



The Correlation between Plant Growth and Intercepted Radiation: An Interpretation in Terms of Optimal Plant Nitrogen Content

RODERICK C. DEWAR

School of Biological Science, University of New South Wales, Sydney NSW 2052, Australia

Received: 1 June 1995 Accepted: 15 March 1996

Photosynthesis of leaves is commonly observed to have a saturating response to increases in their nitrogen (N) content, while the response of plant maintenance respiration is more nearly linear over the normal range of tissue N contents. Hence, for a given amount of foliage, net primary productivity (*NPP*) may have a maximum value with respect to variations in plant N content. Using a simple analytically-solvable model of *NPP*, this idea is formulated and its broad implications for plant growth are explored at the scale of a closed stand of vegetation. The maximum-*NPP* hypothesis implies that *NPP* is proportional to intercepted radiation, as commonly observed. The light utilization coefficient (ϵ), defined as the slope of this relationship, is predicted to be

$$\epsilon = \alpha Y_g (1 - \lambda)^2,$$

where α is the quantum yield, Y_g is the biosynthetic efficiency, and λ is a dimensionless combination of physiological and environmental parameters of the model. The maximum-*NPP* hypothesis is also consistent with observations that whole-plant respiration (R) is an approximately constant proportion of gross canopy photosynthesis (A_c), and predicts their ratio to be

$$R:A_c = 1 - Y_g(1 - \lambda).$$

Using realistic parameter values, predicted values for ϵ and $R:A_c$ are typical of C_3 plants. ϵ is predicted to be independent of plant N supply, consistent with observations that long-term growth responses to N fertilization are dominated by increased light interception associated with increased growth allocation to leaf area. Observed acclimated responses of plants to atmospheric $[CO_2]$, light and temperature are interpreted in terms of the model.

© 1996 Annals of Botany Company

Key words: Allocation, acclimation, carbon-use efficiency, growth, light-use efficiency, model, nitrogen, optimization, photosynthesis, radiation, respiration.

INTRODUCTION

Over the last 20 years, considerable attention has focussed on the relationship between growth rate and the amount of solar radiation intercepted by agricultural crops and tree stands. Monteith (1977) showed that the relationship between annual above-ground dry matter production and intercepted total solar radiation was approximately linear for several agricultural crops in Britain with good access to water and nutrients, and proposed that the slope of this relationship (ϵ) was relatively conservative among crop species. However, subsequent studies have shown that ϵ varies considerably between crop species (e.g. Sivakumar and Virmani, 1984; Prince, 1991). Similar linear relationships have been observed for tree species in terms of both above-ground and total biomass production (Linder, 1985; Cannell *et al.*, 1987; Grace, Jarvis and Norman, 1987; Cannell, Sheppard and Milne, 1988; Dalla-Tea and Jokela, 1991; Hunt, 1994; Landsberg *et al.*, 1996).

In comparing reported values of ϵ , it is important to take account of different measures of growth and radiation used (Prince, 1991). In this paper, ϵ is the ratio of total net primary productivity (*NPP*, both above- and below-ground)

to intercepted photosynthetically-active radiation (PAR). On this basis, reported values of ϵ for crops range from 0.85 to 4.8 g dry matter MJ^{-1} (Prince, 1991). For trees in the absence of climatic limitations (such as drought, high vapour pressure deficits or cold temperatures), ϵ is typically in the range 2.0–3.5 g dry matter MJ^{-1} (Hunt, 1994).

The practical advantage of such a simple predictor of plant growth over more complex approaches is clear. Several authors have used the ‘ ϵ -model’ as a basis for predicting *NPP* at scales ranging from a few hectares (e.g. Kirschbaum *et al.*, 1994) to the entire global land surface (e.g. Potter *et al.*, 1993). However, the physiological basis for a linear relationship between *NPP* and intercepted PAR (although disputed by Demetriades-Shah *et al.*, 1992, 1994; see replies by Arkenbauer *et al.*, 1994; Kiniry, 1994; Monteith, 1994) has received relatively little attention. In view of its empirical nature, it is important to determine the range of validity of this relationship, and to understand the physiological and environmental factors underlying observed variations in ϵ .

The observation that *NPP* is approximately proportional to intercepted PAR seems counter-intuitive because leaf photosynthesis (P_{leaf}) is a non-linear function of leaf

TABLE 1. Symbol definitions. Abbreviations: C, carbon; N, nitrogen; PAR, photosynthetically-active radiation

Symbol	Definition (with relevant equations)	Units
A_c	daily gross canopy photosynthesis (3a)	kg C m ⁻² ground d ⁻¹
A_{leaf}	daily gross leaf photosynthesis	kg C m ⁻² leaf d ⁻¹
$A_{\text{leaf}}(L)$	value of A_{leaf} at L (2a)	kg C m ⁻² leaf d ⁻¹
c_i, c_a	intercellular (i) and ambient (a) [CO ₂]	kg C m ⁻³
CUE	carbon use efficiency (8a, 8b)	dimensionless
g_x	carboxylation conductance (1b)	m s ⁻¹
h	daylength	s d ⁻¹
I	leaf irradiance	W PAR m ⁻² leaf
$\langle I_L \rangle$	mean leaf irradiance at L (2b)	W PAR m ⁻² leaf
$\langle I_c \rangle$	mean irradiance intercepted by the canopy (3b)	W PAR m ⁻² ground
k	canopy light extinction coefficient	m ² ground m ⁻² leaf
k_x	carboxylation coefficient	m ² kg ⁻¹ N s ⁻¹
L	cumulative leaf area index inside the canopy	m ² leaf m ⁻² ground
L_c	canopy leaf area index	m ² leaf m ⁻² ground
n_c	canopy N content	kg N m ⁻² ground
$n_{c,\text{opt}}$	optimal value of n_c (6a)	kg N m ⁻² ground
n_{leaf}	leaf N content	kg N m ⁻² leaf
$n_{\text{leaf}}(L)$	value of n_{leaf} at L (3d)	kg N m ⁻² leaf
$n_{\text{leaf,opt}}(L)$	optimal value of $n_{\text{leaf}}(L)$ (6c)	kg N m ⁻² leaf
n_p	whole-plant N content (4b)	kg N m ⁻² ground
NPP	net primary productivity (5)	kg C m ⁻² ground d ⁻¹
NPP_{max}	maximum value of NPP (7a)	kg C m ⁻² ground d ⁻¹
P_{leaf}	instantaneous gross leaf photosynthesis (1a, 1c)	kg C m ⁻² leaf s ⁻¹
$P_{\text{1max}}(L)$	light-saturated value of P_{leaf} at L (3f)	kg C m ⁻² leaf s ⁻¹
r	maintenance respiration rate per unit tissue N	kg C kg ⁻¹ N d ⁻¹
R	whole-plant respiration	kg C m ⁻² ground d ⁻¹
R_g	whole-plant growth respiration (4d)	kg C m ⁻² ground d ⁻¹
R_m	whole-plant maintenance respiration (4a, 4c)	kg C m ⁻² ground d ⁻¹
S_o	daily PAR incident above the canopy	J PAR m ⁻² ground d ⁻¹
S_c	daily PAR intercepted by the canopy (3c)	J PAR m ⁻² ground d ⁻¹
VPD	vapour pressure deficit	kPa
Y_g	biosynthetic efficiency	dimensionless
α	quantum yield	kg C J ⁻¹ PAR
β	$c_i:c_a$ ratio	dimensionless
ϵ	light utilization coefficient (7b)	kg C J ⁻¹ PAR
λ	parameter combination (6b)	dimensionless
λ_{sw}	sapwood N content: canopy N content	dimensionless
λ_r	fine root N content: canopy N content	dimensionless

irradiance (I). One explanation is that, for a closed stand of vegetation of sufficiently large leaf area index (LAI), the majority of leaves are below light-saturation (e.g. Russell, Jarvis and Monteith, 1989). This explanation has been called into question by Medlyn's (1996) analysis of the detailed canopy photosynthesis model MAESTRO (Wang and Jarvis, 1990), which shows that the contribution from light-saturated leaves to the canopy-averaged slope of the P_{leaf} vs. I relationship is significant. Another explanation has been suggested on the basis of the theoretical result that, if the rate of light-saturated leaf photosynthesis (P_{1max}) is distributed inside the canopy similarly to leaf irradiance (as is often observed), then canopy photosynthesis is proportional to the fraction of incident PAR that is intercepted by the canopy (e.g. Charles-Edwards, 1982; Sellers *et al.*, 1992; Kull and Jarvis, 1995). However, this result relates canopy photosynthesis to P_{1max} at some reference level in the canopy, additional assumptions for which are required to explain a proportionality between canopy photosynthesis and intercepted PAR (see Appendix). A more fundamental limitation of both these explanations is that the analysis of photosynthesis alone cannot explain the linear relationship

between NPP and intercepted PAR. Any physiological interpretation of this relationship must also take account of respiration. This paper presents one such interpretation.

