - (2\theta - 1)s - 2(1 - \theta s)\sigma_b]. \quad \text{eqn 10}$$

## CASE 2: EXTENSION TO WHOLE-CANOPY PHOTOSYNTHESIS

We now extend equation 7 from the leaf level to canopy level. For a canopy of total leaf area index  $L_0$ , total net photosynthesis is given by

$$A_{\text{nd}} = \int_0^{L_0} A_{\text{nd}}(I_d(L)) dL \quad \text{eqn 11}$$

where  $I_d(L)$  is the daily APAR for a cumulative leaf area index  $L$  below the upper surface. As equation 7 predicts that  $A_{\text{nd}}$  is a linear function of  $I_d$ , the integral simplifies to

$$A_{\text{nd}} = \epsilon_{\text{nd}} \int_0^{L_0} I_d(L) dL \quad \text{eqn 12}$$

where  $\epsilon_{\text{nd}}$  is the daily light-use efficiency for net photosynthesis given by equation 10. The integral gives the fraction of incident PAR intercepted by the canopy and can be rewritten as

$$A_{\text{nd}} = \epsilon_{\text{nd}} S_d S_f \quad \text{eqn 13}$$

where  $S_d$  is the total daily incident PAR and  $S_f$  is the fraction of  $S_d$  absorbed by the canopy as a whole.  $S_f$  can be estimated from leaf-area index using a light-attenuation model such as Beer's law for light attenuation through a canopy (Monsi & Saeki 1953), or from remote sensing data.

CASE 3: A SEMI-MECHANISTIC PHOTOSYNTHESIS  
MODEL

Functions describing  $A_{\max}$  and  $\phi$  in terms of more

fundamental biochemical parameters were derived from a semi-mechanistic photosynthesis model (Collatz *et al.* 1991). The non-rectangular hyperbola is now assumed to describe the gradual transition between two limiting rates  $J_C$  and  $J_E$ :

$$\theta A^2 - (J_C + J_E)A + J_E J_C = 0 \quad \text{eqn 14}$$

$J_E$  describes the response of photosynthesis to absorbed PAR under PAR limitation:

$$J_E = C_1 I \quad \text{eqn 15}$$

$$C_1 = \alpha (p_i - \Gamma^*) / (p_i + \Gamma^*) \quad \text{eqn 16}$$

where  $I$  is the absorbed PAR,  $\alpha$  is the intrinsic quantum efficiency for  $\text{CO}_2$  uptake,  $\Gamma^*$  is the  $\text{CO}_2$  compensation point given by

$$\Gamma^* = [\text{O}_2] / 2\tau \quad \text{eqn 17}$$

in which  $\tau$  is an experimentally determined parameter (Brooks & Farquhar 1985) and  $[\text{O}_2]$  is the partial pressure of oxygen,  $p_i$  is the internal partial pressure of  $\text{CO}_2$  given by

$$p_i = P c_i \quad \text{eqn 18}$$

where  $P$  is atmospheric pressure and  $c_i$  is the intercellular concentration (mole fraction) of  $\text{CO}_2$ . Many observations have shown that, for  $\text{C}_3$  species, stomata respond in a way that maintains a constant ratio of intercellular ( $c_i$ ) to ambient ( $c_a$ )  $\text{CO}_2$  concentration of 0.6–0.8 (Wong, Cowan & Farquhar 1979; Long & Hutchin 1991). We therefore introduce a parameter  $\lambda$ , where  $\lambda \approx 0.7$  and  $c_i = \lambda c_a$ .

$J_C$  is the Rubisco-limited rate of photosynthesis defined as:

$$J_C = C_2 V_m \quad \text{eqn 19}$$

$$C_2 = (p_i - \Gamma^*) / \{p_i + K_c(1 + [\text{O}_2]/K_o)\} \quad \text{eqn 20}$$

where  $V_m$  is the maximum catalytic capacity of Rubisco per unit leaf area,  $K_c$  is the Michaelis constant for  $\text{CO}_2$  and  $K_o$  is the competitive inhibition constant for  $\text{O}_2$  with respect to  $\text{CO}_2$  in the Rubisco reaction.

Respiration costs ( $R$ ) are scaled to  $V_m$  by

$$R = b V_m \quad \text{eqn 21}$$

where  $b = 0.015$  (Farquhar, von Caemmerer & Berry 1980). The kinetic parameters,  $K_c$ ,  $K_o$ , and  $\tau$  are temperature dependent; their temperature dependence is modelled using

$$k = k_{25} Q_{10}^{(T-25)/10} \quad \text{eqn 22}$$

where  $k_{25}$  is the value of the parameter at  $25^\circ\text{C}$  and  $Q_{10}$  is the relative change in the parameter for a  $10^\circ\text{C}$  change in temperature. The values of the parameters used in the model and their  $Q_{10}$  values are given in Table 1. Both  $V_m$  and  $R$  are predicted by the model at any temperature  $T$  and so require no *explicit* temperature dependence for the calculation of  $A$  and  $A_{nd}$ .

