THEORETICAL PAPER

Predicting responses of photosynthesis and root fraction to elevated $[CO_2]_a$: interactions among carbon, nitrogen, and growth*

Y. LUO[1], C. B. FIELD[2] & H. A. MOONEY[1]

[1]*Department of Biological Sciences, Stanford University, Stanford, CA 94305, USA, and* [2]*Department of Plant Biology, Carnegie Institution of Washington, Stanford, CA 94305, USA*

ABSTRACT

At elevated atmospheric CO_2 concentrations ($[CO_2]_a$), photosynthetic capacity (A_{max}) and root fraction (η_R, the ratio of root to plant dry mass) increased in some studies and decreased in others. Here, we have explored possible causes of this, focusing on the relative magnitudes of the effects of elevated $[CO_2]_a$ on specific leaf (n_m) and plant (n_p) nitrogen concentrations, leaf mass per unit area (h), and plant nitrogen productivity (α). In our survey of 39 studies with 35 species, we found that elevated $[CO_2]_a$ led to decreased n_m and n_p in all the studies and to increased h and α in most of the studies. The magnitudes of these changes varied with species and with experimental conditions.

Based on a model that integrated $[CO_2]_a$-induced changes in leaf nitrogen into a biochemically based model of leaf photosynthesis, we predicted that, to a first approximation, photosynthesis will be upregulated (A_{max} will increase) when growth at increased $[CO_2]_a$ leads to increases in h that are larger than decreases in n_m. Photosynthesis will be downregulated (A_{max} will decrease) when increases in h are smaller than decreases in n_m. The model suggests that photosynthetic capacity increases at elevated $[CO_2]_a$ only when additional leaf mesophyll more than compensates the effects of nitrogen dilution.

We considered two kinds of regulatory paradigms that could lead to varying responses of η_R to elevated $[CO_2]_a$, and compared the predictions of each with the data. A simple static model based on the functional balance concept predicts that η_R should increase when neither n_p nor h is very responsive to elevated $[CO_2]_a$. The quantitative and qualitative agreement of the predictions with data from the literature, however, is poor. A model that predicts η_R from the relative sensitivities of photosynthesis and relative growth rate to elevated $[CO_2]_a$ corresponds much more closely to the observations. In general, root fraction increases if the response of photosynthesis to $[CO_2]_a$ is greater than that of relative growth rate.

Correspondence: Yiqi Luo, Biological Sciences Center, Desert Research Institute, University of Nevada System, P.O. Box 60220, Reno, NV 89506, USA.

Key-words: atmospheric change; carbon dioxide; functional balance; leaf nitrogen; mathematical model; partitioning; photosynthesis; root:shoot ratio.

INTRODUCTION

The responses of photosynthesis and root fraction (the ratio of root to total plant dry mass) to elevated $[CO_2]_a$ are not consistent among species and vary with growth conditions (Eamus & Jarvis 1989; Farrar & Williams 1991; Stitt 1991). Growth at elevated $[CO_2]_a$ led to increased photosynthetic capacity in *Solanum tuberosum* (Sage, Sharkey & Seemann 1989) but decreased photosynthetic capacity in *Phaseolus vulgaris* (Sage *et al.* 1989). The root fraction increased at elevated $[CO_2]_a$ in *Eucalyptus camaldulensis* (Wong, Kriedemann & Farquhar 1992) but decreased in *Trifolium repens* (Ryle, Powell & Davidson 1992a). The response of photosynthesis in a single species to growth at elevated $[CO_2]_a$ is also sensitive to environmental conditions. For example, the photosynthetic capacity of *Glycine max* increased in elevated $[CO_2]_a$ in plants grown in the field (Campbell, Allen & Bowes 1988), remained unchanged in plants grown in 20 dm^3 pots (Teramura, Sullivan & Ziska 1990), and decreased in plants grown in 4 dm^3 pots (Bunce 1993).

The responses of leaf-level photosynthesis to elevated $[CO_2]_a$ reflect a combination of adjustments in biochemical capacity and changes in leaf morphology. Changes in photosynthetic capacity can be induced by any or all of the interacting reaction complexes, including CO_2 fixation by ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), ribulose bisphosphate (RuBP) regeneration and P_i regeneration (Sage *et al.* 1989; Sage 1990; Stitt 1991). When plants are exposed to elevated $[CO_2]_a$, one initial effect is that photosynthesis is more likely to be limited by the capacity to regenerate RuBP. Over a few days, the amount and activity of Rubisco may be regulated downwards to balance the limitation in the rate of RuBP regeneration (Sage 1990). Morphological changes in elevated $[CO_2]_a$ may involve increased carbohydrate storage, leaf thickness, and mesophyll cell number per unit

storage, leaf thickness, and mesophyll cell number per unit of leaf area (Vu, Allen & Bowes 1989). Downregulation of the amount or activity of Rubisco per unit of leaf mass may be partially or completely compensated by additional growth of mesophyll cells per unit area, tending to preserve the total photosynthetic machinery per unit of leaf area.