The basis for this interpretation is the dependence of photosynthesis and respiration on tissue nitrogen (N) contents. Leaf photosynthesis is commonly observed to have a saturating response to increases in leaf N content except at high irradiance (e.g. Gulmon and Chu, 1981; Evans, 1989), reflecting the role of proteins in the Calvin cycle and thylakoids which represent the majority of leaf N. In contrast, the response of plant maintenance respiration is more nearly linear over the normal range of tissue N contents (e.g. Ryan, 1991, 1995), reflecting the energy requirement for maintaining or re-synthesising degradable products, mostly N-rich proteins. NPP may therefore have a maximum at some optimal value of plant N content.

The aim of this paper is to describe the broad implications of the maximum- NPP hypothesis for plant growth generally, and for the relationship between NPP and intercepted PAR in particular, at the scale of a closed stand of crops or trees. Accordingly, the hypothesis is formulated using a relatively simple leaf photosynthesis model (Thornley and Johnson,

TABLE 2. Standard parameter values (for notation, see Table 1). These values are realistic estimates based on a number of sources. They have been chosen to illustrate the broad implications of the maximum-NPP hypothesis, and do not represent any particular species or data set

Parameter	Standard value	Notes/source
c_a	$1.75 \times 10^{-4} \text{ kg C m}^{-3}$	equivalent to 350 ppmV at 20 °C
h	57600 s d^{-1}	16 h daylength
k	$0.5 \text{ m}^2 \text{ ground m}^{-2} \text{ leaf}$	Jarvis and Leverenz (1983)
k_x	$1.27 \text{ m}^3 \text{ kg}^{-1} \text{ N s}^{-1}$	corresponds to approx. 50% of the maximum slope in Fig. 1 of Evans (1989)*
r	$0.218 \text{ kg C kg}^{-1} \text{ N d}^{-1}$	eqn (6) of Ryan (1991)
Y_g	0.8	Table 2 of Ryan (1991); Johnson (1990)
α	$2.73 \times 10^{-9} \text{ kg C J}^{-1} \text{ PAR}$	equivalent to 0.05 mol $\text{CO}_2 \text{ mol}^{-1}$ quanta typical for C_3 plants (Wong <i>et al.</i> , 1979)
β	0.7	equivalent to 100 W PAR m^{-2} ground or 460 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ over a 16 h day
S_0	$5.76 \text{ MJ PAR m}^{-2} \text{ ground d}^{-1}$	order of magnitude estimates†
λ_{sw}, λ_r	1.0, 1.0	

* The slope of this figure is interpreted as the quantity $\beta c_a k_x$ (in units of $\text{kg C kg}^{-1} \text{ N s}^{-1}$).

† λ_{sw} based on data for *Pinus radiata* (Jeffreys, pers. comm.); λ_r based on ratio of fine root:foliage N concentrations reported for *Pinus radiata* in Kirschbaum *et al.* (1994), together with the assumption that the fine root:foliage biomass ratio ≈ 1 .

1990) which can be examined analytically, in the expectation that the results capture the essential behaviour obtained using more sophisticated leaf photosynthesis models (e.g. Farquhar, Caemmerer and Berry, 1980; Farquhar and Caemmerer, 1982). Respiration is modelled with comparable simplicity. Symbol definitions are given in Table 1, and default parameter values are given in Table 2.

SIMPLE MODEL OF NPP IN RELATION TO NITROGEN CONTENT

Daily gross canopy photosynthesis

Following Thornley and Johnson (1990, their Eqn 9.7i), I assume that the instantaneous rate of gross leaf photosynthesis (P_{leaf}) has a rectangular hyperbolic dependence on the internal leaf $[\text{CO}_2]$ (c_i) and the instantaneous leaf irradiance (I):

$$P_{\text{leaf}} = \frac{\alpha I c_i g_x}{\alpha I + c_i g_x} \quad (1a)$$

where α is the quantum yield, and g_x is the carboxylation conductance. The light-saturated rate of leaf photosynthesis [given from eqn (1a) by $c_i g_x$] is commonly observed to have a strong linear relationship with total leaf N content (Evans,

1989). To express this, I assume that g_x is proportional to total leaf N content (n_{leaf}):

$$g_x = k_x \cdot n_{\text{leaf}} \quad (1b)$$

The parameter k_x varies significantly between species (Evans, 1989).

The widely-observed correlation between stomatal conductance and net leaf photosynthesis (e.g. Wong, Cowan and Farquhar, 1979; Leuning, 1995) may also be introduced implicitly into eqn (1a), by assuming that the ratio c_i/c_a of internal to atmospheric $[\text{CO}_2]$ is a constant, denoted by β . With these assumptions eqn (1a) becomes:

$$P_{\text{leaf}} = \frac{\alpha I \beta c_a k_x n_{\text{leaf}}}{\alpha I + \beta c_a k_x n_{\text{leaf}}} \quad (1c)$$

which describes a saturating function of n_{leaf} at low light and a linear function of n_{leaf} at high light (cf. Gulmon and Chu, 1981; Evans, 1989).

Now consider the daily integral of P_{leaf} . For a leaf at cumulative LAI L inside the canopy, daily gross leaf photosynthesis [$A_{\text{leaf}}(L)$] is approximated by replacing the instantaneous irradiance at that position with its mean value during the day ($\langle I_L \rangle$):

$$A_{\text{leaf}}(L) = h \cdot \frac{\alpha \langle I_L \rangle \beta c_a k_x n_{\text{leaf}}(L)}{\alpha \langle I_L \rangle + \beta c_a k_x n_{\text{leaf}}(L)} \quad (2a)$$

where h is daylength, and $n_{\text{leaf}}(L)$ is the leaf N content at L . Assuming a Beer-Lambert light extinction profile with zero leaf transmission, $\langle I_L \rangle$ is given by (Monsi and Saeki, 1953):

$$\langle I_L \rangle = k \cdot \frac{S_0}{h} \cdot \exp(-kL) \quad (2b)$$

where k is the canopy light extinction coefficient and S_0 is the daily integral of PAR incident above the canopy.

The approximation given by eqn (2a) for the daily integral of leaf photosynthesis is mathematically equivalent to an approximation derived by Charles-Edwards (1982) for the daily integral of canopy photosynthesis when the incident PAR varies sinusoidally during the day (cf. his Eqns 4.12 and 4.1), and which he showed gives a reasonable approximation over the entire range of photosynthetic parameters of interest (see his Fig. 4.2). This approximation has been refined by Sands (1995b), but, for present purposes, eqn (2a) is adequate.

Next consider the spatial integration of $A_{\text{leaf}}(L)$ through the canopy. Following Field (1983) and Hirose and Werger (1987) I assume that, for a given total amount of canopy N (n_c), the distribution of leaf N inside the canopy is that which maximizes gross canopy photosynthesis. This assumption considerably simplifies the spatial integration of A_{leaf} (Marshall and Porter, 1991; Sellers *et al.*, 1992; Sands, 1995a, b; Kull and Jarvis, 1995). The simplification arises because, at each level within the canopy, the optimal value of n_{leaf} (and therefore the light-saturated value of P_{leaf}) is found to be proportional to the fraction of incident PAR that is transmitted to that level [eqns (3d) and (3f) below]. This result enables the canopy integration to be done analytically (Charles-Edwards, 1982). When this procedure

is applied to eqn (2a) (see Appendix), the following expression for daily gross canopy photosynthesis (A_c) is obtained:

$$A_c = h \cdot \frac{\alpha \langle I_c \rangle \beta c_a k_x n_c}{\alpha \langle I_c \rangle + \beta c_a k_x n_c} \quad (3a)$$

Here, $\langle I_c \rangle$ is the mean instantaneous irradiance intercepted by the canopy:

$$\langle I_c \rangle = \frac{S_c}{h} \quad (3b)$$

where S_c is daily intercepted PAR. If L_c denotes the total canopy LAI, S_c is given by:

$$S_c = S_o \cdot [1 - \exp(-kL_c)] \quad (3c)$$

Comparing the expressions for daily leaf photosynthesis [$A_{\text{leaf}}(L)$, eqn (2a)] and daily canopy photosynthesis [A_c , eqn (3a)], it is seen that, when a fixed amount of N is distributed optimally within the canopy, the canopy acts essentially as a ‘big leaf’ with canopy N content (n_c) playing the role of leaf N content [$n_{\text{leaf}}(L)$] and mean intercepted irradiance ($\langle I_c \rangle$) playing the role of mean leaf irradiance ($\langle I_l \rangle$).