The same optimization procedure was applied as before, but with the optimization constraint  $\partial A_{nd} / \partial V_m = 0$ , giving:

$$A_d = I_d C_1 [1 - \sigma_c] \quad \text{eqn 23}$$

$$A_{nd} = I_d (C_1 / C_2) [C_2 - (2\theta - 1) \times s - 2(C_2 - \theta s)\sigma_c] \quad \text{eqn 24}$$

$$V_m = I_d (C_1 / C_2) (1/b) [(2\theta - 1) \times s - (2\theta s - C_2)\sigma_c] \quad \text{eqn 25}$$

where

$$\sigma_c = [1 - (C_2 - s) / (C_2 - \theta s)]^{1/2} \quad \text{eqn 26}$$

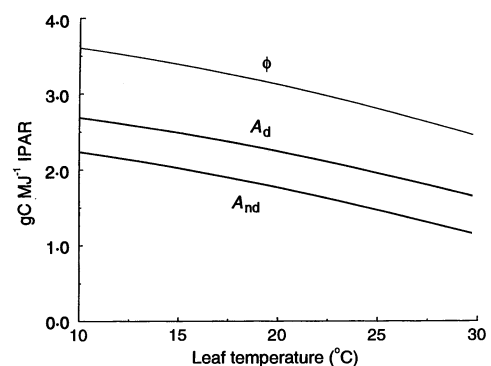
Figure 1 shows the modelled values and temperature response for the  $\epsilon$  of  $A_d$ ,  $A_{nd}$  and quantum efficiency ( $\phi$  or  $C_1$ ). The model predicts that daily photosynthesis is linearly dependent on APAR and that it also depends on mean leaf temperature and daylength. Modelled values of  $V_m$  also depend linearly on APAR.

The shape parameter describes the degree of convexity of the transition between limitation of photosynthesis by light and by the maximum photosynthetic rate. Experimental studies suggest that  $\theta$  should approach unity when the light response is determined for increasingly smaller photosynthetic units (from

**Table 1.** Values of parameters and constants used in the photosynthesis model

Symbol	Value	Units	$Q_{10}$	Description
$K_c$	30*	Pa	2.1	Michaelis constant of $\text{CO}_2$
$K_o$	30*	kPa	1.2	Inhibition constant of $\text{O}_2$
$\tau$	2600†		0.57	$\text{CO}_2/\text{O}_2$ specificity ratio
$\alpha$	0.08*			$\text{C}_3$ intrinsic quantum efficiency
$\phi$	0.053‡			$\text{C}_4$ quantum efficiency
$b$	0.015§			$R_d/V_m$ ratio
$\lambda$	0.7¶			optimal $c_i/c_a$ ratio
$c_a$	355	$\mu\text{mol mol}^{-1}$		Current ambient $\text{CO}_2$
$P$	100	kPa		Atmospheric pressure
$\text{O}_2$	20.9	kPa		Partial pressure $\text{O}_2$

\*Collatz *et al.* 1991; †Brooks & Farquhar 1985; ‡Ehleringer & Björkman 1977; §Farquhar, von Caemmerer & Berry 1980; ¶Wong, Cowan & Farquhar 1979.



**Fig. 1.** Modelled optimal light-use efficiency (LUE or  $\epsilon$ ) for gross photosynthesis ( $A_d$ ), net photosynthesis ( $A_{nd}$ ) and quantum efficiency ( $\phi$ ).

whole leaves to single-cell preparations and chloroplast preparations) (Terashima & Saeki 1985). Estimates of  $\theta$  at the leaf level range around 0.6–0.8; we use a value of 0.7 (McMurtrie & Wang 1993). The sensitivity of modelled  $\epsilon$  to  $\theta$  is shown in Fig. 2.

The optimization procedure can also be applied to a simplified version of the  $C_4$  photosynthesis model of Collatz, Ribas-Carbo & Berry (1992). In the  $C_4$  case,  $C_2$  in equation 19 is set to 1 and  $C_1$  in equation 15 is set to 0.0534 (Ehleringer & Björkman 1977). This calculation gives optimal LUEs for  $C_4$  photosynthesis that are independent of  $c_a$  and temperature over a range of non-extreme values.