Aspects of the variable responses of root fraction (η_R) to increased $[CO_2]_a$ were predicted by some models in the literature, but none of the published explanations appears to be completely general. The functional balance hypothesis of Brouwer (1962) and Davidson (1969) predicts that increased shoot activity (photosynthesis) should always be balanced by increased root mass. Yet, an increase in leaf mass per area resulting from carbohydrate storage tends to reduce shoot activity, making it difficult to predict whether growth at elevated $[CO_2]_a$ will lead to increased photosynthesis per unit of shoot mass. Using the functional balance concept and a cost–benefit analysis, Hilbert, Larigauderie & Reynolds (1991) predicted that η_R should be largely unaffected by $[CO_2]_a$. The carbon/nitrogen substrate ratio, proposed by Reynolds & Thornley (1982) to regulate η_R, fails to explain CO_2 effects on the root fraction of *Raphanus sativas* × *raphanistrum* (Chu, Coleman & Mooney 1992).

A plant is a complex system with the potential to maintain root:shoot balance through a number of mechanisms (Mooney & Chiariello 1984). In elevated $[CO_2]_a$, enhanced shoot function may be balanced by adjustments not only in root fraction but also in other physiological and morphological processes. For example, leaf mass per unit area (h) and nitrogen productivity (α, dry matter production per unit of nitrogen) usually increase with $[CO_2]_a$ (Sage et al. 1989; Field et al. 1992). If photosynthesis per unit area increases less than h, activity per unit of leaf mass decreases. In addition, increased α means that less nitrogen is needed to produce a unit of plant biomass, suggesting that the nitrogen requirements of a shoot of a given size can be met by a smaller root system. Thus, functional balance may be consistent with decreased η_R as a consequence of other physiological and morphological adjustments that affect root fraction.

The work presented here was intended to provide a new framework for predicting variable responses of photosynthesis and root fraction to elevated $[CO_2]_a$. We reviewed the effects of elevated $[CO_2]_a$ on leaf (n_m) and plant (n_p) nitrogen concentrations, h, and α. To model the response of photosynthesis to elevated $[CO_2]_a$, we integrated the $[CO_2]_a$-induced changes in n_m and h into the biochemically based model of Farquhar, von Caemmerer & Berry (1980) via the photosynthesis–nitrogen relationship (Field 1983; Harley et al. 1992). In order to understand the response of η_R to elevated $[CO_2]_a$, we explored two kinds of approach. One is based on the hypothesis that η_R is regulated by the balance between root and shoot functions. The second approach is based on the hypothesis that η_R is controlled by the relative responses of photosynthesis and growth. We compared the observations with model predic-

tions and proposed possible mechanisms for the responses of photosynthesis and root fraction to elevated $[CO_2]_a$.

MODELS

The leaf photosynthesis model

Plant growth at elevated $[CO_2]_a$ leads to changes in the biochemical capacity of photosynthesis but not in the nature of the photosynthetic reactions. Thus, a model that captures the essential features of photosynthesis for plants grown in ambient $[CO_2]_a$ should be adaptable for plants grown in elevated $[CO_2]_a$ (Harley et al. 1992). We explored leaf-level responses to growth at elevated $[CO_2]_a$ with the widely used model of Farquhar et al. (1980), modified by Sharkey (1985) to include the possibility of P_i limitation. We made the maximum carboxylation rate (V_{cmax}), the maximum electron transport rate (J_{max}), the phosphate release rate in triose phosphate utilization (TPU), and dark respiration (ρ) linear functions of nitrogen per unit leaf area [n_a, g(N) m(leaf area)$^{-2}$; Field 1983; Harley et al. 1992] (see Appendix 1). The latter is related to leaf nitrogen per unit of leaf mass [n_m, g(N) g(dry wt)$^{-1}$] and leaf mass per unit of area [h, g(dry wt) m(leaf area)$^{-2}$] by

$$n_a = n_m h. \tag{1}$$

To explore the effects of $[CO_2]_a$-induced changes in n_m and h on photosynthesis, we focused on the relative responses $n_{m,e}/n_{m,a}$ and h_e/h_a, where the subscripts a and e refer to plants grown at ambient (350 μmol mol^{-1}) and elevated (700 μmol mol^{-1}) $[CO_2]_a$, respectively. Note that, when $(n_{m,e}/n_{m,a}) \times (h_e/h_a) = 1$, leaf nitrogen per unit of area does not change in response to growth at elevated $[CO_2]_a$. Nitrogen per unit of area decreases in response to growth at elevated $[CO_2]_a$ when $(n_{m,e}/n_{m,a}) \times (h_e/h_a) < 1$ and increases when $(n_{m,e}/n_{m,a}) \times (h_e/h_a) > 1$.