Relative distribution of leaf N and light-saturated photosynthesis

As mentioned above, the optimal leaf N content at cumulative LAI L is found to be proportional to the transmission fraction, $\exp(-kL)$:

$$n_{\text{leaf}}(L) = n_{\text{leaf}}(0) \cdot \exp(-kL) \quad (3d)$$

where $n_{\text{leaf}}(0)$, the N content of unshaded leaves at the top of the canopy, is given in terms of the total canopy N content (n_c) by (see Appendix):

$$n_{\text{leaf}}(0) = \frac{kn_c}{1 - \exp(-kL_c)} \quad (3e)$$

Likewise, the profile of light-saturated leaf photosynthesis is given by:

$$P_{\text{imax}}(L) = P_{\text{imax}}(0) \cdot \exp(-kL) \quad (3f)$$

where $P_{\text{imax}}(0) = \beta c_a k_x n_{\text{leaf}}(0)$ is the value at the top of the canopy [from eqn (1c)]. Only the relative distribution of n_{leaf} and P_{imax} is determined by this procedure. As eqn (3e) shows, their absolute values depend on the canopy N content, LAI and light extinction coefficient. Evidence for this general pattern of n_{leaf} and P_{imax} within canopies now exists over a wide range of species and ecosystems (Field, 1983; Hirose and Werger, 1987; Sellers *et al.*, 1992).

Maintenance respiration, growth respiration and NPP

The relationship between maintenance respiration and tissue N content is approximately linear (e.g. Ryan, 1991, 1995). Therefore, I assume that whole-plant maintenance respiration (R_m) is given by:

$$R_m = rn_p \quad (4a)$$

where n_p is the whole-plant N content and r is the daily rate

of maintenance respiration per unit of N. For simplicity, I assume that the value of r is the same in all plant parts; the model could easily be modified to incorporate differences in r between plant parts, due to variability in enzyme turnover rates, for example (Penning de Vries, 1975; Szaniawski and Kielkiewicz, 1982). It is also assumed that eqn (4a) includes the respiratory cost associated with maintaining ion gradients (Penning de Vries, 1975), and that root respiration associated with the active uptake of ions is proportional to the rate of biomass construction (Johnson, 1983, 1990) and can be included implicitly as a component of growth respiration (see below).

Plant N content may be expressed in terms of canopy N content:

$$n_p = (1 + \lambda_{\text{sw}} + \lambda_r) n_c \quad (4b)$$

where λ_{sw} and λ_r are the ratios of the N contents of live sapwood and fine roots, respectively, to the N content of the canopy. For non-woody plants, $\lambda_{\text{sw}} = 0$, while for mature trees, λ_{sw} does not include N in dead, non-respiring heartwood. Analysis of nutrient data collected over 4 years from a stand of *Pinus radiata* growing near Canberra showed an approximately linear relationship between the above-ground N content of new wood grown each year and the N content of foliage of the same age (Jeffreys, pers. comm.), suggesting that λ_{sw} may be conservative. In the model, λ_{sw} and λ_r are external parameters which are assumed to be constant, although the consequences of varying their values will be considered below. Equations (4a) and (4b) give:

$$R_m = r(1 + \lambda_{\text{sw}} + \lambda_r) n_c \quad (4c)$$

Growth respiration (R_g) is proportional to *NPP* (e.g. Thornley and Johnson, 1990):

$$R_g = \frac{1 - Y_g}{Y_g} \cdot NPP \quad (4d)$$

where Y_g is the biosynthetic efficiency of conversion of sugars to structural dry matter. For simplicity I make the assumption that Y_g is a constant, which ignores the higher construction costs of proteins compared with carbohydrates (Williams *et al.*, 1987) and the resulting variation in Y_g due to changes in tissue composition.

Net primary productivity, which is equal to $A_c - R_m - R_g$, is then given by:

$$NPP = Y_g (A_c - R_m) \quad (5)$$

where A_c and R_m are related to canopy N content by eqns (3a) and (4c), respectively. An equivalent relationship between *NPP* and whole-plant N content may be obtained using eqn (4b).

IMPLICATIONS OF THE MAXIMUM-NPP HYPOTHESIS

Optimal canopy N content

In the above model, daily gross canopy photosynthesis [A_c , eqn (3a)] is a saturating function of canopy N content (n_c), essentially because the canopy acts like a ‘big leaf’ [cf. eqn (2a)]. In contrast, plant maintenance respiration [R_m ,

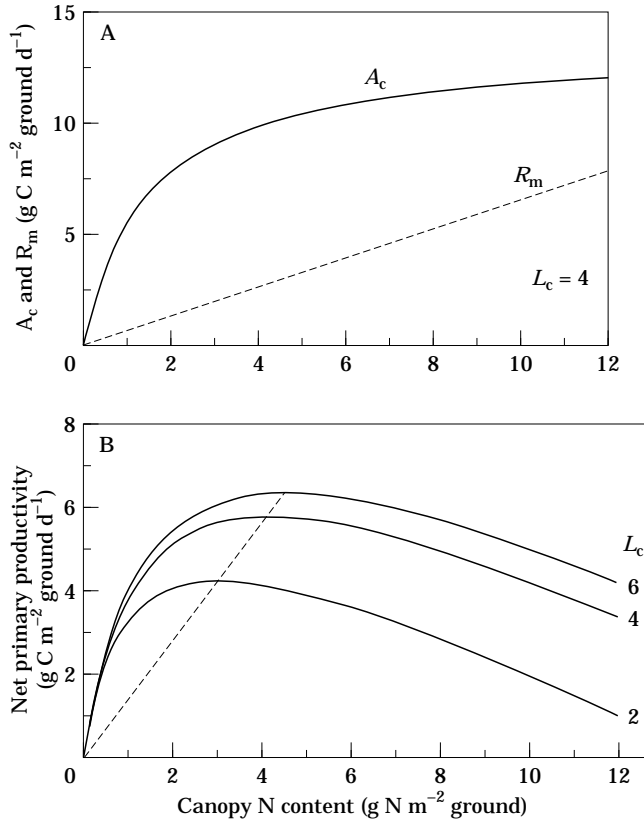


FIG. 1. A, The dependence of gross canopy photosynthesis [A_c , eqn (3a)] and whole-plant maintenance respiration [R_m , eqn (4c)] on canopy N content (n_c), for canopy LAI $L_c = 4$. B, (—) The dependence of net primary productivity [NPP , eqn (5)] on canopy N content, for canopy LAI $L_c = 2, 4$ and 6 . (---) The linear relationship between the maximum NPP [NPP_{max} , eqn (7a)] and optimal canopy N content [$n_{c,opt}$, eqn (6a)] as L_c varies. Parameter values are given in Table 2.

eqn (4c)] increases linearly with n_c (Fig. 1A). Hence, for a given canopy LAI (L_c), there is an optimal canopy N content ($n_{c,opt}$)—and a corresponding optimal plant N content—at which NPP [eqn (5)] has a maximum value (NPP_{max}). This is illustrated in Fig. 1B for $L_c = 2, 4$ and 6 with the parameter values in Table 2, for which $n_{c,opt} = 3.0, 4.1$ and 4.5 g N m⁻² ground and $NPP_{max} = 4.2, 5.8$ and 6.4 g C m⁻² ground d⁻¹, respectively. Note the result that NPP_{max} is proportional to $n_{c,opt}$ (Fig. 1B), further implications of which are derived below [eqn (7a)].

More generally, the value of $n_{c,opt}$ for a given L_c can be obtained analytically from eqns (3a), (4c) and (5), with the result:

$$n_{c,opt} = \frac{\alpha \langle I_c \rangle}{\beta c_a k_x} \left(\frac{1}{\lambda} - 1 \right) \quad (6a)$$

where λ is a dimensionless parameter combination given by:

$$\lambda = \sqrt{\frac{r(1 + \lambda_{sw} + \lambda_r)}{h\beta c_a k_x}} \quad (6b)$$

Equations (6a) and (3b) imply that $n_{c,opt}$ is proportional to intercepted PAR (S_c). The parameter λ characterises the relative N-sensitivities of maintenance respiration (numer-

ator) and light-saturated canopy photosynthesis (denominator), as may be seen from eqn (4c) and from the large $\langle I_c \rangle$ limit of eqn (3a). As shown below, λ plays a central role in determining the light utilization and carbon balance characteristics of the stand.

To recap the analysis so far, two optimization steps have been used to obtain the optimal canopy N content [eqn (6a)]. In step 1, daily gross canopy photosynthesis was maximized with respect to the *relative* distribution of leaf N inside the canopy, for fixed values of n_c and L_c . This is equivalent to maximizing NPP at fixed n_c , provided the relationship between leaf maintenance respiration and leaf N content does not vary significantly through the canopy (e.g. due to spatial variations in temperature). In step 2, NPP was then maximized with respect to n_c for a given value of L_c . The net result is the same as if we had performed an unconstrained optimization of NPP with respect to the *absolute* distribution of leaf N inside the canopy, for a given value of L_c .