## Materials and methods

### PREDICTING LUE FOR NET PHOTOSYNTHESIS

The optimized model allows us to predict LUE as a function of temperature and ambient  $CO_2$  concentration ( $c_a$ ). The model presented here does not account for the effects of environmental stresses on reducing LUE. Thus, the LUEs predicted by the model may be regarded as being predictions of the optimal LUE attainable for a given temperature and  $c_a$  and under conditions where restricted N supply does not hinder the attainment of this optimum.

There is abundant evidence that photosynthetic properties acclimate to temperature (e.g. Berry & Björkman 1980). Thus rather than assuming that leaf photosynthetic properties are invariant with temperature, a more realistic approach may be to assume that LUE declines steeply at very low or very high temperatures where photosynthesis is inhibited, but that otherwise enzyme activities adjust (to different climates and during the seasonal cycle) so as to maintain optimal net photosynthesis according to the principles outlined above. The model derived in case 3 captures the variation of this optimal net photosynthesis with temperature over a range of non-extreme temperatures ( $\approx 10$ – $30$  °C). This temperature dependence consists of a gradual decrease in the LUE with increasing temperature. Temperature extremes may further limit LUE in ways we do not consider here.

Similarly, we hypothesize that plant responses to  $CO_2$  may entail optimization of leaf characteristics.

### PREDICTING LUE FOR NET PRIMARY PRODUCTION

In order to compare the resulting estimates of LUE with most experimental measurements of LUE we need to estimate the LUE for net primary production. Formally, this would require modelling of the respiration costs for different ecosystems and plant tissues. However, for simplicity we use the general finding that whole plant respiration consumes 30–70% of total carbon fixation (Hagihara & Hozumi 1991; Ryan 1991; Sprugel & Benecke 1991).

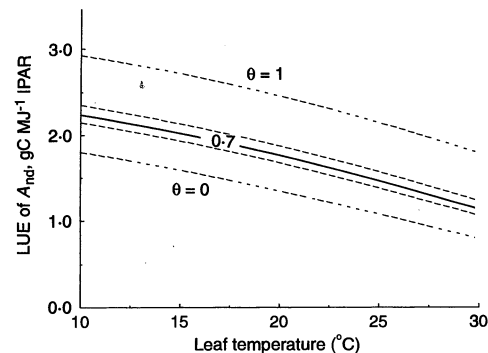


Fig. 2. Modelled response of light-use efficiency (LUE) for net photosynthesis ( $A_{nd}$ ) to the shape parameter ( $\theta$ ). The solid line shows LUE for  $\theta=0.7$ , the dotted lines directly above and below are for  $\theta=0.8$  and  $\theta=0.6$  respectively, and the outlying upper and lower lines are for  $\theta=1$  and  $\theta=0$  respectively.

### PREDICTING FOLIAGE NITROGEN CONTENT

Many studies of naturally growing plants have reported a strong linear correlation between  $A_{max}$  and foliage nitrogen content (Field & Mooney 1986; Hirose & Werger 1987a; Field 1988, 1991). Although the relationship has been shown to hold across a broad range of vegetation types, it is essentially an empirical observation (Field 1991). However, this observation allows us the possibility of relating modelled estimates of  $A_{max}$  to foliage N content. The model calculates optimal values for the maximum catalytic capacity of Rubisco ( $V_m$ ), and we assume a linear relationship between leaf N content and the value of  $V_m$  at a reference temperature (25 °C) giving

$$N = p V_m^{25} + N_o \quad \text{eqn 27}$$

where  $N$  is the foliage nitrogen content,  $V_m^{25}$  the value of  $V_m$  at 25 °C, and  $p$  and  $N_o$  are parameters. For a fixed enzyme content  $V_m$  has a strong dependence on temperature which we model using the  $Q_{10}$  function with a  $Q_{10}$  of 2.0 at all temperatures. The value predicted for  $V_m$  at a temperature  $T$  can then be used to calculate leaf N content using

$$N = p V_m e^{-0.0693(T-25)} + N_o \quad \text{eqn 28}$$

where  $V_m$  is the maximum catalytic capacity of Rubisco predicted by the model at a temperature  $T$ . Equation 28 may be implemented on an area basis to calculate  $N$  content per unit leaf area or on a mass basis to calculate  $N$  content per unit leaf mass. The correlation has sometimes but not always been found to be stronger when both photosynthesis and  $N$  are expressed on a leaf mass basis (Evans 1989b).

