

Interactive effects of atmospheric carbon dioxide and leaf nitrogen concentration on canopy light use efficiency: a modeling analysis

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Received March 2, 1995

Summary Potential increases in plant productivity in response to increasing atmospheric CO₂ concentration are likely to be constrained by nutrient limitations. However, the interactive effects of nitrogen nutrition and CO₂ concentration on growth are difficult to define because both factors affect several aspects of growth, including photosynthesis, respiration, and leaf area. By expressing growth as a product of light intercepted and light use efficiency (ϵ), it is possible to decouple the effects of nutrient availability and CO₂ concentration on photosynthetic rates from their effects on other aspects of plant growth. I used measured responses of leaf photosynthesis to leaf nitrogen (N) content and CO₂ concentration to parameterize a model of canopy radiation absorption and photosynthesis, and then used the model to estimate the response of ϵ to elevated CO₂ concentration for *Pinus radiata* D. Don, *Nothofagus fusca* (Hook. f.) Ørst. and *Eucalyptus grandis* W. Hill ex Maiden. Down-regulation of photosynthesis at elevated CO₂ was represented as a reduction in either leaf N content or leaf Rubisco activity.

The response of ϵ to elevated CO₂, which differed among the three species, was analyzed in terms of the underlying relationships between leaf photosynthesis and leaf N content. The response was independent of leaf N content when photosynthesis was down-regulated to the same extent at low and high leaf N content. Interactive effects of N availability and CO₂ on growth are thus likely to be the result of either differences in down-regulation of photosynthesis at low and high N availability or interactive effects of CO₂ and N availability on other aspects of plant growth.

Keywords: canopy model, elevated CO₂, photosynthetic down-regulation.

Introduction

The present increase in atmospheric CO₂ concentration is well documented (Watson et al. 1990), but its long-term effects on growth of terrestrial vegetation are less well understood (Eamus and Jarvis 1989). Although plant photosynthetic productivity increases in response to short-term exposure to elevated CO₂ (e.g., Kimball 1983, Cure and Acock 1986, Stitt 1991), other environmental factors also limit plant productivity, and

may moderate the response of vegetation to elevated CO₂ in the longer term (Gunderson and Wullschleger 1994, Sage 1994). It has been suggested that soil fertility, in particular, may constrain any CO₂-induced increase in productivity (Kramer 1981, Bazzaz and Fajer 1992). Because nutrient availability is often limiting in terrestrial ecosystems (Tamm 1991), it could have a large impact on the ability of nonagricultural systems to respond to elevated CO₂.

Conflicting results have been obtained from studies of the effect of soil nutrition on the response of vegetation to elevated CO₂. Thus, CO₂ stimulation of growth was reduced at low nutrient availability in wheat (Sionit et al. 1981), a C₃ grass (Larigauderie et al. 1988), willow (Silvola and Alholm 1992), three out of four species of eucalypts (Wong et al. 1992), and wild cherry (Wilkins et al. 1994). However, in other experiments, the percentage stimulation of growth at elevated CO₂ was similar in both high and low nutrient treatments (cotton, Wong 1979; soybean, Sionit 1983 and Cure et al. 1988; Noogoora burr, Hocking and Meyer 1985; yellow poplar, Norby and O'Neill 1991; and sweet chestnut, El Kohen and Mousseau 1994).

Although it is not clear how low nutrient availability will affect plant responses to elevated CO₂, it is evident that the interactive effects of CO₂ and nutrition on plant growth are complex (Eamus and Jarvis 1989, Mousseau and Saugier 1992). Insight into such complex growth responses may be gained by expressing growth as a function of several independent factors, and investigating the responses of the individual factors. One such method of analyzing plant growth responses is the light use efficiency approach (Monteith 1977) in which growth of vegetation over time (i.e., annual C uptake, G , g C m⁻² year⁻¹) is modeled as:

$$G = \epsilon \phi_{\text{abs}} Y_g (1 - R), \quad (1)$$

where ϵ is the photosynthetic light use efficiency of the canopy (g C MJ⁻¹), ϕ_{abs} is the photosynthetically active radiation absorbed by the canopy (MJ m⁻² year⁻¹), Y_g is the conversion efficiency of photosynthate to biomass, and $(1 - R)$ represents the fraction of photosynthate that is not respired (Jarvis and Leverenz 1983). Equation 1 separates the effects on growth of photosynthetic rates (that affect ϵ), leaf area (that affect ϕ_{abs}),

and respiration. The light use efficiency approach has been used to investigate the effects of nitrogen fertilization and irrigation on plant growth (Gallagher and Biscoe 1978, Legg et al. 1979, Cannell et al. 1987, Garcia et al. 1988), but has rarely been used to interpret responses to elevated CO₂ (but see Gifford and Morison 1993, Pinter et al. 1994). In this paper I used the light-use efficiency approach to evaluate the contribution of changes in photosynthetic rate to the overall growth response of plants to elevated CO₂. I estimated light use efficiency with MAESTRO (Wang and Jarvis 1990a), a detailed model of radiation absorption and photosynthesis integrated through the canopy and over time. The model MAESTRO (Wang and Jarvis 1990a) was used to predict the interactive effects of changes in atmospheric CO₂ concentration and leaf nitrogen (N) content on ϵ , based on the observed responses of leaf photosynthesis.