Optimal leaf N distribution

Equation (3d) gives the relative distribution of leaf N after step 1 of the optimization, which depends on the value of n_c [see eqn (3e)]. The absolute distribution of leaf N after step 2, as predicted by the maximum- NPP hypothesis, is obtained by substituting eqn (6a) for the optimal value of n_c into eqns (3d) and (3e). The result for the optimal leaf N content at cumulative LAI L inside the canopy is:

$$n_{leaf,opt}(L) = \frac{\alpha \langle I_L \rangle}{\beta c_a k_x} \left(\frac{1}{\lambda} - 1 \right) \quad (6c)$$

where $\langle I_L \rangle$ [eqn (2b)] is the mean leaf irradiance at L . Note the ‘big leaf’ correspondence between eqns (6a) and (6c). In contrast to eqn (6a), however, eqn (6c) is independent of canopy LAI (L_c), the implications of which are discussed below.

Figure 2A illustrates the dependence of $n_{leaf,opt}(0)$, the optimal N content of an unshaded leaf at the top of the canopy, on the mean incident irradiance (S_o/h), for various parameter combinations that affect the value of λ (lines ‘a’–‘d’). Figure 2B shows that $n_{leaf,opt}(0)$ is predicted to decrease with increasing atmospheric $[CO_2]$, except at very low $[CO_2]$. Similar results are obtained for optimal leaf N contents inside the canopy.

NPP and intercepted PAR

The maximum value of NPP is found by substituting the optimal value of canopy N content [eqn (6a)] into eqns (3a), (4c) and (5), with the result:

$$NPP_{max} = \alpha Y_g (1 - \lambda)^2 S_c \quad (7a)$$

Thus, if canopy N content varies with canopy LAI according to the maximum- NPP hypothesis [eqn (6a)], then net primary productivity is proportional to intercepted PAR. This result reflects the predictions that NPP_{max} is proportional to $n_{c,opt}$ (Fig. 1B) and that $n_{c,opt}$ is proportional to intercepted PAR [eqn (6a)].

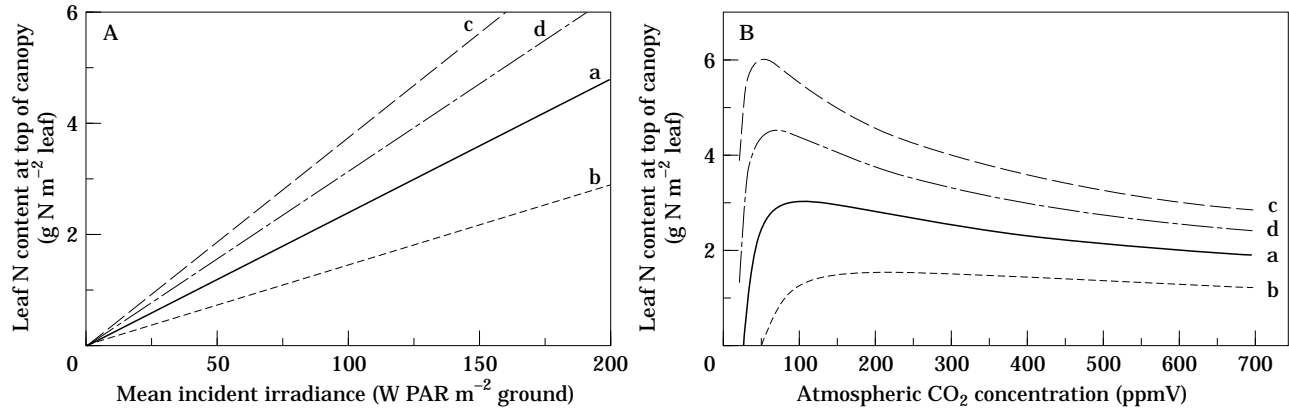


FIG. 2. The optimal N content of an unshaded leaf at the top of the canopy [$n_{\text{leaf,opt}}(0)$, eqn (6c)] as a function of (A) mean incident irradiance there (S_0/h) and (B) atmospheric $[\text{CO}_2]$ (c_a). In each figure, curve 'a' is obtained with all other parameters set to their standard values (Table 2). Curves 'b' and 'c' are obtained when the ratio r/k_x (where r is maintenance respiration per unit N and k_x is the carboxylation coefficient) is twice or half its standard value, respectively. Curve 'd' is obtained when the contribution to maintenance respiration from sapwood is zero ($\lambda_{\text{sw}} = 0$). These responses are independent of canopy LAI (L_c). Similar results are obtained for the optimal N content of leaves inside the canopy.

TABLE 3. Percentage responses of the light utilization coefficient [ϵ , eqn (7b)] and carbon use efficiency [CUE, eqn (8b)] to a 10% increase in various physiological and environmental parameters from their standard values (Table 2). See Table 1 for parameter definitions

Parameter	ϵ	CUE
α	+10.0	0.0
Y_g	+10.0	+10.0
r	-3.6	-1.9
λ_{sw} or λ_r	-1.2	-0.7
h, β, c_a or k_x	+3.5	+1.7
VPD*	-1.4	-0.7

* VPD responses derived from the relationship $\beta = 1 - (1 + \text{VPD}/0.35)/25$ (based on Leuning, 1995). The standard value of VPD (giving $\beta = 0.7$) is 2.275 kPa.

The light utilization coefficient (ϵ), defined as the slope of the linear relationship between NPP_{max} and S_c , is:

$$\epsilon = \alpha Y_g (1 - \lambda)^2 \quad (7b)$$

Equation (7b) describes how the value of ϵ is reduced below its theoretical maximum—given by the quantum yield (α)—due to the effects of growth respiration (described by Y_g) and maintenance respiration [described by the factor $(1 - \lambda)^2$]. As noted previously, λ characterises the relative N-sensitivities of maintenance respiration and light-saturated canopy photosynthesis, and is seen here to be crucial in determining the light utilization coefficient. With the standard parameter values in Table 2, eqn (6b) predicts $\lambda \approx 0.27$, giving $(1 - \lambda)^2 \approx 0.53$. With $Y_g = 0.8$, eqn (7b) then predicts that the effect of growth and maintenance respiration in this case is to decrease ϵ to 42% of its theoretical maximum value, giving $\epsilon = 2.33 \text{ g dry matter MJ}^{-1} \text{ PAR}$ (assuming dry matter is 50% carbon).

The analytical result given by eqns (6b) and (7b) identifies several physiological and environmental factors which may underlie observed variations in the light utilization coefficient. A numerical sensitivity analysis of the factors affecting ϵ is presented in Table 3.

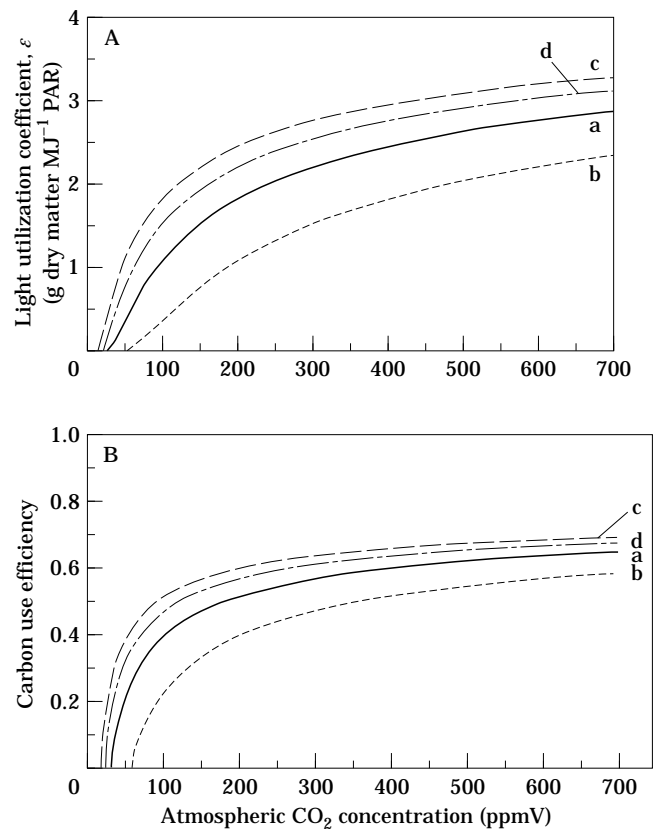


FIG. 3. The predicted dependence of (A) the light utilization coefficient [ϵ , eqn (7b)] and (B) the carbon-use efficiency [CUE, eqn (8b)] on atmospheric $[\text{CO}_2]$ (c_a). In (A), to convert from $\text{kg C J}^{-1} \text{ PAR}$ to $\text{g dry matter MJ}^{-1} \text{ PAR}$, eqn (7b) was multiplied by 2×10^9 (assuming dry matter is 50% carbon). Curves 'a'–'d' as in Fig. 2.