We implemented equation 28 with  $V_m$  measured in units of  $\mu\text{mol(C)}\text{g}^{-1}\text{s}^{-1}$  and  $N$  in units of  $\text{mg N g}^{-1}$ . Parameter values were obtained from Field (1983) who measured the  $N$  content and  $V_m$  of 10 leaves of the chaparral shrub *Lepechinia calycina* grown at different irradiances. His regression of  $V_m$  against  $N$  gives values for  $p=23$  and  $N_o=-0.16$ . Although only measured

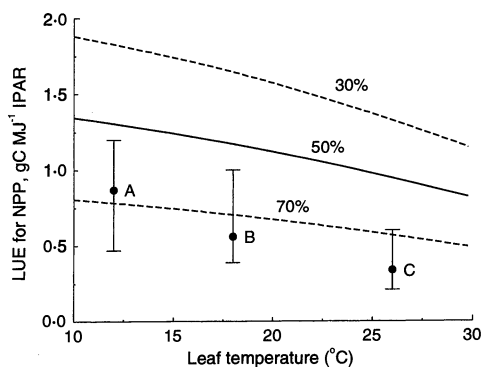
for one species these parameter values were used because they were obtained from direct and consistent measurements of the variation of  $V_m$  with leaf  $N$  concentration. For comparison, parameter values were also estimated from the VINE data set of Field & Mooney (1986). This data set includes measurements of  $N$  vs  $A_{max}$  for 137 leaves from 21 species, including trees, shrubs and herbs, from widely varying environments. Although these data give values for the variation of  $A_{max}$  with leaf  $N$  content, parameter values were estimated by assuming a reference temperature of 25 °C. Equation 19 ( $C_2=0.27$  at 25 °C) was used to convert from  $A_{max}$  to  $V_m$  (setting  $J_C=A_{max}$ ). Using the regression given in Fig. 1.2 of Field & Mooney (1986) we estimated parameter values of  $p=25$  and  $N_0=7.15$ . This more generalized relationship of  $V_m$  to  $N$  gives a similar slope to that obtained from Field (1983).

## Results

### ESTIMATES OF LUE

Figure 3 shows the LUE values predicted between 10 °C and 30 °C with whole-plant respiration costs taken as 30%, 50% and 70% of gross photosynthesis. LUE in Fig. 3 is expressed as net primary production in grams of carbon (gC) per unit of intercepted photosynthetically active radiation (IPAR). Taking whole-plant respiration as 50% of gross photosynthesis gives predicted LUE values that vary from 1.34 gC MJ<sup>-1</sup> IPAR at 10 °C down to 0.81 gC MJ<sup>-1</sup> IPAR at 30 °C (to convert from LUE in gC MJ<sup>-1</sup> absorbed PAR to gC MJ<sup>-1</sup> IPAR we assume a leaf absorptance to PAR of 0.86).

Russell *et al.* (1989), in a review of empirical studies, found measured values of LUE for crop ecosys-



**Fig. 3.** Modelled optimal light-use efficiency (LUE) for net primary production (NPP). The solid line shows LUEs calculated assuming whole-plant respiration costs of 50% and the upper and lower dotted line are calculated assuming respiration of 30% and 70% of gross photosynthesis respectively. Dots and tick marks indicate the mean and range of LUE estimated from measurements (Ruimy *et al.* 1994) for: A, temperate/subpolar coniferous forests; B, temperate deciduous forests; C, tropical/subtropical forests. Values are plotted at an estimated mean growing season temperature for each biome.

tems of 1.1–1.4 gC MJ<sup>-1</sup> IPAR. Cannell *et al.* (1987) measured values of 1.58 and 1.13 gC MJ<sup>-1</sup> IPAR for stands of short-rotation willows, growing with and without irrigation. If respiration costs are estimated as 30% of gross photosynthesis instead of 50% then the modelled LUE at 20 °C changes from 1.1 gC MJ<sup>-1</sup> IPAR to 1.57 gC MJ<sup>-1</sup> IPAR, which accounts for the highest measured value of LUE. Thus, values of LUE measured for crop ecosystems growing under optimum conditions are in the same range as values predicted by the model.

Linder (1985) measured an average value of the LUE for above-ground biomass of 0.8 gC MJ<sup>-1</sup> IPAR in evergreen broad-leaved and coniferous plantations of up to 55 years of age in Australia, England and Sweden (converted using a carbon-to-dry organic matter ratio of 0.475). If we further assume that below-ground production represents 20–40% of above-ground production (Ruimy, Saugier & Dedieu 1994) then Linder's data imply a LUE  $\approx$  1 gC MJ<sup>-1</sup> IPAR. A number of these plantations were fertilized and most suffered little water stress, so this value may be considered close to an optimal value for forest ecosystems. Thus, Linder's estimate of average LUE in forest plantations is also consistent with the modelled optimal LUE.