The rate of leaf photosynthesis is assumed to be controlled by (1) the rate of regeneration of ribulose-1,5-bisphosphate (RuBP), (2) the activity of the carbon-fixing enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), and (3) the rate of regeneration of inorganic phosphate (Pi) (Farquhar and von Caemmerer 1982, Sharkey 1985). Each of these processes has been shown to depend on leaf N content (Harley et al. 1992); however, because the rate of photosynthesis per unit leaf N (N use efficiency) varies among species (Evans 1989), I incorporated the published relationships between photosynthesis and leaf N content for three species into the model.

Down-regulation of photosynthesis affects light use efficiency. Therefore, I incorporated into the model two hypotheses to explain down-regulation of photosynthesis at elevated CO₂: (1) a decrease in leaf N content (Ceulemans and Mousseau 1994, Thomas et al. 1994), and (2) a decrease in Rubisco content (Besford et al. 1990, Sage 1994). Both hypotheses predict reduced Rubisco activity at elevated CO₂, but they differ on whether the activities of other photosynthetic processes are also reduced. The model was used to estimate light use efficiency at a range of leaf N contents, and two atmospheric CO₂ concentrations (350 and 700 ppmv), for the following assumptions: (1) no photosynthetic down-regulation; (2) a 10% decrease in leaf N content at elevated CO₂; (3) a 20% decrease in leaf N content at elevated CO₂; (4) a 20% decrease in Rubisco activity at elevated CO₂; and (5) a 40% decrease in Rubisco activity at elevated CO₂. In cases (4) and (5), there were no indirect effects of elevated CO₂ on any processes other than Rubisco activity.

Model description

Leaf photosynthesis

I used Farquhar and von Caemmerer's (1982) model of leaf photosynthesis, as modified by Sharkey (1985), to determine the rate of photosynthesis (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$):

$$A = \left(1 - \frac{\Gamma^*}{C_i}\right) \min(W_c, W_j, W_p) - 0.6R_d, \quad (2)$$

where Γ^* is the CO₂ compensation point in the absence of dark respiration (ppmv), R_d is the rate of dark respiration (assumed to be reduced by 40% in the light; $\mu\text{mol m}^{-2} \text{s}^{-1}$), C_i is the intercellular CO₂ concentration (ppmv), W_c is the rate of carboxylation when Rubisco activity is limiting, W_j is the rate of carboxylation when RuBP regeneration is limiting, and W_p is the rate of carboxylation when Pi regeneration is limiting.

The rate of carboxylation when Rubisco limits photosynthesis (W_c) is given by:

$$W_c = V_{\text{cmax}} \frac{C_i}{C_i + k_c(1 + O_i/k_o)}, \quad (3)$$

where V_{cmax} is the maximum rate of carboxylation ($\mu\text{mol m}^{-2} \text{s}^{-1}$), O_i is the intercellular oxygen concentration (ppmv), and k_c and k_o are the Michaelis-Menten constants ($\mu\text{mol mol}^{-1}$) for Rubisco catalytic activity for CO₂ and O₂, respectively.

The rate of carboxylation when RuBP regeneration limits photosynthesis (W_j), which occurs when light is limiting, is given by:

$$W_j = \frac{J}{4} \frac{C_i}{C_i + 2\Gamma^*}, \quad (4)$$

where J is the rate of electron transport ($\mu\text{mol m}^{-2} \text{s}^{-1}$), and is a saturating function of the absorbed quantum flux, Q ($\mu\text{mol m}^{-2} \text{s}^{-1}$):

$$\theta J^2 - (\alpha Q + J_{\text{max}})J + \alpha Q J_{\text{max}} = 0, \quad (5)$$

where J_{max} is the maximum rate of electron transport ($\mu\text{mol m}^{-2} \text{s}^{-1}$), α is the quantum yield of electron transport (mol mol^{-1}), and θ is a constant (= 0.9) that defines the curvature of the light response of J .

The rate of carboxylation when Pi regeneration limits photosynthesis (W_p), which occurs when the rate of use of the end-products of photosynthesis is limiting, such that:

$$A = 3\text{TPU} - 0.6R_d, \quad (6)$$

where TPU is the rate of phosphate release in triose phosphate utilization ($\mu\text{mol m}^{-2} \text{s}^{-1}$) (Harley et al. 1992).

Equation 2 describes the rate of CO₂ utilization by the chloroplast. The rate of supply of CO₂ is determined by stomatal conductance (g_s , $\mu\text{mol m}^{-2} \text{s}^{-1}$), which is predicted by the model of Leuning (1995):

$$g_s = g_0 + \frac{aA}{(C_a - \Gamma^*)(1 + D/D_0)}, \quad (7)$$

where C_a is the atmospheric CO₂ concentration (ppmv), D is the saturation vapor deficit of air (Pa), and g_0 , a and D_0 are empirical constants ($g_0 = 0 \mu\text{mol m}^{-2} \text{s}^{-1}$; $a = 30$; and $D_0 = 350$ Pa). It is assumed that leaf boundary layer resistance is negligible. When $g_0 = 0$, as is assumed here, Equation 7 implies that stomatal conductance varies such that the ratio C_i/C_a is constant when C_a and leaf N concentration are varied, except at

low values of A ; this result is often reported (Wong et al. 1979, Wong et al. 1985, Spencer and Bowes 1986, Sage 1994, Thomas et al. 1994).