Figure 3A illustrates ϵ as an increasing function of atmospheric $[\text{CO}_2]$ (c_a). Curve 'a' is the response of ϵ to c_a when all other parameters are set to their standard values (Table 2). When the value of the maintenance respiration coefficient (r) is decreased from twice to one half of its standard value, the value of ϵ at $c_a = 350 \text{ ppmV}$ increases by

71% from 1.67 to 2.86 g dry matter MJ⁻¹ PAR (curves 'b' and 'c', respectively). Note from eqn (6b) that λ , and hence ϵ , depends only on the ratio of r to the carboxylation coefficient, k_x . Therefore, curves 'b' and 'c' also illustrate the case where k_x is increased from one half to twice its standard value, with r fixed; recall that the parameter k_x determines the rate at which light-saturated leaf photosynthesis increases with increasing leaf N content [eqn (1b)], which varies significantly among species (Evans, 1989). Curve 'd' illustrates the effect of setting the parameter λ_{sw} to zero, representing a non-woody plant for which the contribution to maintenance respiration from sapwood is zero. Compared with the standard case (curve 'a'), this has the effect of increasing the value of ϵ at $c_a = 350$ ppmV by 14%, from 2.33 to 2.65 g dry matter MJ⁻¹ PAR.

Equations (6b) and (7b) also imply that ϵ depends positively on daylength (h). This means that, for a given daily intercepted PAR (S_c), NPP is greatest when the mean intercepted irradiance ($\langle I_c \rangle$) is low [see eqn (3b)]. This simply reflects the saturating character of the response of instantaneous leaf photosynthesis to leaf irradiance [eqn (1c)]. Finally, eqns (6b) and (7b) imply that ϵ depends positively on the $c_1:c_a$ ratio (β). A recent model of stomatal conductance (Leuning, 1995) predicts that β decreases linearly with increasing vapour pressure deficit (VPD), and implies here that ϵ also decreases (Table 3).

Carbon use efficiency

The relationship between respiration and gross canopy photosynthesis may be expressed in terms of the carbon-use efficiency (CUE), defined by:

$$CUE = \frac{NPP}{A_c} = 1 - \frac{R}{A_c} \quad (8a)$$

where R is the total respiration rate (growth + maintenance). The CUE predicted by the maximum- NPP hypothesis is obtained by combining eqns (3a) and (6a) to calculate A_c , and substituting eqn (7a) for NPP_{max} , with the result:

$$CUE = Y_g(1 - \lambda) \quad (8b)$$

Like the light utilization coefficient, CUE is predicted to be a conservative quantity, or, equivalently, respiration is predicted to be proportional to photosynthesis. This result reflects the optimal balance between maintenance respiration and photosynthesis implied by the maximum- NPP hypothesis.

The maximum- NPP hypothesis implies that CUE and ϵ are closely related quantities. A comparison of eqns (7b) and (8b) shows that, apart from the quantum yield (α), the same physiological and environmental factors are predicted to underlie variations in both ϵ and CUE (Table 3). For example, CUE , like ϵ , is predicted to increase with increasing atmospheric $[CO_2]$ (Fig. 3B). The maximum theoretical value of CUE is equal to 1. According to eqn (8b), this is reduced by growth and maintenance respiration (described by the parameters Y_g and λ , respectively), in a similar way to the reduction in ϵ from its maximum value (α). With the standard parameter values in Table 2, eqn (8b) predicts

$CUE \approx 0.58$, so that in this case 42% of gross photosynthesis is consumed in growth and maintenance respiration.

A further consequence of eqns (7b) and (8b) is that the ratio of ϵ to CUE^2 is equal to the ratio of the quantum yield to the biosynthetic efficiency:

$$\frac{\epsilon}{CUE^2} = \frac{\alpha}{Y_g} \quad (8c)$$

and is independent of λ . The quantum yield varies little between C_3 species and is weakly dependent on temperature (Ehleringer and Björkman, 1977). The biosynthetic efficiency is also generally independent of growth temperature (e.g. Szaniawski and Kielkiewicz, 1982); for a known plant composition, Y_g may be calculated from the construction efficiency of individual compounds, and is typically in the range 0.75–0.85 (Johnson, 1990). Therefore, $\epsilon:CUE^2$ may be a more conservative parameter across different species and environments than either ϵ or CUE alone.

Allocation: manipulating N supply to maximize NPP

The ability of a growing stand of vegetation to maintain optimal leaf N contents as LAI increases depends on the capacity of plant roots to take up sufficient N from the soil. This requirement leads naturally to a goal-seeking interpretation of fine root:foliage allocation, according to which plants manipulate their N supply in order to maximize NPP for a given amount of foliage. The quantitative dependence of N uptake rate and plant N content on root biomass and soil N availability is beyond the scope of this paper (see e.g. Clarkson, 1985). Qualitatively however, if the dependence is positive (as seems plausible), then an increase in the availability of soil N enables plants to maintain optimal leaf N contents with lower allocation to root biomass relative to foliage biomass. The converse holds if soil N availability decreases.

The long-term result of N fertilization, therefore, will be an increase in intercepted PAR. Moreover, it follows from the maximum- NPP hypothesis that this is the sole factor through which NPP is increased by N fertilization. This conclusion may be seen directly from eqn (7b), which implies that the value of ϵ is independent of the rate of N supply. This result is also reflected in eqn (6c), which implies that the predicted optimal distribution of leaf N (and therefore of light-saturated leaf photosynthesis) inside the canopy is independent of total canopy LAI (L_c) and N supply, and simply extends further down as L_c increases in response to N fertilization. Note therefore that maintenance of the optimal leaf N distribution does not imply that plants are free of N-limitation; it simply implies that growth responses to N fertilization occur through an increase in intercepted PAR caused by increased foliage allocation, rather than through an increase in ϵ .

How are the predictions of the maximum- NPP hypothesis modified when allocation to fine roots *vs.* foliage is insufficient to maintain optimal leaf N contents (e.g. in low fertility soils)? There are two possibilities: either the linear relationship between NPP and intercepted PAR remains valid and is characterised by a reduced (N-dependent) value

of ϵ , or the relationship becomes non-linear in which case the rationale for the ϵ -model breaks down.

It is easy to show from eqns (3a), (4c) and (5) that, when n_c is sub-optimal, the linear relationship between NPP and intercepted PAR breaks down. The apparent value of the light utilization coefficient (i.e. the ratio of NPP to intercepted PAR) then depends on both n_c and L_c . Thus, only when n_c and L_c are related by eqn (6a) is NPP proportional to intercepted PAR. This suggests that, under conditions of severe N limitation, an apparent N-dependence of the light utilization coefficient may be observed, but that it could be misleading to interpret such a dependence within the context of the ϵ -model if NPP is no longer proportional to S_c .

DISCUSSION

Conservative nature of ϵ and CUE

The maximum- NPP hypothesis provides a physiological interpretation of the well documented proportionality between NPP and intercepted PAR. In the examples illustrated in Fig. 3A using realistic parameter values, the predicted values of ϵ (1.5–3.0 g dry matter MJ⁻¹ PAR) are typical of C₃ plants growing at current (1995) atmospheric [CO₂], in the absence of severe climatic limitations (such as drought, high vapour pressure deficits or cold temperatures) or severe nutrient limitation (Prince, 1991; Hunt, 1994; Landsberg *et al.*, 1996). The analytical results identify several physiological and environmental factors which may explain observed variations in ϵ , as summarised in Table 3. The parameter combination λ , a measure of the relative N-sensitivities of maintenance respiration and light-saturated photosynthesis, emerges as a critical factor in determining ϵ . The implications of the present analysis for the long-term response of forests to increased [CO₂] and N deposition have been examined by Medlyn and Dewar (1996).

The closely-related prediction that respiration is proportional to photosynthesis, as intercepted PAR varies, is supported by data from a diverse range of species. Gifford (1994) measured the ratio $R:A_c$ of plants of seven species, including perennials and annuals, grown for periods of up to 9 months at different constant temperatures. $R:A_c$ was found to be remarkably constant as plant size varied over two orders of magnitude (as well as being only weakly dependent on temperature). The value of $R:A_c$ (≈ 0.4) was also conservative among species [and close to the value of 0.42 predicted by eqns (8a) and (8b) using the default parameters in Table 2].

$R:A_c$ has also been observed to be relatively conservative among different forest ecosystems. In the studies referred to by Gifford (1994), $R:A_c$ on an annual basis was 0.58 for a 48 year old *Liriodendron tulipifera* forest (Reichle *et al.*, 1973), and 0.53 for an oak-pine forest (Woodwell and Botkin, 1970). In a study of four *Pinus* species (Ryan *et al.*, 1994), the ratio of annual whole-plant respiration to annual net daylight canopy assimilation was generally in the range 0.54–0.64 (except for two stands of *P. sylvestris* for which the ratio was about 0.33). These data are in broad agreement with the numerical examples illustrated in Fig. 3B, where it

is predicted that 40–60% of gross photosynthesis is consumed in respiration at current atmospheric [CO₂].