Ruimy *et al.* (1994), in a review of the literature on LUE measurements for natural ecosystems, calculated mean LUE values of 0.87 gC MJ<sup>-1</sup> IPAR for temperate/subpolar coniferous forests, 0.56 gC MJ<sup>-1</sup> IPAR for temperate deciduous forests and 0.34 gC MJ<sup>-1</sup> IPAR for tropical/subtropical forests. These figures show a clear decrease in LUE with temperature, as predicted in Fig. 3. From the data presented in Ruimy *et al.* (1994) we selected the maximum recorded values of the LUE for above-ground production, yielding maximum LUE values of 1.2 gC MJ<sup>-1</sup> IPAR for temperate/subpolar coniferous forests, 1.0 gC MJ<sup>-1</sup> IPAR for temperate deciduous forests and 0.6 gC MJ<sup>-1</sup> IPAR for tropical/subtropical forests. Thus the maximum values for LUE lie within the range of our modelled optimal LUEs, except for the value for tropical/subtropical forests. This value could also be reconciled with the model if respiration costs were assumed to be as high as 70% of gross photosynthesis for tropical/subtropical forests. The mean values cited by Ruimy *et al.* (1994) show that on average, LUE values in natural ecosystems (as opposed to agricultural crops and forest plantations) are considerably lower than the predicted optimal values.

Wofsy *et al.* (1993) measured the mean effective quantum efficiency (defined as the number of CO<sub>2</sub> molecules fixed per day by the canopy per incident photon) and maximum quantum efficiency in a temperate deciduous forest, using eddy correlation to measure the CO<sub>2</sub> flux. Midsummer values averaged 0.02 or  $\approx$  1.1 gC MJ<sup>-1</sup> IPAR for the mean effective quantum efficiency and 0.04–0.055 or  $\approx$  2–3 gC MJ<sup>-1</sup> IPAR for the maximum quantum efficiency. Using the same method, Fan *et al.* (1990) measured a value

for the mean effective quantum efficiency of 0.015 or  $\approx 0.83 \text{ gCMJ}^{-1}$  IPAR for a tropical forest in central Amazonia, and Grace *et al.* (1995) measured a value for the quantum efficiency of 0.025 or  $\approx 1.6 \text{ gCMJ}^{-1}$  IPAR for a tropical forest in Rondônia, Brazil. The measurements of mean effective quantum efficiency can be directly compared with the modelled LUE for gross photosynthesis (making the approximation that 100% of incident PAR is intercepted by the canopy) which ranges from 1.6 to  $2.7 \text{ gCMJ}^{-1}$  IPAR between  $30^\circ\text{C}$  and  $10^\circ\text{C}$ . Thus the measurements of LUE for gross photosynthesis in natural ecosystems, made using the eddy correlation method, are also lower than the predicted optimal values.

The fixed LUE of  $1.25 \text{ gCMJ}^{-1}$  IPAR used by Heimann & Keeling (1989) coincides with the highest optimal LUEs predicted by our model. Potter *et al.* (1993) calculated a much lower global LUE of  $0.389 \text{ gCMJ}^{-1}$  IPAR by calibrating their model against measurements of net primary production. Knorr & Heimann (1995) estimated a global LUE of  $0.54 \text{ gCMJ}^{-1}$  IPAR by calibrating a LUE model against measured seasonal variations of atmospheric  $\text{CO}_2$  concentration, after accounting for reductions in LUE owing to drought. Our modelled optimal LUE values are thus considerably larger than these globally calibrated mean values. We suggest that this is because the predicted optimal LUE represents a maximal value that is reduced in natural ecosystems by drought, temperature and nutrient stresses.

#### OPTIMAL VALUES OF $V_m$

Predicted optimal values of  $V_m$  (the maximum catalytic capacity of Rubisco) vary linearly with APAR. Canopy-averaged values of the optimal  $V_m$  (expressed per unit leaf area) predicted by the model decrease as leaf area index (LAI) increases, because the proportion of shaded leaves increases.