The temperature dependence of TPU is taken from Harley et al. (1992), and those of J_{\max} and V_{cmax} are taken from Kirschbaum (1986), with the modification that both quantities decline linearly to zero between 10 and 0 °C. Other temperature dependences in the model are taken from McMurtrie and Wang (1993).

Relationship between leaf photosynthesis and leaf N content at current CO₂ concentration

The three parameters determining the light-saturated rate of leaf photosynthesis, A_{sat} , namely J_{\max} , V_{cmax} and TPU, are linearly related to leaf N content (Table 1). Because Rubisco content increases with increasing leaf N, V_{cmax} is related to leaf N content (Seemann et al. 1987). Similarly, N is needed for chlorophyll and various components of the electron transport chain (Evans 1989) and hence J_{\max} scales with leaf N. The link between TPU and leaf N is not clearly understood, but TPU may scale with N simply because J_{\max} and V_{cmax} do (see von Caemmerer and Farquhar 1984, Evans 1989, Stütt 1991). This assumption was used to derive relationships between TPU and leaf N content. Because photosynthesis was not limited by Pi regeneration in most of the studies used to compile Table 1, I derived the N-dependence of TPU for several species based on the relationship between J_{\max} and TPU developed by Wullschlegel (1993):

$$\text{TPU} = 0.06J_{\max} \quad (r^2 = 0.844). \quad (8)$$

Three of the sets of relationships given in Table 1, for *Eucalyptus grandis*, *Nothofagus fusca* and *Pinus radiata*, were used to parameterize MAESTRO.

Parameterization of canopy model

The leaf photosynthesis model was scaled up to the canopy using the model MAESTRO (Wang and Jarvis 1990a). MAESTRO calculates canopy radiation absorption and consequent

photosynthesis on an hourly time step. Penetration of radiation is calculated using the method of Norman and Welles (1983). Diffuse and direct components of radiation are treated separately, with multiple scattering considered as described by Norman (1979). Photosynthesis is calculated as a function of absorbed quantum flux density. Leaf temperatures are assumed equal to air temperatures. Leaf N content is assumed to decline exponentially through the canopy. I assumed no effect of low water potentials on photosynthesis, in order to focus only on N limitations.

MAESTRO was parameterized for the *Pinus radiata* Biology of Forest Growth (BFG) site near Canberra, Australia (35°21' S, 148°56' E, elevation 625 m above sea level; see Benson et al. (1992) for a full site description). Stocking density, green crown height and crown radius were 700 stems ha⁻¹, 8.5 m and 2.83 m, respectively. Tree crowns were assumed to be of equal dimensions and equally spaced. Projected leaf area index was 7. Leaf area distribution was assumed to follow beta distributions given by Wang et al. (1990), and the "clumping factor" (Wang and Jarvis 1990b) was 0.7. The leaf angle distribution was assumed to be spherical.

The distribution of leaf N through the canopy was calculated based on data from biomass harvests on all experimental plots at BFG (Snowdon and Benson 1992). In these harvests, tree crowns were divided into quarters vertically, and the N content and leaf area in each section were measured. These data were fitted to the model of Hirose and Werger (1987):

$$N_i = N_0 \exp(-kL_i/L_t), \quad (9)$$

where N_i is the leaf N content above canopy height i (g m⁻²), L_i is leaf area index above canopy height i , L_t is the total leaf area index (= 7), N_0 is a parameter determining total canopy N content (g m⁻²), and k is a constant (average value = 0.86) determining rate of decline of N content with increasing canopy depth. Equation 9 was used to calculate leaf N content for five vertical levels in the canopy at varying N_0 .

MAESTRO requires hourly radiation and temperature data as input. Daily values of incident radiation and average daily

Table 1. Relationships between J_{\max} , V_{cmax} and TPU, and leaf N content used in modeling.