The conventional hypothesis that maintenance costs will eventually offset photosynthetic carbon gains as trees increase in size (e.g. Kozłowski, Kramer and Pallardy, 1991) is not supported by these and other data (Ryan and Waring, 1992). In terms of the present model, the data suggest that λ_{sw} , the ratio of sapwood N content to canopy N content, is relatively conservative.

Acclimated responses to temperature, [CO₂] and light

According to eqns (6b) and (8b), the insensitivity of $R:A_c$ to growth temperature observed by Gifford (1994) could be the result of approximately equal temperature sensitivities for the maintenance respiration and carboxylation coefficients (r and k_x). As Gifford (1994) noted, this long-term acclimated response of $R:A_c$ contrasts with the expectation from short-term experiments showing that the temperature sensitivity of maintenance respiration is greater than that of photosynthesis. Gifford's (1994) results, when combined with the prediction here that the same physiological factors (apart from the quantum yield) underlie variations in both ϵ and CUE, then suggest that ϵ will also be insensitive to growth temperature. This suggestion is supported by Hunt's (1994) analysis of ϵ for a range of boreal, temperate, sub-tropical and tropical tree species. The implication here is that long-term growth responses to temperature, like N supply, are dominated by changes in leaf growth.

Figure 3 illustrates the predicted responses of ϵ and CUE to increasing [CO₂]. In experiments with eight diverse species (Gifford, 1991), CUE never decreased but increased by between 0.5 and 15% when plants were grown in 2 × normal [CO₂]. These increases are broadly consistent with the range of responses illustrated in Fig. 3B (curve 'b' predicts an 18% increase in CUE as [CO₂] increases from 350 to 700 ppm). The model suggests that observed variations among species in the CO₂-sensitivity of CUE may be interpreted in terms of species-specific factors which determine the value of λ , particularly the physiological parameters r and k_x (cf. curves 'b' and 'c', Fig. 3B). However, Gifford (1991) found that increases in CUE at elevated [CO₂] were accompanied by increases in the efficiency of growth respiration (Y_g); variations in Y_g have not been considered in the present analysis.

In a free-air CO₂ enrichment experiment on cotton (*Gossypium hirsutum*), Pinter *et al.* (1994) observed an average increase in ϵ of 25% as [CO₂] increased from 370 to 550 ppm; curve 'b' in Fig. 3A predicts a 22% increase in ϵ over the same range of [CO₂]. Although these comparisons do not constitute detailed validation of the model, they illustrate that, with realistic parameter values, the predicted CO₂ responses of ϵ and CUE are broadly consistent with the magnitude of observed responses. Table 3 shows that the CO₂ sensitivity of ϵ is predicted to be approximately twice that of CUE.

The prediction that leaf [N] decreases with increasing atmospheric [CO₂] (except at low [CO₂], Fig. 2B) is consistent with numerous studies on a variety of plants grown at

ambient and elevated $[\text{CO}_2]$ (Luo, Field and Mooney, 1994). However, the predicted CO_2 response of leaf $[\text{N}]$ on an area basis does not take into account increases in leaf mass per unit area which often accompany, and sometimes offset, decreases in leaf $[\text{N}]$ on a dry weight basis.

The predicted proportionality between leaf N per unit area at cumulative LAI L and the corresponding mean leaf irradiance $\langle I_L \rangle$ [eqn (6c), Fig. 2A] implies that the rate of light-saturated photosynthesis is also proportional to $\langle I_L \rangle$. This is broadly consistent with the general pattern observed in plants grown under different irradiances (e.g. Björkman, 1981; Charles-Edwards, 1982). Although $\langle I_L \rangle$ in eqn (6c) is the mean leaf irradiance over a day, it would be unrealistic to apply eqn (6c) on a daily basis to plants growing in the field; $\langle I_L \rangle$ more likely represents the average irradiance over some longer period, perhaps a week or more, appropriate to acclimation (e.g. Evans, 1993).

Long-term growth response to N fertilization

The maximum-NPP hypothesis implies that growth responses to N fertilization are due to increased intercepted PAR, and not to increased ϵ (predicted to be independent of N supply). This prediction is borne out by a number of fertilization experiments on trees (e.g. *Eucalyptus globulus*: Cromer *et al.*, 1975; Cromer and Williams, 1982; Linder, 1985; *Pinus elliottii* and *Pinus taeda*: Dalla-Tea and Jokela, 1991) and crops (e.g. *Triticum aestivum*: Garcia *et al.*, 1988; *Sorghum bicolor*: Monteith, pers. comm.; but see Green, 1987). A positive correlation between foliage allocation and N supply, as implied here, has been observed in numerous fertilization studies and in comparisons between plants growing on fertile *vs.* nutrient poor soils (e.g. Cannell and Dewar, 1994; Gower *et al.*, 1996). Apparent nutritional effects on ϵ based on measurements of above-ground productivity may reflect changes in allocation between above- and below-ground plant parts (e.g. Gower *et al.*, 1996). Table 3 suggests that the sensitivity of ϵ to VPD is also relatively small; field evidence supports the implication that the main effect of increasing VPD , like that of decreasing N supply, is to decrease leaf growth (Legg *et al.*, 1979).

The closely-related prediction that leaf N content is independent of N supply [eqn (6c)] is consistent with the general behaviour of *Eucalyptus* (Cromer and Williams, 1982), but appears to be inconsistent with much of the literature on measured foliar responses to N fertilization in trees and crops generally. There are two ways in which this apparent inconsistency might be explained without rejecting the maximum-NPP hypothesis. First, commonly observed increases in leaf $[\text{N}]$ may be a transient response to fertilization, whereas the predicted constancy of leaf $[\text{N}]$ may be more relevant on longer time scales (greater than the response time of root:foliage allocation). This view is supported by a 7-year N fertilization experiment on Douglas-fir stands (Brix, 1983), where annual biomass production per unit foliage biomass (which was positively correlated with leaf $[\text{N}]$) increased during the first 3–4 years, but was at or below control level after 7 years.

Second, the model predicts that N fertilization also has no effect on the light-saturated rate of photosynthesis (P_{max} ,

assumed to be proportional to leaf N). This prediction appears to be more consistent with observations than the corresponding prediction for leaf N. For example, several conifer studies have reported that fertilization has little or no effect on leaf photosynthesis, despite large increases in leaf N content (Gower *et al.*, 1994, 1996). One explanation is that much of the extra leaf N is partitioned into non-photosynthetic compounds (Evans and Seemann, 1989). While the maximum-NPP hypothesis has been formulated here for simplicity in terms of total tissue N contents, it would be more appropriate to apply its predictions only to the component of N involved in the trade-off between photosynthesis and maintenance respiration.

Therefore a consistent picture of responses to N fertilization, at least for conifers, might be that, in the short term, plants take up as much extra N as possible, in order to maintain a competitive advantage and to guard against possible future shortage, with most of this extra N being partitioned to non-photosynthetic compounds. In the longer term, the extra N is used for new growth with an increased allocation to foliage but with no increase in ϵ , in accordance with the maximum-NPP hypothesis.

Range of validity of the ϵ -model

This analysis supports the conclusion of Garcia *et al.* (1988), from experiments on winter wheat, that ϵ is not significantly affected by mild nutrient stress. As shown here, the linear relationship between NPP and intercepted PAR is likely to remain valid under increased N limitation as long as increased root allocation is able to maintain optimal leaf N contents, but will eventually break down under severe N stress. Analysis of data from five *Pinus* stands by McMurtrie *et al.* (1994) suggests that the ϵ -model is also likely to break down under conditions of drought, high vapour pressure deficits or cold temperatures.

Conclusions

The present analysis could be refined by incorporating such features as a more sophisticated leaf photosynthesis model (e.g. Farquhar *et al.*, 1980; Farquhar and Caemmerer, 1982), a distinction between photosynthetic and non-photosynthetic N pools (e.g. Kull and Jarvis, 1995) or between direct-beam and diffuse radiation (e.g. Sinclair, Murphy and Knoerr, 1976), differences in enzyme turnover rates between different plant parts (e.g. Penning de Vries, 1975), and variations in the efficiency of growth respiration (Gifford, 1991). These and other refinements may be required when evaluating the maximum-NPP hypothesis for individual species or datasets.

However, the simplified analysis presented here has focussed instead on the broad implications of the maximum-NPP hypothesis for plant growth generally, with the following conclusions: (a) The hypothesis provides a physiological interpretation of the well documented conservative nature of ϵ and CUE. (b) The analytical results identify several physiological and environmental factors which may underlie observed variations in ϵ and CUE. (c) Model predictions are qualitatively consistent with ac-

climated plant responses to $[\text{CO}_2]$ and light, and suggest that ϵ , like CUE , may be relatively insensitive to growth temperature. (d) The hypothesis provides a goal-seeking interpretation of fine root:foliage allocation, consistent with observations that long-term growth responses to N fertilization are dominated by increased light interception. (e) The relationship between NPP and intercepted PAR may become non-linear when N stress cannot be alleviated by increased root allocation.