For all calculations with the photosynthesis model, intercellular $[CO_2]$ was iteratively calculated from measurement $[CO_2]$, stomatal conductance, and photosythesis (Appendix 1). To delineate the zones of upregulated and downregulated photosynthesis for plants grown at elevated $[CO_2]_a$, we numerically searched for the value of h_e/h_a at each $n_{m,e}/n_{m,a}$ such that photosynthetic capacity at CO_2 saturation (A_{max}) for plants grown at $[CO_2]_a = 700$ μmol mol^{-1} was equal to that for plants grown at $[CO_2]_a = 350$ μmol mol^{-1}. Values of h_e/h_a larger and smaller than this result in, respectively, upregulated and downregulated photosynthesis. A similar search for the value of h_e/h_a for each $n_{m,e}/n_{m,a}$ where the rate of photosynthesis in leaves grown and measured at $[CO_2]_a = 700$ μmol mol^{-1} is the same as that in leaves grown and measured at $[CO_2]_a = 350$ μmol mol^{-1} locates the boundary between downregulated and depressed photosynthesis.

The root fraction model based on the functional balance concept

Brouwer (1962) first proposed a functional equilibrium concept. Davidson (1969) extended this concept with the

postulate that total shoot activity should be proportional to total root activity as

$$\eta_S \sigma_S \propto \eta_R \sigma_R , \tag{2}$$

where σ_S is the shoot activity and is expressed in terms of total plant growth [g(plant dry wt) g(shoot dry wt)$^{-1}$ d^{-1}], σ_R is the root activity [g(plant dry wt) g(root dry wt)$^{-1}$ d^{-1}], η_S is the shoot fraction [g(shoot dry wt) g(plant dry wt)$^{-1}$], and η_R is the root fraction [g(root dry wt) g(plant dry wt)$^{-1}$]. With these definitions, the proportionality in Eqn 2 becomes an equality. In terms of the variables used here,

$$\sigma_S = \frac{A_d}{h} \tag{3}$$

and

$$\sigma_R = \frac{N_u}{n_p}, \tag{4}$$

where A_d is the daily net assimilation rate [g(dry wt) m(leaf area)$^{-2}$ d^{-1}], N_u is the nitrogen uptake rate [g(N) g(root dry wt)$^{-1}$ d^{-1}], and n_p is the plant nitrogen concentration [g(N) g(dry wt)$^{-1}$]. Using Eqns 3 and 4 to substitute for σ_S and σ_R, replacing η_S with $1 - \eta_R$, and rearranging, we obtain

$$\eta_R = \frac{A_d n_p}{h N_u + A_d n_p} . \tag{5}$$

With this formulation, η_R should depend on the relative effects of elevated [CO_2]$_a$ on photosynthesis, leaf mass per unit area, plant nitrogen, and nitrogen uptake rate.

The root fraction model based on the photosynthesis:growth balance concept

An alternative model for η_R is derived from the photosynthesis:growth balance concept. The relative growth rate of a plant [R, g(dry wt) g(dry wt)$^{-1}$ d^{-1}] is determined by the daily net assimilation rate (A_d), the leaf weight ratio [η_L, g(leaf dry wt) g(plant dry wt)$^{-1}$], and the leaf mass per unit area (h) (Lambers & Poorter 1992) as

$$R = A_d \frac{\eta_L}{h} . \tag{6}$$

The plant relative growth rate is also proportional to n_p according to the concept of nitrogen productivity (Ågren 1985):

$$R = \alpha n_p \tag{7}$$

where α is the plant nitrogen productivity [g(dry wt) g(N)$^{-1}$ d^{-1}].

The concept of nitrogen productivity has been very useful in explaining the response of η_R to the rate of nitrogen supply (Ågren 1985; Ågren & Ingestad 1987). We used it

here as a possible approach to understanding responses of η_R to elevated [CO_2]$_a$. For a herbaceous plant without a significant amount of stem tissue, $\eta_S = \eta_L$. Making this substituting and solving Eqn 6 for η_R we obtain

$$\eta_R = 1 - \frac{Rh}{A_d} , \tag{8}$$

and substitution for R from Eqn 7 gives

$$\eta_R = 1 - \frac{n_p \alpha h}{A_d} \tag{9}$$

With this formulation, the root fraction (η_R) should depend on the relative effects of [CO_2]$_a$ on growth (or nitrogen and nitrogen productivity), photosynthesis, and leaf mass per unit area. Note that with the formulation based on nitrogen productivity (Eqn 9) increased n_p leads to decreased η_R, whereas in the formulation based on functional balance (Eqn 5), increased n_p leads to increased η_R.