| Species | J_{\max} | V_{cmax} | TPU | Reference |
|--|----------------------------|--------------------------|---------------------------|-----------------------------|
| <i>Alocasia macrorrhiza</i> (L.) G. Don | 70.7N - 10.35 ^a | 43.1N - 5.0 | 4.24N - 0.62 ^c | Sims and Pearcy 1989 |
| <i>Colocasia esculenta</i> (L.) Schott | 78.3N - 7.65 ^a | 55.5N - 14.5 | 4.7N - 0.46 ^c | Sims and Pearcy 1989 |
| <i>Eucalyptus grandis</i> W. Hill ex Maiden. | 58N ^a | 31.0N + 16.7 | 3.48N ^c | Leuning et al. 1991 |
| <i>Gossypium hirsutum</i> L. | 70.6N - 3.3 ^b | 33.8N - 5.4 ^b | 4.15N + 0.51 ^b | Harley et al. 1992 |
| <i>Lepeshinia calycina</i> Benth. Epl. | 82.3N + 12.3 ^a | 35.8N + 12.4 | 4.94N + 0.74 ^c | Field 1983 |
| <i>Nothofagus fusca</i> (Hook. f.) Ørst. | 32.9N + 6.6 ^a | 14N + 2.3 | 1.97N + 0.39 ^c | D.Y. Hollinger, pers. comm. |
| <i>Pinus radiata</i> D. Don | 50.3N - 44.9 | 30.2N - 28.3 | 3.02N - 2.7 ^c | Kirschbaum et al. 1994 |
| <i>Quercus lobata</i> Nee | 63.2N + 34.22 ^a | 22.8N + 6.8 | 3.79N - 2.05 ^c | Hollinger 1984 |

^a J_{\max} was multiplied by either 4 or 4/4.5 to standardize units of expression.

^b Values were referenced to 25 °C based on temperature dependences given by Harley et al. (1992).

^c Calculated from J_{\max} by Equation 8.

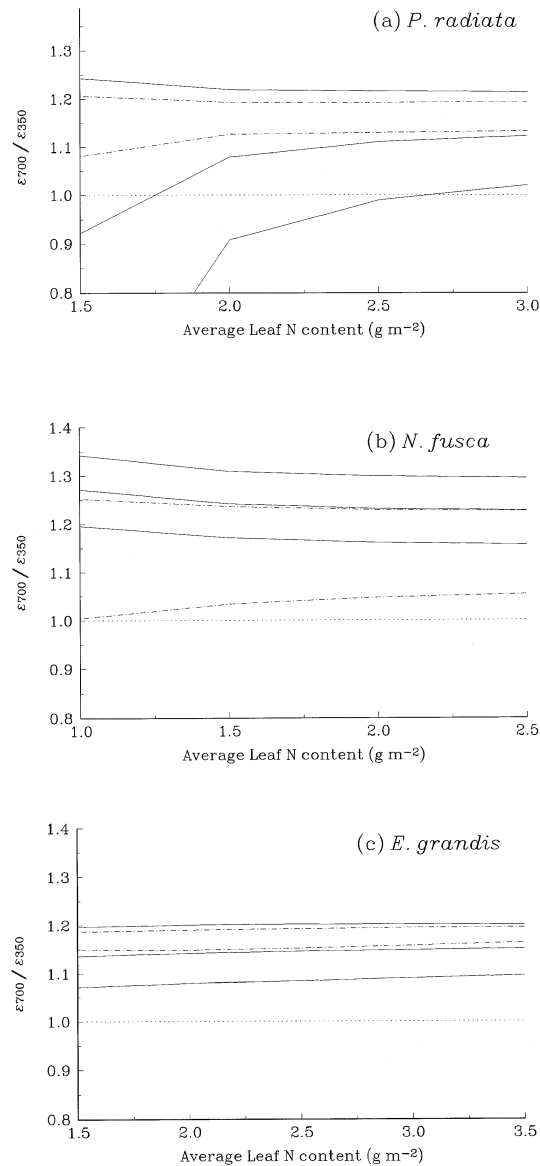


Figure 1. Ratio of ϵ at 700 ppmv CO_2 (ϵ_{700}) to ϵ at 350 ppmv CO_2 (ϵ_{350}) versus average leaf N content. Values of ϵ were calculated with the model MAESTRO. Relationships between the leaf photosynthetic parameters J_{\max} , V_{cmax} and TPU, and leaf N content from three different species were used: (a) *P. radiata*; (b) *N. fusca*; and (c) *E. grandis*. The range of average leaf N content for each species is the range of leaf N content reported in the study listed in Table 1. Five assumptions about down-regulation of photosynthesis at elevated CO_2 were made: (1) no down-regulation = uppermost solid line; (2) a 10% decrease in leaf N content = middle solid line; (3) a 20% decrease in leaf N content = lowest solid line; (4) a 20% decrease in leaf Rubisco activity = upper broken line; and (5) a 40% decrease in leaf Rubisco activity = lower broken line. Dotted line indicates the value of $\epsilon_{700}/\epsilon_{350}$ at which there is no response of ϵ to an increase in CO_2 .

temperatures recorded at the BFG site were obtained for the period July 1, 1985 to June 30, 1986. Daily mean temperatures over this period averaged 19 °C. Hourly radiation was calculated from daily values (Gates 1980), and temperatures were assumed to vary sinusoidally during the day.

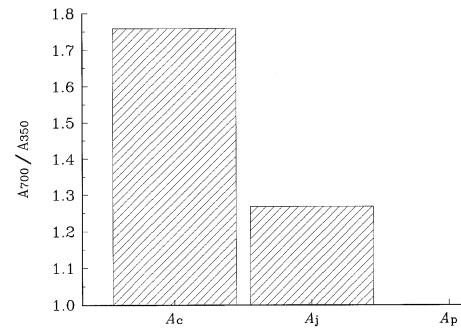


Figure 2. The response of leaf photosynthesis to elevated CO_2 when photosynthesis is limited by Rubisco activity (A_c), RuBP regeneration (A_j), or Pi regeneration (A_p). Calculations were made using Equations 3–6 and a leaf temperature of 25 °C. Symbols: $A_{350} = A$ at current ambient CO_2 , and $A_{700} = A$ at elevated CO_2 .