ACKNOWLEDGEMENTS

I thank Roger Gifford, Mark Jeffreys, Belinda Medlyn, Ross McMurtrie and John Monteith for valuable discussions, access to unpublished work, and constructive comments on an earlier version of this paper. I acknowledge financial support from the NGAC Dedicated Research Grants Scheme and the Australian Research Council.

APPENDIX

Derivation of daily gross canopy photosynthesis [A_c , eqn (3a)] from daily gross leaf photosynthesis [A_{leaf} , eqn (2a)]

A_c is derived from A_{leaf} by integrating eqn (2a) through the canopy:

$$A_c = \int_0^{L_c} h \cdot \frac{\alpha \langle I_L \rangle \beta c_a k_x n_{\text{leaf}}(L)}{\alpha \langle I_L \rangle + \beta c_a k_x n_{\text{leaf}}(L)} dL \quad (\text{A1})$$

where $\langle I_L \rangle$ [eqn (2b)] and $n_{\text{leaf}}(L)$ are the mean leaf irradiance and leaf N content, respectively, at cumulative LAI L inside the canopy. The total canopy N content is given by:

$$n_c = \int_0^{L_c} n_{\text{leaf}}(L) dL \quad (\text{A2})$$

It is then assumed that, for a given value of n_c , the distribution of leaf N inside the canopy is that which maximizes A_c . It is straightforward to show that the optimal value of $n_{\text{leaf}}(L)$ is proportional to $\langle I_L \rangle$ (e.g. Sands, 1995a). Hence:

$$n_{\text{leaf}}(L) = n_{\text{leaf}}(0) \exp(-kL) \quad (\text{A3})$$

where $n_{\text{leaf}}(0)$ is the N content of an unshaded leaf at the top of the canopy [giving eqn (3d)]. $n_{\text{leaf}}(0)$ is obtained in terms of n_c by substituting eqn (A3) into eqn (A2) and integrating, with the result [eqn (3e)]:

$$n_{\text{leaf}}(0) = \frac{kn_c}{1 - \exp(-kL_c)} \quad (\text{A4})$$

By substituting eqns (A2–A4) into eqn (A1), the canopy integral may be performed analytically, giving canopy photosynthesis as a function of canopy N content [eqn (3a)]:

$$A_c = h \cdot \frac{\alpha \langle I_c \rangle \beta c_a k_x n_c}{\alpha \langle I_c \rangle + \beta c_a k_x n_c} \quad (\text{A5})$$

where $\langle I_c \rangle$ is the mean irradiance intercepted by the canopy [eqns (3b) and (3c)]. Using eqn (A4) to eliminate n_c from eqn (A5), canopy photosynthesis can also be expressed in terms

of the light-saturated rate of leaf photosynthesis at the top of the canopy [$P_{\text{imax}}(0) = \beta c_a k_x n_{\text{leaf}}(0)$]:

$$A_c = \frac{\alpha h P_{\text{imax}}(0)}{\alpha S_o k + h P_{\text{imax}}(0)} S_c \quad (\text{A6})$$

where S_c is the daily intercepted PAR [eqn (3c)]. In general, eqn (A6) does not imply that canopy photosynthesis is proportional to intercepted PAR (cf. Kull and Jarvis, 1995). Only in the special case where $n_{\text{leaf}}(0)$ is independent of canopy LAI (L_c) and proportional to the mean leaf irradiance above the canopy [given by kS_o/h , see eqn (2b)] does eqn (A6) predict that A_c is proportional to S_c . It is this case which emerges as a direct consequence of the maximum-NPP hypothesis [see eqn (6c) with $L = 0$]. From the additional implication that plant respiration is proportional to A_c [eqns (8a) and (8b)], the maximum-NPP hypothesis also predicts that NPP is proportional to S_c [eqn (7a)].

LITERATURE CITED

- Arkenbauer TJ, Weiss A, Sinclair TR, Blum A. 1994. In defense of radiation use efficiency: a response to Demetriades-Shah *et al.* (1992). *Agricultural and Forest Meteorology* **68**: 221–227.
- Björkman O. 1981. Responses to different quantum flux densities. In: Lange OL, Noble PS, Osmond CB, Ziegler H, eds. *Encyclopedia of plant physiology, New Series*, Vol. 12A. New York: Springer-Verlag, 57–107.
- Brix H. 1983. Effects of thinning and nitrogen fertilization on growth of Douglas-fir: relative contribution of foliage quantity and efficiency. *Canadian Journal of Forest Research* **13**: 167–175.
- Cannell MGR, Dewar RC. 1994. Carbon allocation in trees: a review of concepts for modelling. *Advances in Ecological Research* **25**: 59–104.
- Cannell MGR, Milne R, Sheppard LJ, Unsworth MH. 1987. Radiation interception and productivity of willow. *Journal of Applied Ecology* **24**: 261–268.
- Cannell MGR, Sheppard LJ, Milne R. 1988. Light use efficiency and woody biomass production of poplar and willow. *Forestry* **61**: 123–136.
- Charles-Edwards DA. 1982. *Physiological determinants of crop growth*. Sydney: Academic Press.
- Clarkson DT. 1985. Factors affecting mineral nutrient acquisition by plants. *Annual Review of Plant Physiology* **36**: 77–115.
- Cromer RN, Raupach M, Clarke ARP, Cameron JN. 1975. Eucalypt plantations in Australia—the potential for intensive production and utilization. *Appita* **29**: 165–173.
- Cromer RN, Williams ER. 1982. Biomass and nutrient accumulation in a planted *E. globulus* (Labill.) fertilizer trial. *Australian Journal of Botany* **30**: 265–278.
- Dalla-Tea F, Jokela EJ. 1991. Needlefall, canopy light interception, and productivity of young intensively managed slash and loblolly pine stands. *Forest Science* **37**: 1298–1313.
- Demetriades-Shah TH, Fuchs M, Kanemasu ET, Flitcroft I. 1992. A note of caution concerning the relationship between cumulated intercepted solar radiation and crop growth. *Agricultural and Forest Meteorology* **58**: 193–207.
- Demetriades-Shah TH, Fuchs M, Kanemasu ET, Flitcroft I. 1994. Further discussions on the relationship between cumulated intercepted solar radiation and crop growth. *Agricultural and Forest Meteorology* **68**: 231–242.
- Ehleringer J, Björkman O. 1977. Quantum yields for CO_2 uptake in C_3 and C_4 plants. Dependence on temperature, CO_2 , and O_2 concentrations. *Plant Physiology* **59**: 86–90.
- Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* **78**: 9–19.
- Evans JR. 1993. Photosynthetic acclimation and nitrogen partitioning within a lucerne canopy. II. Stability through time and comparison