McMurtie & Wang (1993) used  $V_m = 72 \mu\text{mol m}^{-2} \text{ s}^{-1}$  at  $25^\circ\text{C}$  in modelling a forest stand with a LAI that increased from 0.5 to 8.5 over an 8-year period, and daily irradiances of  $\approx 0\text{--}20 \text{ MJ IPAR m}^{-2} \text{ day}^{-1}$ . Over this range of irradiances, our model predicts a range of canopy averaged  $V_m$  values of up to  $44 \mu\text{mol m}^{-2} \text{ s}^{-1}$  at  $25^\circ\text{C}$  and a LAI of 8.5 and up to  $140 \mu\text{mol m}^{-2} \text{ s}^{-1}$  at  $25^\circ\text{C}$  and a LAI of 0.5. Thus, the model predicts optimal values of  $V_m$  that vary with environment but the range of values predicted is in agreement with previous models. Wullschleger (1993) reported values of  $V_m$  for 109  $\text{C}_3$  plant species. Reported values ranged from 6 to  $194 \mu\text{mol m}^{-2} \text{ s}^{-1}$  with a mean value across all species of  $64 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , in agreement with the range of values predicted by our model.

#### FOLIAGE IN CONCENTRATIONS

Estimates of optimal foliage-N represent an upper

limit to the amount of N required by foliage. If less N is available for foliage then leaf N concentrations may be reduced and/or total leaf area may be reduced. Both effects will reduce whole-canopy photosynthesis per unit ground area to below the optimum rate. Our model predicts (1) that foliage-N should increase linearly with increasing PAR and (2) that foliage-N should increase nearly exponentially with decreasing growing season temperatures, provided that N supply is sufficient to maintain these levels.

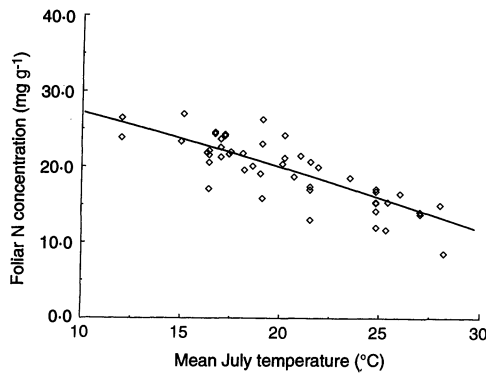
Yin (1993) compiled measurements of foliar N concentrations in 49 deciduous broad-leaf forests distributed across North America. These measurements are shown in Fig. 4, plotted against the mean July temperatures given for each site by Yin (1993). For deciduous forests foliar N concentrations were strongly correlated with mean July temperatures, with foliar N concentrations increasing as mean July temperature decreased (Yin 1993).

In order to make explicit predictions of foliar N concentrations in deciduous forests at the height of the growing season, for comparison with these data, we used values for mean July temperature, PAR and day-length as inputs. A standard algorithm (Prentice, Sykes & Cramer 1993) was used to calculate PAR and day length. Temperature and cloudiness data were obtained from Leemans & Cramer (1991). Values for the three variables were then used to estimate the range of optimal foliage N contents for deciduous forests growing anywhere in the Northern Hemisphere with a mean July temperature between  $10^\circ\text{C}$  and  $30^\circ\text{C}$ . The estimates of foliage N concentration were made using an average value for the foliar biomass of deciduous forests of  $407 \text{ g (dry mass) m}^{-2}$  (ground area) calculated from data presented in Yin (1993). We assumed that deciduous forests intercept 90% of PAR during the peak of growing season. Figure 4 shows the agreement obtained. The increase in foliar N concentration associated with decreasing mean July temperatures is partially counteracted by decreasing irradiance (which acts to decrease foliar N concentration). The result is an almost linear increase in foliar N concentration with decreasing temperature (Fig. 4).

Figure 4 shows that the measured foliage-N contents are close to predicted optimal values. This does not imply the absence of nitrogen limitation. Instead, it invites the speculation that if nitrogen is limiting to primary production (as appears to be the case, for example, for the boreal forest) the effect may be a reduction of foliage biomass (and thus leaf area index) rather than a reduction in foliar N concentrations to suboptimal levels.

Implemented over the entire growing season, the model would not predict a constant value for foliar N concentration. Instead, the model would predict foliar N concentrations to be highest in spring and early summer (both low temperature and, later, high PAR demand high foliar N concentrations), declining from





**Fig. 4.** The data points (diamonds) show measurements of foliage N concentration in 49 deciduous broad-leaf forests distributed across North America plotted against mean July temperature (Yin 1993). The solid line shows a regression ( $y = 33.36 - 0.5543x - 0.0057x^2$ ) of the range of values of foliar N concentration predicted by the model for Northern Hemisphere deciduous forests.

late summer onward as PAR declines. This prediction is qualitatively in agreement with measurements of seasonal changes in foliar N concentration in leaves of temperate deciduous trees (Reich *et al.* 1991) whereas a consistent pattern was observed of an increase in leaf N (most clearly seen in N per unit leaf area) until early- to mid-summer, followed by a gradual decline until the end of the growing season.