Results

Figure 1 illustrates the increase in annual light use efficiency predicted for a doubling in CO_2 , from 350 to 700 ppmv, for the three species and five scenarios regarding down-regulation of photosynthesis. The increase in light use efficiency represents the increase in photosynthetic production that would be expected from the effects of elevated CO_2 on leaf photosynthetic rates alone.

On the assumption that there is no down-regulation of photosynthesis at elevated CO_2 , there is little effect of leaf N content on the response of ϵ to elevated CO_2 , but there are considerable differences in response among species (Figure 1). The CO_2 -induced increase in ϵ is predicted to be about 20% for *E. grandis*, 25% for *P. radiata*, and 35% for *N. fusca*.

Inspection of the leaf photosynthesis model (especially Equations 3–5) shows that the response of leaf photosynthesis to elevated CO_2 does not change with changing leaf N content provided that the process that is limiting photosynthesis does not change. If, as Equation 7 implies, C_1/C_a does not change with leaf N content, and respiration rate is small compared to photosynthetic rate, then the ratio of leaf photosynthesis at 700 ppmv CO_2 to that at 350 ppmv CO_2 (A_{700}/A_{350}) is independent of leaf N content; however, the value of this ratio depends on which process is limiting photosynthesis. Figure 2 shows the response, at 25 °C, of leaf photosynthesis to a doubling of CO_2 when photosynthesis is limited by Rubisco activity, RuBP regeneration or Pi regeneration. (Note that the CO_2 responses of Rubisco-limited photosynthesis, A_c , and RuBP-regeneration-limited photosynthesis, A_j , both increase with increasing temperature, but that at any given temperature, the CO_2 response of A_c is greater than that of A_j .) The response of A to elevated CO_2 is highest when Rubisco activity is limiting photosynthesis (A_c), and is intermediate when RuBP regeneration is limiting (A_j), and there is no response if the rate of Pi regeneration is limiting (A_p) (cf. Stitt 1991). If control of photosynthesis shifts from one process to another at elevated CO_2 , then the CO_2 response lies between the CO_2 responses for the two processes. The response of ϵ to a doubling of C_a should therefore depend on the proportions of photosynthesis that are

controlled by each limitation.

The MAESTRO model was used to calculate the proportions of annual canopy photosynthesis that are controlled by each limitation, for each species at CO₂ concentrations of 350 and 700 ppmv and for low and high average canopy N content (Figure 3). Canopy N content does not greatly affect the proportions of photosynthesis controlled by each limitation, but there are species-specific differences. The proportion of photosynthesis that is Rubisco-limited is higher for *N. fusca*

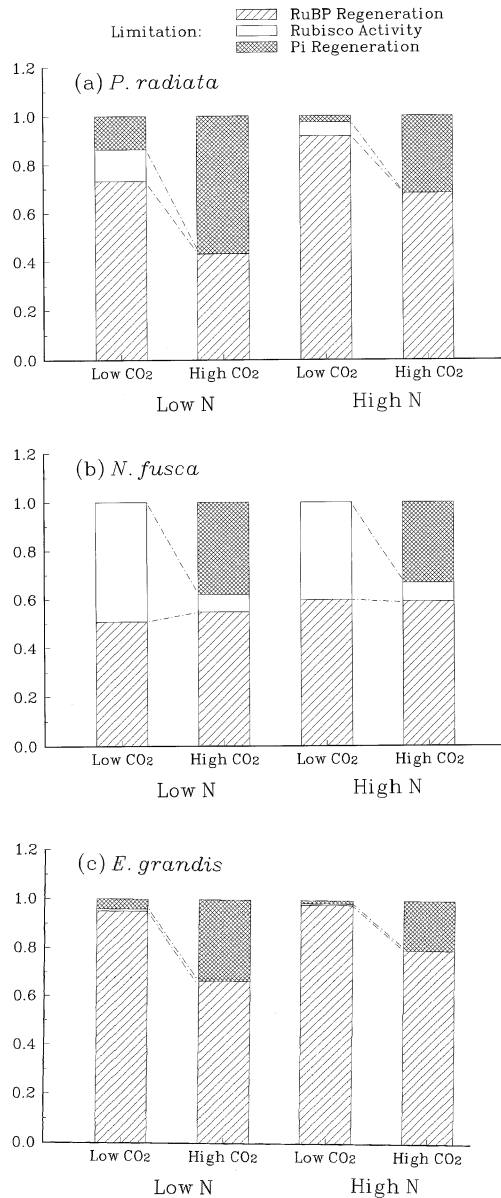


Figure 3. The proportions of annual canopy photosynthesis that are limited by each of the three potential limitations, at the lowest and highest average leaf N content for each species, and at current (350 ppmv) and elevated (700 ppmv) C_a: (a) *P. radiata*; (b) *N. fusca*; and (c) *E. grandis*. Dotted lines indicate how the proportions of annual canopy photosynthesis controlled by each limitation change when the atmospheric CO₂ concentration is doubled from 350 to 700 ppmv.

than for the other two species. Because Rubisco-limited photosynthesis is most responsive to CO₂, the CO₂-induced increase in ϵ is higher for *N. fusca* than for the other species (Figure 1).