The daily net assimilation rate (A_d) was calculated by integrating the daily course of leaf photosynthesis (Hirose & Werger 1987; Hilbert *et al.* 1991), which was predicted from the photosynthesis model with a daily course of light intensities given by Hirose & Werger (1987):

$$I = I_0 \sin^2[\pi(t-6)/12] \quad (6 \leq t < 18),$$
$$I = 0 \qquad\qquad (0 \leq t < 6, \; 18 \leq t < 24), \tag{10}$$

where I is the instantaneous photon flux density (PFD, μmol m^{-2} s^{-1}), I_0 is the maximum PFD (= 1000 μmol m^{-2} s^{-1}) at noon ($t = 12$), and t is solar time (h). For this calculation, we made the following assumptions: the leaf temperature was 25 °C; all leaves were horizontal and fully illuminated and the leaf nitrogen concentration was proportional to plant nitrogen with a proportionality that did not change with [CO_2]$_a$ (Coleman & Bazzaz 1992). The daily photosynthesis was converted to dry weight by dividing by 1·54 (Hilbert *et al.* 1991).

The photosynthesis model (Appendix 1) makes daily net assimilation rate (A_d) a function of n_m and h. By running the photosynthesis model in a range of n_m and h, and substituting for A_d in Eqns 5 and 9, we can predict the response of η_R to n_m and h. With the assumption that the proportionality does not change with [CO_2]$_a$, we can substitute n_p for n_m. Thus, the root fraction (η_R) can be predicted from n_p, N_u, and h in Eqn 5 and from n_p, α, and h in Eqn 9. Of these, the nitrogen uptake rate (N_u) is assumed to be unaffected by growth at elevated [CO_2]$_a$. As with n_m and h, we plotted the relative responses of n_p, α, R, and A_d as X_e/X_a, where X_e and X_a are the values of the parameters for plants grown under, respectively, elevated and ambient [CO_2]$_a$.

To identify zones of the parameter space where the model predicts increased and decreased η_R, we numerically searched for the combinations of $n_{p,e}/n_{p,a}$ and h_e/h_a (Eqn 5), R_e/R_a and ($A_{d,e}/h_e$)/($A_{d,a}/h_a$) (Eqn 8), or $n_{p,e}/n_{p,a}$, h_e/h_a and α_e/α_a (Eqn 9) that gave the same root fraction for plants grown at elevated and ambient [CO_2]$_a$.

RESULTS AND DISCUSSION

Leaf and plant carbon and nitrogen

We reviewed the effects of increased $[CO_2]_a$ on specific leaf nitrogen concentration (n_m), leaf mass per unit area (h), plant nitrogen concentration (n_p), and nitrogen productivity (α) for 35 species in 39 published studies. Plant growth periods in those experiments ranged from 22 d to 27 months. For the experiments with multiple nitrogen treatments, data for the highest nitrogen treatment were chosen.

Specific leaf (n_m) and plant (n_p) nitrogen concentration always decreased in elevated $[CO_2]_a$. The decreases in n_m ranged from 2% for *Abutilon theophrasti* (Coleman & Bazzaz 1992) to 57% for *Brassica oleracea* (Sage *et al.*

1989). Decreases in n_p varied from 2% for *Trifolium repens* (Ryle *et al.* 1992a) to 37% for *Triticum aestivum* (Hocking & Meyer 1991a) (Table 1). Leaf mass per unit area (h) and plant nitrogen productivity (α) almost always increased with $[CO_2]_a$. Changes in h ranged from –4% for *Trifolium repens* (Ryle *et al.* 1992a) to +129% for *Gossypium hirsutum* (Delucia, Sasek & Strain 1985). Changes in α varied from –5% for *Eucalyptus pauciflora* to +80% for *Triticum aestivum* (Hocking & Meyer 1991a) (Table 1).

Plants grown in elevated $[CO_2]_a$ frequently accumulate carbohydrate in leaves and other tissues as starch, soluble sugars and structural compounds. Increased h results from both increased growth of mesophyll tissues and starch accumulation in leaves. Decreased nitrogen in leaves may be a consequence of a combination of dilution from in-

Table 1. Relative changes in specific leaf nitrogen concentration $(n_{m,e}/n_{m,a})$, leaf mass per unit area (h_e/h_a), plant nitrogen productivity (α_e/α_a), and plant nitrogen concentration $(n_{p,e}/n_{p,a})$ in elevated $[CO_2]_a$ in comparison to those in ambient $[CO_2]_a$