#### CO<sub>2</sub> RESPONSES

For C<sub>3</sub> plants both the modelled quantum efficiency and the ratio  $R/A_{\max}$  change with the ambient CO<sub>2</sub> concentration; both effects increase the optimal LUE as the ambient CO<sub>2</sub> concentration ( $c_a$ ) increases. The dependence of LUE on  $c_a$  is stronger at higher temperatures (Fig. 5). Thus, for a doubling in  $c_a$  from 355 to 710  $\mu\text{mol mol}^{-1}$  the model predicts an increase of 16% in the LUE for net photosynthesis at 10 °C, 31% and 20 °C and 63% on 30 °C (Fig. 3).

Kimball *et al.* (1993) reviewed the findings of a large number of greenhouse and growth chamber studies and found that plant growth and yield typically increases by 30% or more with a doubling of CO<sub>2</sub> concentration. This estimate was based on studies of C<sub>3</sub> plants mostly growing under optimum conditions of water and soil nutrients (Kimball *et al.* 1993). It has also been observed experimentally that the effect of increasing CO<sub>2</sub> concentrations is greater at higher temperatures (e.g. Idso *et al.* 1987; Drake & Leadley 1991; Silvola & Ahlholm 1992; Kimball *et al.* 1993).

When  $c_a$  is increased, the model calculates a new optimal value for  $V_m$ . For the CO<sub>2</sub> doubling, the model predicts a modest reduction in  $V_m$  of  $\approx 5\%$  at 10–20 °C. This implies a similar decrease in dark respiration costs and a smaller decrease in foliar N concentration (4% at 20 °C, if specific leaf area remains constant).

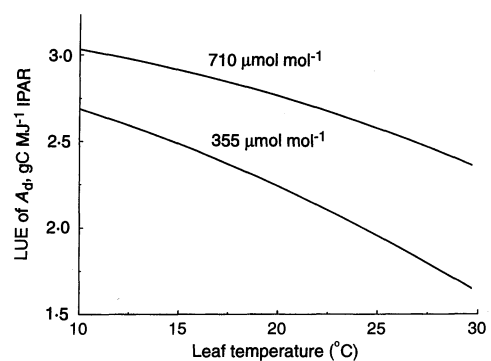
This predicted decrease in  $V_m$  and foliar N concentration is qualitatively in agreement with results

obtained from experimental studies. Sage, Sharkey & Seemann (1989) studied the response of five C<sub>3</sub> species grown at CO<sub>2</sub> partial pressures of 300 and 900–1000 microbars. The extent of the downward acclimation of Rubisco content at high CO<sub>2</sub> was found to be highly species specific. However, the Rubisco activation state was consistently observed to be lower by 19–48%. Silvola & Ahlholm (1992) grew Willows (*Salix × dasyclados*) at different CO<sub>2</sub> concentrations and fertilization levels. They found an average decrease in foliar N concentration of  $\approx 19\%$  for an increase in CO<sub>2</sub> concentration from 300 to 1000  $\mu\text{g g}^{-1}$ . For the same CO<sub>2</sub> increase the model predicts a decrease of  $\approx 7\%$  in foliar N concentration. Thus, the predicted decrease in  $V_m$  is a real phenomenon, though its magnitude is less than found in experimental studies.

Stomatal conductance is not modelled explicitly here. However, there is an implied decrease in stomatal conductance as CO<sub>2</sub> increases. This is because the ratio of intercellular to ambient CO<sub>2</sub> concentration is held constant as ambient CO<sub>2</sub> increases. For a doubling of  $c_a$  stomatal conductance is thus predicted to decrease by 42% at 10 °C, 35% at 20 °C and 19% at 30 °C; the decrease in stomatal conductance is greater at lower temperatures because of the temperature dependence of the increase in LUE. These figures compare well with average decreases in stomatal conductance measured in greenhouse and growth chamber studies of  $\approx 37\%$  for a doubling of CO<sub>2</sub> (Kimball *et al.* 1993).

#### Discussion and conclusions

We have shown using the hypothesis of optimal N allocation that the standard non-rectangular hyperbola formulation for the instantaneous response of leaf net photosynthesis to APAR leads to a linear equation for the time-integrated response of canopy net photosynthesis to APAR. When the limiting rates in this equation are derived using a semi-mechanistic model of photosynthesis (Collatz *et al.* 1991), the resulting pre-



**Fig. 5.** Light-use efficiency (LUE) of gross photosynthesis ( $A_d$ ) predicted by the model at atmospheric CO<sub>2</sub> concentrations of 355  $\mu\text{mol mol}^{-1}$  and 710  $\mu\text{mol mol}^{-1}$ .

dictions of light-use efficiency (LUE) compare well with the range of LUEs measured for crops and forest plantations. For natural ecosystems, measured maximal LUE values lie at the bottom of the range of optimal LUE values predicted by our model, while measured mean LUEs are somewhat lower than those predicted by our model. We suggest that this is because the predicted optimal LUE values represent a maximal value that is reduced in natural ecosystems.