The proportion of photosynthesis controlled by each of the limitations is determined largely by the ratio of the maximum rates of RuBP-regeneration and Rubisco activity (J_{\max}/V_{\max}). (The ratio of J_{\max}/TPU is assumed to be constant (Equation 8).) Rubisco activity is more often the limiting factor when J_{\max}/V_{\max} is high than when this ratio is low. The J_{\max}/V_{\max} ratio is higher for *N. fusca* than for *P. radiata* or *E. grandis* (Figure 4), which explains the high proportion of photosynthesis that is Rubisco-limited for *N. fusca*. Thus, the response of ϵ to a doubling in CO₂, in the absence of down-regulation of photosynthesis, is largely determined by the relative rates of RuBP regeneration (J_{\max}) and carboxylation (V_{\max}).

Next, consider the increase in ϵ predicted when photosynthesis is assumed to be down-regulated in response to elevated CO₂ as a result of a decrease in leaf N content. MAESTRO was run with leaf N content decreased by 10 and 20%. Figure 1 shows that the effect of a decrease in leaf N content is much greater for *P. radiata* than for *N. fusca* and *E. grandis*. This is because of differences in N use efficiency among the species. The effect of decreasing leaf N content on the response of ϵ to elevated CO₂ depends on the steepness of the relationship between ϵ and leaf N content (Figure 5). Because this relationship is steepest for *P. radiata*, a decrease in leaf N content has a greater effect on ϵ for *P. radiata* than for the other two species.

Differences in the response of ϵ to leaf N content among the three species are explained in Figure 6, which shows that ϵ is a saturating function of J_{\max} . Saturation occurs because increasing J_{\max} increases the rate of photosynthesis in leaves that are below light saturation, and at high values of J_{\max} , only a small proportion of the canopy is below light saturation. Species with a high value of J_{\max} per unit N, such as *E. grandis*, tend to operate on the saturated part of the ϵ - J_{\max} curve, and so a decrease in J_{\max} , as a result of a decrease in leaf N content,

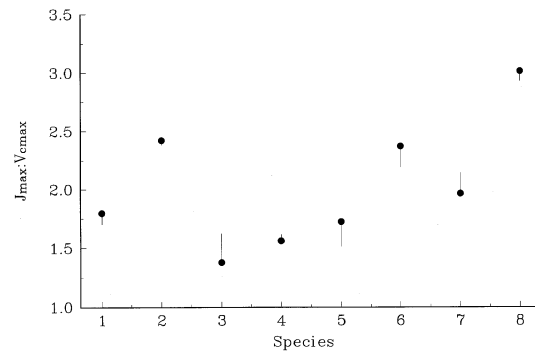


Figure 4. Ratio of J_{\max}/V_{\max} for each species. The ratio was calculated for the range of published leaf N contents; the resulting range in J_{\max}/V_{\max} is indicated by the vertical lines. Circles show the J_{\max}/V_{\max} at the lowest leaf N content considered. Species are: 1 = *P. radiata*, 2 = *N. fusca*, 3 = *E. grandis*, 4 = *A. macrorrhiza*, 5 = *C. esculenta*, 6 = *G. hirsutum*, 7 = *L. calycina*, and 8 = *Q. lobata*.

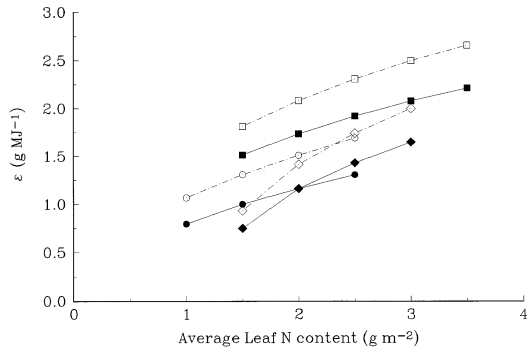


Figure 5. Response of canopy light-use efficiency to average canopy leaf N content for *P. radiata* (\diamond , \blacklozenge); *N. fusca* (\circ , \bullet); and *E. grandis* (\square , \blacksquare), at $\text{CO}_2 = 350$ ppmv (filled symbols) and at $\text{CO}_2 = 700$ ppmv (open symbols).