- with a theoretical optimum. *Australian Journal of Plant Physiology* **20**: 69–82.
- Evans JR, Seemann JR. 1989.** The allocation of protein nitrogen in the photosynthetic apparatus: costs, consequences and control. In: Briggs WR, ed. *Photosynthesis*. New York: Allan R. Liss, 183–205.
- Farquhar GD, Caemmerer S von. 1982.** Modelling of photosynthetic response to environmental conditions. In: Lange OL, Nobel PS, Osmond CB, Ziegler H, eds. *Physical plant ecology II. Water relations and carbon assimilation*. Berlin: Springer-Verlag, 550–587.
- Farquhar GD, Caemmerer S von, Berry JA. 1980.** A biochemical model of photosynthetic CO₂ fixation in leaves of C₃ species. *Planta* **149**: 78–90.
- Field C. 1983.** Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* **56**: 341–347.
- García R, Kanemasu ET, Blad BL, Bauer A, Hatfield JL, Major DJ, Reginato RJ, Hubbard KG. 1988.** Interception and use efficiency of light in winter wheat under different nitrogen regimes. *Agricultural and Forest Meteorology* **44**: 175–186.
- Gifford RM. 1991.** *Impact of increasing atmospheric carbon dioxide concentration on the carbon balance of vegetation*. Australia, Energy Research and Development Corporation Project Report No. ERDC 37.
- Gifford RM. 1994.** The global carbon cycle: a viewpoint on the missing sink. *Australian Journal of Plant Physiology* **21**: 1–15.
- Gower ST, Gholz HL, Nakane K, Baldwin VC. 1994.** Production and carbon allocation patterns of pine forests. *Ecological Bulletins* **43**: 115–135.
- Gower ST, Running SW, Gholz HL, Haynes BE, Hunt RE, Ryan MG, Waring RH, Cropper WP. 1996.** Influence of climate and nutrition on carbon allocation and net primary production of four conifer forests. *Tree Physiology* (in press).
- Grace JC, Jarvis PG, Norman JM. 1987.** Modelling the interception of solar radiant energy in intensively managed stands. *New Zealand Journal of Forest Science* **17**: 193–209.
- Green CF. 1987.** Nitrogen nutrition and wheat growth in relation to absorbed solar radiation. *Agricultural and Forest Meteorology* **41**: 207–248.
- Gulmon SL, Chu CC. 1981.** The effects of light and nitrogen on photosynthesis, leaf characteristics, and dry matter allocation in the chaparral shrub, *Diplacis aurantiacus*. *Oecologia* **49**: 207–212.
- Hirose T, Werger MJA. 1987.** Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* **72**: 520–526.
- Hunt RE. 1994.** Relationship between woody biomass and PAR conversion efficiency for estimating net primary production from NDVI. *International Journal of Remote Sensing* **15**: 1725–1730.
- Jarvis PG, Leverenz JW. 1983.** Productivity of temperate, deciduous and evergreen forests. In: Lange OL, Nobel PS, Osmond CB, Ziegler H, eds. *Physiological plant ecology IV ecosystem processes: mineral cycling, productivity and man's influence. Encyclopedia of plant physiology, New Series Vol. 12D*. Berlin: Springer-Verlag, 233–280.
- Johnson IR. 1983.** Nitrate uptake and respiration in roots and shoots: a model. *Physiologia Plantarum* **58**: 145–147.
- Johnson IR. 1990.** Plant respiration in relation to growth, maintenance, ion uptake and nitrogen assimilation. *Plant, Cell and Environment* **13**: 319–328.
- Kiniry JR. 1994.** A note of caution concerning the paper by Demetriades-Shah *et al.* (1992). *Agricultural and Forest Meteorology* **68**: 229–230.
- Kirschbaum MUF, King DA, Comins HN, McMurtrie RE, Medlyn BE, Pongracic S, Murty D, Keith H, Raison RJ, Khanna PK, Sheriff DW. 1994.** Modelling forest response to increasing CO₂ concentration under nutrient-limited conditions. *Plant, Cell and Environment* **17**: 1081–1099.
- Kozłowski T, Cramer P, Pallardy S. 1991.** *The physiological ecology of woody plants*. San Diego: Academic Press.
- Kull O, Jarvis PG. 1995.** The role of nitrogen in a simple scheme to scale up photosynthesis from leaf to canopy. *Plant, Cell and Environment* **18**: 1174–1182.
- Landsberg JJ, Prince SD, Jarvis PG, McMurtrie RE, Luxmoore R, Medlyn BE. 1996.** Energy conversion and use in forests: the analysis of forest production in terms of radiation utilization efficiency (ϵ). In: Gholz HL, Nakane K, Shimoda H, eds. *The use of remote sensing in the modeling of forest productivity*. Kluwer Academic Publications (in press).
- Legg BJ, Day W, Lawlor DW, Parkinson KJ. 1979.** The effects of drought on barley growth: models and measurements showing the relative importance of leaf area and photosynthetic rate. *Journal of Agricultural Science (Cambridge)* **92**: 703–716.
- Leuning R. 1995.** A critical appraisal of a combined stomatal-photosynthesis model for C₃ plants. *Plant, Cell and Environment* **18**: 339–355.
- Linder S. 1985.** Potential and actual production in Australian forest stands. In: Landsberg JJ, Parsons W, eds. *Research for forest management*. Australia: CSIRO, 11–35.
- Luo Y, Field CB, Mooney HA. 1994.** Predicting responses of photosynthesis and root fraction to elevated [CO₂]_a: interactions among carbon, nitrogen and growth. *Plant, Cell and Environment* **17**: 1195–1204.
- McMurtrie RE, Gholz HL, Linder S, Gower ST. 1994.** Climatic factors controlling productivity of pine stands: a model-based analysis. *Ecological Bulletins (Copenhagen)* **43**: 173–188.
- Marshall B, Porter JR. 1991.** Concepts of nutritional and environmental interactions determining plant productivity. In: Porter JR, Lawlor DW, eds. *Plant growth: interactions with nutrition and environment*. Cambridge: Cambridge University Press, 99–124.
- Medlyn BE. 1996.** *The representation of photosynthetic productivity in an ecosystem model used to assess plant responses to climate change*. PhD Thesis, University of New South Wales, Sydney.
- Medlyn BE, Dewar RC. 1996.** A model of the long-term response of carbon allocation and productivity of forests to increased CO₂ concentration and nitrogen deposition. *Global Change Biology* **2**: (in press).
- Monsi M, Saeki T. 1953.** Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Japanese Journal of Botany* **14**: 22–52.
- Monteith JL. 1977.** Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London, Series B* **281**: 277–294.
- Monteith JL. 1994.** Validity of the correlation between intercepted radiation and biomass. *Agricultural and Forest Meteorology* **68**: 213–220.
- Penning de Vries FWT. 1975.** The cost of maintenance processes in plant cells. *Annals of Botany* **39**: 77–92.
- Pinter PJ Jr, Kimball BA, Mauney JR, Hendrey GR, Lewin KF, Nagy J. 1994.** Effects of free-air carbon dioxide enrichment on PAR absorption and conversion efficiency by cotton. *Agricultural and Forest Meteorology* **70**: 209–230.
- Potter CS, Randerson JT, Field CB, Matson PA, Vitousek PM, Mooney HA, Klooster SA. 1993.** Terrestrial ecosystem production: a process model based on global satellite and surface data. *Global Biogeochemical Cycles* **7**: 811–841.
- Prince SD. 1991.** A model of regional primary production for use with coarse resolution satellite data. *International Journal of Remote Sensing* **12**: 1313–1330.
- Reichle DE, Dinger BE, Edwards NT, Harris WF, Phillip S. 1973.** Carbon flow and storage in a forest ecosystem. In: Woodwell GM, Pecan EV, eds. *Carbon and the biosphere*. Washington DC: US Atomic Energy Commission, 345–365.
- Russell G, Jarvis PG, Monteith JL. 1989.** Absorption of radiation by canopies and stand growth. In: Russell G, Marshall B, Jarvis PG, eds. *Plant canopies: their growth, form and function*. Cambridge: Cambridge University Press, 21–39.
- Ryan MG. 1991.** Effects of climate change on plant respiration. *Ecological Applications* **1**: 157–167.
- Ryan MG. 1995.** Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content. *Plant, Cell and Environment* **18**: 765–772.
- Ryan MG, Linder S, Vose JM, Hubbard RM. 1994.** Dark respiration of pines. *Ecological Bulletins (Copenhagen)* **43**: 50–63.
- Ryan MG, Waring RH. 1992.** Maintenance respiration and stand development in a subalpine lodgepole pine forest. *Ecology* **73**: 2100–2108.
- Sands PJ. 1995a.** Modelling canopy production: I. Optimal distribution

- of photosynthetic resources. *Australian Journal of Plant Physiology* **22**: 593–601.
- Sands PJ. 1995b.** Modelling canopy production: II. From single-leaf photosynthetic parameters to daily canopy photosynthesis. *Australian Journal of Plant Physiology* **22**: 603–614.
- Sellers PJ, Berry JA, Collatz GJ, Field CB, Hall FG. 1992.** Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing and Environment* **42**: 187–216.
- Sinclair TR, Murphy CE, Knoerr KR. 1976.** Development and evaluation of simplified models for simulating canopy photosynthesis and transpiration. *Journal of Applied Ecology* **13**: 813–839.
- Sivakumar MVK, Virmani SM. 1984.** Crop productivity in relation to interception of photosynthetically active radiation. *Agricultural and Forest Meteorology* **31**: 131–141.
- Szaniawski RK, Kielkiewicz M. 1982.** Maintenance and growth respiration in shoots and roots of sunflower plants grown at different root temperatures. *Physiologia Plantarum* **54**: 500–504.
- Thornley JHM, Johnson IR. 1990.** *Plant and crop modelling*. Oxford: Clarendon Press.
- Wang Y-P, Jarvis PG. 1990.** Description and validation of an array model—MAESTRO. *Agricultural and Forest Meteorology* **51**: 257–280.
- Williams K, Percival F, Merino J, Mooney HA. 1987.** Estimation of tissue construction cost from heat of combustion and organic nitrogen content. *Plant, Cell and Environment* **10**: 725–734.
- Wong SC, Cowan IR, Farquhar GD. 1979.** Stomatal conductance correlates with photosynthetic capacity. *Nature* **282**: 424–426.
- Woodwell GM, Botkin DB. 1970.** Metabolism of terrestrial ecosystems by gas-exchange techniques. In: Reichle DE, ed. *Analysis of temperate forest ecosystems*. Berlin: Springer-Verlag, 73–85.