Species	$n_{m,e}/n_{m,a}$	h_e/h_a	α_e/α_a	$n_{p,e}/n_{p,a}$	Reference
Abutilon theophrasti	0·98	0·99	1·48	0·85	Coleman & Bazzaz (1992)
Acer rubrum		1·22			Miao, Wayne & Bazzaz (1992)
Amaranthus retroflexus	0·89	1·15	·12	0·82	Coleman & Bazzaz (1992)
Artemisia tridentata	0·74	1·25			Johnson & Lincoln (1991)
Betula alleghaniensis	0·69				Rochefort & Bazzaz (1992)
Betula lenta	0·78				Rochefort & Bazzaz (1992)
Betula papyrifera	0·71				Rochefort & Bazzaz (1992)
Betula pendula	0·86	1·13			Pettersson & McDonald (1992)
Betula populifolia	0·69				Rochefort & Bazzaz (1992)
Betula populifolia		1·18			Miao *et al.* (1992)
Brassica oleracea	0·43	1·73			Sage, Sharkey & Seemann (1989)
Calluna vulgaris	0·60				Woodin *et al.* (1992)
Chenopodium album	0·69	1·73			Sage *et al.* (1989)
Eucalyptus camaldulensis	0·74	1·45	1·30	0·79	Wong, Kriedemann & Farquhar (1992)
Eucalyptus cypellocarpa	0·75	1·45	1·30	0·83	Wong *et al.* (1992)
Eucalyptus grandis		1·76			Conroy, Milham & Barlow (1992)
Eucalyptus pauciflora	0·79	1·35	0·95	0·81	Wong *et al.* (1992)
Eucalyptus pulverulenta	0·83	1·36	1·22	0·89	Wong *et al.* (1992)
Gliricidia sepium	0·68	1·41	1·38	0·85	Thomas *et al.* 1991
Glycine max	0·79*	1·24			Campbell, Allen & Bowes (1988)
Glycine max		1·31			Vu, Allen & Bowes (1989)
Gossypium hirsutum	0·48	1·79			Wong (1990)
Gossypium hirsutum		2·29			Delucia, Sasek & Strain (1985)
Liriodendron tulipifera	0·68	1·15			Norby *et al.* (1992)
Lolium perenne	0·64	1·13	·10	0·96	Ryle, Powell & Tewson (1992b)
Opuntia ficus-indica		1·14**			Luo & Nobel (1993)
Phaseolus vulgaris		1·04			Radoglou, Aphalo & Jarvis (1992)
Phaseolus vulgaris	0·57	1·23			Sage *et al.* (1989)
Picea glauca		1·19			Brown & Higginbotham (1986)
Populus tremuloides		1·32			Brown & Higginbotham (1986)
Quercus alba	0·81				Norby, O'Neill & Luxmoore (1986)
Raphanus sativas × *raphanistrum*	0·77	1·52	·72	0·82	Chu, Coleman & Mooney (1992)
Salix × *dasyclados*	0·83				Silvola & Ahlholm (1992)
Scirpus olneyi	0·90				Curtis, Drake & Whigham (1989)
Solanum melongena	0·88	·53			Sage *et al.* (1989)
Solanum tuberosum	0·72	·60			Sage *et al.* (1989)
Spartina patens	0·93				Curtis *et al.* (1989)
Trifolium repens	0·90	0·96	1·09	0·98	Ryle, Powell & Davidson (1992a)
Triticum aestivum	0·65	0·97	1·80	0·63	Hocking & Meyer (1991a)

* Calculated from leaf soluble protein.
** Cladode weight per unit of surface area.

creased carbohydrate and decreased investment in Rubisco and other enzymes (Stitt 1991). Decreased nitrogen content in other parts is attributable to starch accumulation (Hocking & Meyer 1991b; Conroy 1992), changes in tissue chemical composition (Wong 1990; Wong *et al.* 1992), and shifts in plant size (Coleman, McConnaughay & Bazzaz 1993). Increases in nitrogen productivity are due to growth stimulation by higher carbohydrate availability.
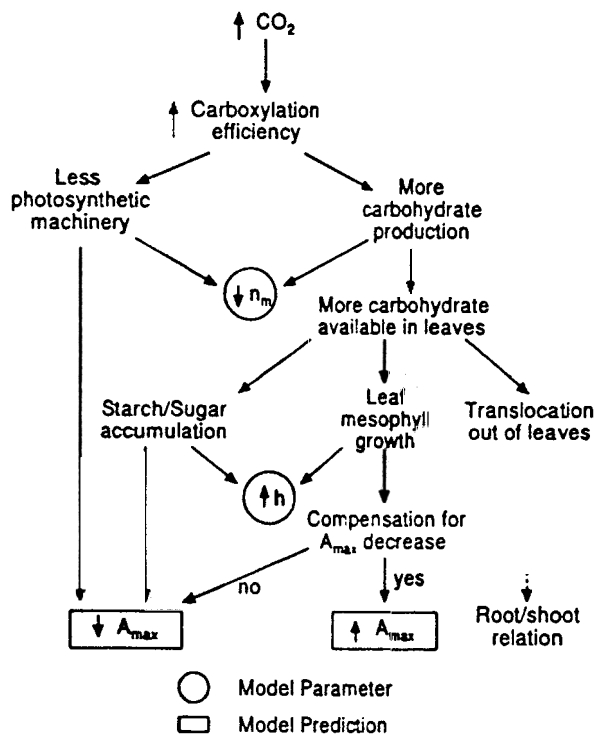
Photosynthetic response to elevated [CO₂]ₐ