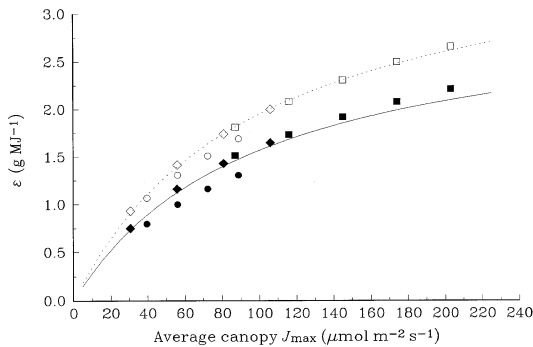


Figure 6. Response of canopy light use efficiency to average canopy J_{\max} for *P. radiata*, *N. fusca*, and *E. grandis*. Symbols as in Figure 5. Lines indicate rectangular hyperbolae fitted to values of canopy light use efficiency predicted by MAESTRO for all eight species listed in Table 1. Solid line, $\text{CO}_2 = 350$ ppmv; dashed line, $\text{CO}_2 = 700$ ppmv.

has little effect on ϵ . On the other hand, for species with a low J_{\max} per unit N, such as *P. radiata*, ϵ responds approximately linearly to decreasing J_{\max} , and thus is markedly affected by decreases in leaf N content. This explanation does not apply to *N. fusca* because the relationship between ϵ and J_{\max} for *N. fusca* is different from that for the other species (Figure 6). For *N. fusca*, the J_{\max}/V_{cmax} ratio is high (Figure 4), indicating that Rubisco activity more often limits annual canopy photosynthesis in this species than in *P. radiata* and *E. grandis*; consequently, the value of ϵ is reduced for a given J_{\max} .

In Figure 1, the response of ϵ to elevated CO_2 , assuming a 10% decrease in leaf N content, lies about halfway between the response assuming no change in leaf N and the response assuming a 20% decrease in leaf N content, suggesting that the stimulation of ϵ at elevated CO_2 decreases linearly as leaf N content declines. The same cannot be said of the decreases in leaf Rubisco activity. For *P. radiata* and *E. grandis*, a 20% decrease in leaf Rubisco activity has little effect on the response of ϵ to elevated CO_2 , whereas a 40% decrease in Rubisco activity has a large effect. At elevated CO_2 , Rubisco activity may decrease without having an impact on leaf photo-

synthesis or ϵ , because the efficiency of the enzyme is increased. The extent to which Rubisco activity can be decreased at elevated CO_2 without affecting ϵ depends on how often Rubisco activity limits photosynthesis at current ambient CO_2 ; this is indicated by the ratio of J_{\max}/V_{cmax} (Figure 4). For *N. fusca*, which was strongly limited by Rubisco activity, a reduction in Rubisco activity decreases the response of ϵ to elevated CO_2 considerably more than for *P. radiata* or *E. grandis*.

Discussion

The effect on growth of changes in photosynthetic rates in response to elevated CO_2 depends on the relationship between leaf photosynthesis and leaf N content. Assuming that there is no down-regulation of photosynthesis at elevated CO_2 , growth responses due to increased photosynthetic rates range from 20% in *E. grandis* and *P. radiata* to 35% in *N. fusca*. A 10% decrease in leaf N content reduces the CO_2 -induced stimulation of ϵ to 15% in *E. grandis* and leads to a decrease of ϵ in *P. radiata*. A 40% reduction in Rubisco activity reduces the CO_2 -induced increase in ϵ to 15% in *E. grandis* and to zero in *N. fusca*.

The responses to elevated CO_2 are strongly dependent on (1) the N use efficiency of photosynthesis, and (2) the ratio of J_{\max}/V_{cmax} . There is a general understanding of how nitrogen use efficiency varies among species (Lambers and Poorter 1992), but there is a need to develop explicit relationships, such as those given in Table 1, for different species. It would also be useful to know how these relationships vary over time and through the canopy.

It is not clear why the ratio of J_{\max}/V_{cmax} differs among species (Figure 4). The mean \pm standard deviation of J_{\max}/V_{cmax} in a survey of 109 species was 2.27 ± 0.55 (Wullschlegel 1993). The J_{\max}/V_{cmax} ratio was lowest in conifers and highest in monocotyledonous crop species, vegetables and sclerophyllous shrubs; however, consistent differences among species have yet to be established.

A clearer understanding of the relationship between leaf photosynthesis and N may help to elucidate the mechanism(s) underlying down-regulation. If down-regulation is caused by a decrease in leaf N content alone, the relationships between J_{\max} , V_{cmax} and TPU, and leaf N will not change; however, if acclimation of photosynthesis to elevated CO_2 involves a shift of resources away from Rubisco, then these relationships will change. Harley et al. (1992) found that leaf N content of cotton did not decrease significantly at elevated CO_2 , but the relationship between V_{cmax} and leaf N content was decreased at elevated CO_2 , indicating some down-regulation of Rubisco activity. In loblolly pine, however, down-regulation of photosynthesis at elevated CO_2 was completely explained by a decrease in leaf N content (Thomas et al. 1994). Both hypotheses are thus supported by the data. Because both hypotheses predict that Rubisco activity is decreased at elevated CO_2 , studies that only report changes in Rubisco activity at elevated CO_2 , without reference to leaf N content, provide little information about the process that is driving down-regulation.