We have formally considered only the case where N supply is not limiting. Where N is limiting we might expect vegetation to optimize foliage area and foliage N concentration simultaneously. The model described here could be extended to consider this joint optimization problem. However, the agreement obtained between modelled optimal foliage N concentrations and field measurements along a latitudinal transect suggests that the first-order effect of limited N supply may be to reduce foliage area, rather than to reduce foliage N concentration to suboptimal levels. Thus the LUE values predicted by the model may still be applicable under N limitation but calculation of photosynthesis for prognostic models of global NPP will require that the N limitation of foliage area is also modelled.

This approach to modelling NPP would have the advantage of not requiring parameters to be specified for each biome. In particular, values of  $V_m$  (the maximum catalytic capacity of Rubisco) are predicted on the basis of environmental variation and photosynthetic pathway, and not prescribed for each biome as in many current models. We conclude that optimization theory can provide a useful way of integrating diverse experimental observations into a framework for global-scale modelling of terrestrial carbon fluxes.

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#### Appendix A: Second order solution to photosynthesis model equations

The Taylor series about the mean value of daytime irradiance  $I_d$  is, neglecting third and higher order terms:

$$A_n = A_n(I_a) + (I - I_a)I_a \left(\frac{\partial A_n}{\partial I}\right)_{I_a} + (1/2)(I - I_a)^2 \left(\frac{\partial^2 A_n}{\partial I^2}\right)_{I_a} \quad \text{eqn A1}$$

We model the daily radiation curve (Monteith 1981) with

$$I(t) = (\pi I_d / 2t_d) \sin(\pi t / t_d) \quad \text{eqn A2}$$

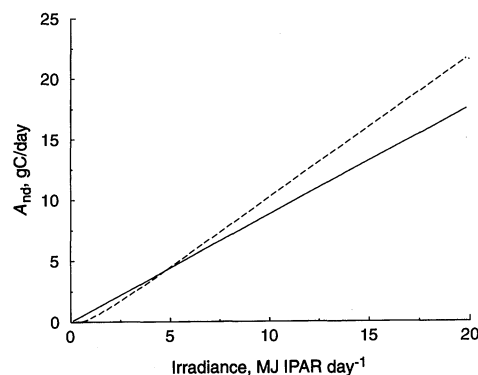
where  $I(t)$  is the rate of PAR absorbed at time  $t$  after sunrise,  $I_d$  is the total daily absorbed PAR and  $t_d$  is the day-length. Equation A1 can be integrated over the daylight hours using equation A2 and over darkness hours assuming  $A_n = -R$ :

$$A_{nd} = A_n(I_a)t_d + 0.5(\pi/4 - I_a)I_d \left(\frac{\partial^2 A_n}{\partial I^2}\right)_{I_a} - a(24 - t_d)A_{max} \quad \text{eqn A3}$$

To optimize equation A3 we set

$$\partial A_n / \partial V_m = 0. \quad \text{eqn A4}$$

Solution of equation A4 yields optimum values for  $V_m$ , and  $A_{nd}$ . Figure A1 shows the response of  $A_{nd}$  to  $I_d$  as calculated using both the first and second order approximations. The second order equation predicts a near-linear response of  $A_{nd}$  to  $I_d$ , except that the intercept gives zero  $A_{nd}$  at a value of  $I_d > 0$ . At low values of  $I_d$  the second order equation predicts slightly lower values of  $A_{nd}$  than the first order equation, whilst at higher values of  $I_d$  the second order equation predicts increasingly higher values of  $A_{nd}$  than the first order equation. These differences are smaller than the sensitivity



**Fig. A1.** Response of daily net photosynthesis ( $A_{nd}$ ) to the daily total of intercepted PAR. The solid line shows daily net photosynthesis as calculated using the first order approximation and the dotted line shows daily net photosynthesis calculated using the second order approximation.

of the model to changes in the value of other parameters such as  $\theta$ . A counter-intuitive result is that, if  $I_d$  is sufficiently high, a sinusoidal variation in daytime irradiance allows a somewhat more efficient use of  $I_d$  than does a constant average daytime irradiance.

Including the effects of a diurnal variation in temperature would not alter the values of  $A_{nd}$  predicted by the second equation but would somewhat lower values of  $A_{nd}$  predicted by the second order equation.