Based on relative changes in h and n_m at elevated $[CO_2]_a$, we predicted zones of upregulated, downregulated and depressed photosynthesis (Fig. 1). Whenever $(n_{m,e}/n_{m,a}) \times (h_e/h_a) > 1$, leading to increased area-based leaf nitrogen concentration (n_a), predicted photosynthesis is upregulated, i.e. photosynthetic capacity increases, and the rate of photosynthesis under growth conditions is much higher for plants grown in elevated than in ambient $[CO_2]_a$. If $(n_{m,e}/n_{m,a}) \times (h_e/h_a) < 1$, predicted photosynthesis may be either downregulated or depressed. It is downregulated when photosynthetic capacity decreases but photosynthesis measured under growth conditions is still greater for plants grown at elevated than at ambient $[CO_2]_a$. If h changes only a little but n_m decreases considerably, photosynthetic capacity decreases markedly, and predicted photosynthetic rate at the growth $[CO_2]_a$ is lower for plants grown at elevated than at ambient $[CO_2]_a$. We defined this case as depressed photosynthesis.

The model prediction is quite consistent with published data (Fig. 1). Two species, *Solanum tuberosum* and *Chenopodium album* (Sage *et al.* 1989), fell in the predicted zone of upregulated photosynthesis. Their measured photosynthetic capacity (A_{max}) was higher for plants grown in elevated $[CO_2]_a$ than for plants grown in ambient $[CO_2]_a$. For a third species predicted to be in the zone of downregulated photosynthesis, *Glycine max*, the measured photosynthesis was upgraded (Campbell *et al.* 1988). For the five species predicted to be in the zone of downregulated photosynthesis, the predictions are consistent with measurements for four species, *Gossypium hirsutum* (Delucia *et al.* 1985), *Lolium perenne* (Ryle, Powell & Tewson 1992b), *Phaseolus vulgaris* (Sage *et al.* 1989) and *Trifolium repens* (Ryle *et al.* 1992a, c). For the fifth species, *Brassica oleracea* (Sage *et al.* 1989), the measurement was in the zone of depressed photosynthesis (Sage *et al.* 1989). In this case, the Rubisco activation state decreased by 25% in elevated $[CO_2]_a$, contributing to depression of photosynthesis.

Growth at elevated $[CO_2]_a$ leads to increased carboxylation efficiency, i.e. the carboxylation rate per unit of photosynthetic machinery. In response, investment in photosynthetic machinery may be reduced, leading to downregulated photosynthetic capacity (A_{max}) (Fig. 2). If growth at elevated $[CO_2]_a$ leads to more carbohydrate production, the availability of carbohydrate is increased. The additional carbohydrate has three possible fates. It could be stored as starch and/or soluble sugars in leaves, used for
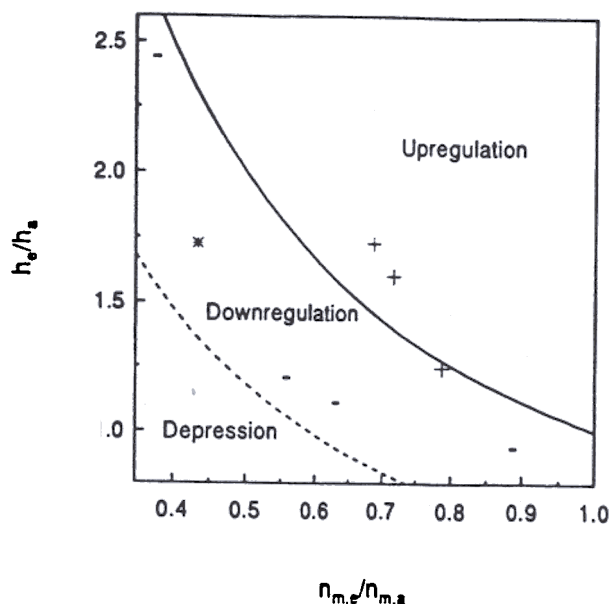
Figure 1. Three response zones of upregulated, downregulated and depressed photosynthesis predicted from relative changes in specific leaf nitrogen concentration $(n_{m,e}/n_{m,a})$ and leaf mass per unit area (h_e/h_a) in elevated $[CO_2]_a$. Symbols represent observed responses of photosynthesis from data in the literature: + for upregulation; – for downregulation; and * for depression. For *Gossypium hirsutum* (Delucia *et al.* 1985), $n_{m,e}/n_{m,a}$ was calculated from changes in chlorophyll content.