I conclude that leaf N content often does not markedly affect the response of ϵ to elevated CO₂. Only under the assumption of decreased leaf N content for *P. radiata* was there an interactive effect of leaf N and CO₂, indicating that any interactive effects of N availability and CO₂ on growth are likely to result from either (1) differences in down-regulation of photosynthesis at low and high N availability, or (2) interactive effects of CO₂ and N availability on the other components of Equation 1, such as leaf area expansion and respiration. It has been suggested that down-regulation of photosynthesis is stronger when nitrogen availability is limiting (Sage 1994). If so, and if down-regulation is due to one of the two hypotheses considered above, then either leaf N content or Rubisco activity should decrease, in response to elevated CO₂, more strongly when N availability is limiting. The data summarized in Table 2 indicate that there was no consistent pattern of responses of leaf N content or Rubisco activity at high and low N, indicating that down-regulation was not necessarily stronger at low N availability.

Other components of Equation 1 are also strongly affected both by N and CO₂ availability. Respiration increases with increasing tissue N concentration (Ryan 1991) and commonly decreases at elevated CO₂ (Bunce 1994). Absorbed photosynthetically active radiation depends on canopy leaf area, which generally increases with N availability (Brix 1983, Cromer et al. 1993) and often increases with increasing CO₂ (Ceulemans and Mousseau 1994). The response of leaf area to elevated CO₂ might be expected to be greater at high fertility, because more nutrients are available to support canopy expansion. This was found by El Kohen and Mousseau (1994); leaf area in their unfertilized *Castanea sativa* plants did not change between CO₂ treatments, but it increased 24% in the fertilized plants.

Table 2. Percentage changes in leaf N per unit area and Rubisco activity per unit leaf N in response to growth at elevated CO₂, at different nutrient supply rates.

| Species | Low N | High N | Reference |
|----------------------------------|-------|--------|--------------------------|
| Leaf N per unit area | | | |
| <i>Betula nana</i> | +1 | 0 | Oberbauer et al. 1986 |
| <i>Bromus mollis</i> | -3 | -4 | Larigauderie et al. 1988 |
| <i>Carex bigelowii</i> | +14 | +2 | Oberbauer et al. 1986 |
| <i>Eucalyptus camaldulensis</i> | -11 | -12 | Wong et al. 1992 |
| <i>Eucalyptus cypellocarpa</i> | -11 | -10 | Wong et al. 1992 |
| <i>Eucalyptus pauciflora</i> | -9 | -7 | Wong et al. 1992 |
| <i>Eucalyptus pulverulenta</i> | -2 | +2 | Wong et al. 1992 |
| <i>Ledum palustre</i> | -8 | +10 | Oberbauer et al. 1986 |
| <i>Liriodendron tulipifera</i> | -17 | -11 | Norby and O'Neill 1991 |
| <i>Pinus taeda</i> | -30 | -18 | Thomas et al. 1994 |
| <i>Pinus taeda</i> | -14 | -29 | Tissue et al. 1993 |
| <i>Populus × euramericana</i> | -4 | +10 | Curtis et al. 1995 |
| <i>Prunus avium</i> seedlings | -27 | -16 | Wilkins et al. 1994 |
| <i>Prunus avium</i> cuttings | +7 | -20 | Wilkins et al. 1994 |
| <i>Triticum aestivum</i> | 0 | -13 | Delgado et al. 1994 |
| Rubisco activity per unit leaf N | | | |
| <i>Pinus taeda</i> | -37 | -19 | Tissue et al. 1993 |
| <i>Prunus avium</i> | +41 | -16 | Wilkins et al. 1994 |

However, Norby and O'Neill (1991) found that leaf area decreased slightly in both low-nutrient and high-nutrient treatments of *Liriodendron tulipifera*, and Wong (1979) found leaf area increased equally (~50%) in cotton plants at all nutrient levels.

In conclusion, I investigated how observed changes in leaf photosynthetic rates at elevated CO₂ impact on total plant growth. The model used to scale up from leaf photosynthesis to canopy light use efficiency, MAESTRO, is based on the radiation interception characteristics of a forest canopy. The results are therefore most applicable to tree species. However, comparison with the CO₂ response of light use efficiency reported in a FACE (free-air CO₂ exchange) experiment with cotton grown at 370 ppmv (ambient) and 550 ppmv (elevated) CO₂ indicates that crop species are likely to respond in a similar way (Pinter et al. 1994, Idso et al. 1994). Photosynthesis in cotton does not appear to be down-regulated at elevated CO₂ (Idso et al. 1994). Based on the scenario used for the cotton study, MAESTRO predicts an increase in light use efficiency of 20% (data not shown), whereas the CO₂ response of light use efficiency in the cotton experiment was 25%. The difference may be partly explained by the high temperatures experienced by the cotton crop (daily mean of 28.7 °C, compared to the daily mean of 19 °C used in the MAESTRO simulations). Because photosynthetic rates respond more strongly to elevated CO₂ at high temperatures than at low temperatures (Long 1991), a higher CO₂-induced response of ϵ would be expected at high temperatures.

Acknowledgments

This work was supported by the NGAC Dedicated Greenhouse Research Grants Scheme. I thank Drs. Ross McMurtrie, Roddy Dewar and Peter Harley for helpful comments on the manuscript.

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