Figure 2. Proposed mechanisms for the responses of photosynthesis to elevated $[CO_2]_a$. Photosynthetic capacity (A_{max}) increases in elevated $[CO_2]_a$ only when the additional leaf mesophyll growth more than compensates the effect of nitrogen dilution on A_{max}.

leaf structural growth, or translocated out of the leaves. If the additional carbohydrate is stored as starch and/or soluble sugars in leaves, the photosynthetic capacity (A_{max}) can be downregulated through nitrogen dilution and feedback inhibition by end-products (Stitt 1991). If the additional carbohydrate is used for leaf mesophyll growth, the nitrogen dilution may be partially or completely compensated by extra layers of mesophyll cells (Vu *et al.* 1989). If the compensation is partial, photosynthetic capacity (A_{max}) is still downregulated. When the compensation is more than complete, photosynthetic capacity (A_{max}) should be upregulated. If all of the additional carbohydrate is translocated out of leaves, leaf properties may hardly change. Both reduced photosynthetic machinery and increased carbohydrate production lead to decreased n_m, whereas increased starch/sugar accumulation and mesophyll growth lead to increased h (Fig. 2).

Responses of root fraction to elevated $[CO_2]_a$

The prediction based on the functional balance concept (Eqn 5) suggests that η_R should increase with increasing A_d and decrease with decreasing n_p, increasing h, and increasing N_u. The nitrogen uptake rate per unit of root dry mass (N_u) did not appear to change in *Raphanus sativas* × *raphanistrum* (Chu *et al.* 1992), *Abutilon theophrasti* or *Amaranthus retroflexus* (Coleman & Bazzaz 1992) but increased for the nitrogen-fixing species *Trifolium repens* (Ryle *et al.* 1992a). With the assumption that N_u does not change with growth at different $[CO_2]_a$, changes in η_R can be predicted from only n_p and h.

The model predicts that η_R increases when neither n_p nor h is very responsive to elevated $[CO_2]_a$ (Fig. 3). The data suggest that essentially the opposite is the case. The root fraction (η_R) actually increased only when the $[CO_2]_a$ response of n_p was large (Fig. 3).

The model based on the balance between photosynthesis and growth (Eqn 8) suggests that η_R should increase whenever growth at elevated $[CO_2]_a$ leads to an increase in A_d/h that is greater than the increase in R (Fig. 4). In cases where A_d/h increases more than R in elevated $[CO_2]_a$, increased η_R is effectively the mechanism that returns photosynthesis and growth (Eqn 8) or photosynthesis and nitrogen productivity (Eqn 9) to balance. Insensitivity of R could be a consequence of genetically determined low growth potential, nutrient limitation (Chapin 1980, 1991), or some combination of the two.

The photosynthesis:growth formulation in Eqn 9 predicts that η_R should increase when elevated $[CO_2]_a$ leads to a large decrease in n_p and little increase in h and α (Fig. 5a). This formulation leads to a much better fit to observations than does the formulation based on functional balance, explaining 13 of 19 cases (Fig. 5b). Of the six cases where the prediction is qualitatively incorrect, two observed data differ from the predictions by less than 10% and another two by less than 20%. The two species with much smaller $\eta_{R,e}/\eta_{R,a}$ than predicted are *Lolium perenne*, which distributed much less nitrogen to leaves in elevated
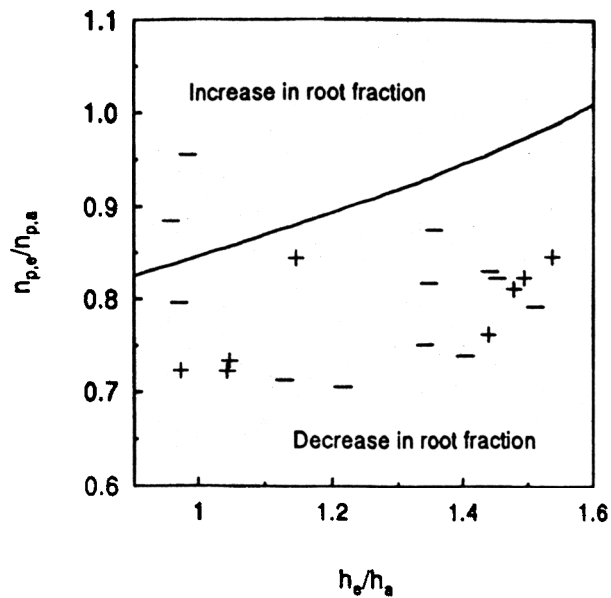
Figure 3. Predicted zones of increased and decreased root fraction in elevated $[CO_2]_a$, based on the regulatory paradigm of functional balance between roots and shoots. The root fraction should increase when growth at elevated $[CO_2]_a$ leads to changes in plant nitrogen concentration ($n_{p,e}/n_{p,a}$) and leaf mass per unit area (h_e/h_a) being above the line. Symbols represent data from the literature: + for increased root fraction in elevated $[CO_2]_a$ and - for decreased root fraction.
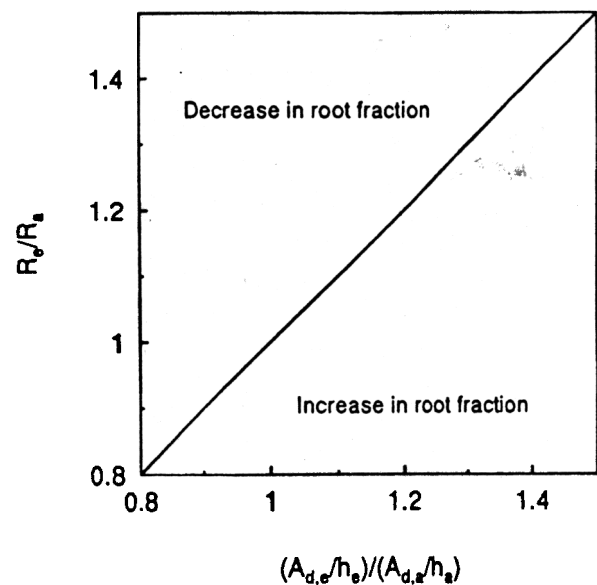
Figure 4. Predicted zones of increased and decreased root fraction for plants grown in elevated $[CO_2]_a$, based on the regulatory paradigm of photosynthesis:growth balance. The root fraction should increase when growth at elevated $[CO_2]_a$ leads to responses of photosynthesis per unit shoot mass $[(A_{d,e}/h_e)/(A_{d,a}/h_a)]$ that are larger than changes in relative growth rate (R_e/R_a).
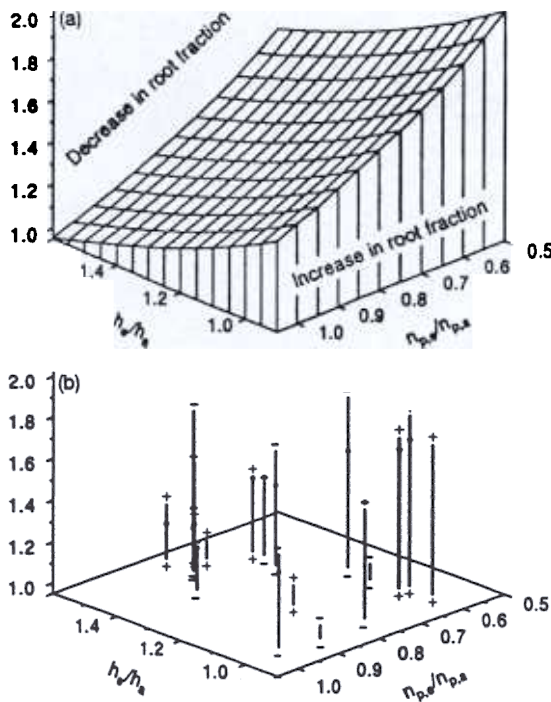
Figure 5. The responses of root fraction to elevated $[CO_2]_a$ as determined from the responses of plant nitrogen concentration $(n_{p,e}/n_{p,a})$, leaf mass per unit area (h_e/h_a), and nitrogen productivity (α_e/α_a). (a) The predicted zero-response surface of the root fraction to elevated $[CO_2]_a$, where photosynthesis and growth are balanced without any changes in root fraction. The root fraction should decrease when growth at elevated $[CO_2]_a$ leads to changes in $n_{p,e}/n_{p,a}$, h_e/h_a and α_e/α_a such that these parameters fall above the surface. (b) Observed data from the literature. Dots in the data lines indicate the cross-points with the zero-response surface.

$[CO_2]_a$ (Ryle *et al.* 1992b), and *Trifolium repens*, a nitrogen-fixing species that responded to elevated $[CO_2]_a$ with large increases in nitrogen uptake per unit root mass (Ryle *et al.* 1992a).

Plant responses to elevated $[CO_2]_a$ tend to maintain a balance between photosynthesis and growth, but species differ in the distribution of the adjustments among various components, including η_R. In *Brassica oleracea*, photosynthetic capacity in elevated $[CO_2]_a$ (Sage *et al.* 1989) was depressed to such an extent that photosynthesis:growth balance could be maintained without adjustments in biomass allocation. In *Triticum aestivum* (Hocking & Meyer 1991a), a 55% increase in carbon assimilation in elevated $[CO_2]_a$ was compensated by a 37% decrease in n_p, a 22% increase in h, and an 85% increase in α with virtually no change in η_R. For *Abutilon theophrasti*, h and n_p changed little in elevated $[CO_2]_a$ but α increased by 48% (Coleman & Bazzaz 1992). In this case, enhanced shoot function in elevated $[CO_2]_a$ was more than compensated by increased α (or decreased nitrogen demand) and η_R decreased to balance photosynthesis and growth. In contrast, for *Eucalyptus cypellocarpa*

with a $1\cdot2$ mol m^{-3} NO_3 nitrogen treatment, h increased by 48% and n_p decreased by 23% in elevated $[CO_2]_a$, but α increased by only 11% (Wong *et al.* 1992). Although enhanced shoot function in elevated $[CO_2]_a$ was partially diminished by increased h, total nitrogen demand still increased, leading to increased η_R. For the nitrogen-fixing species *Trifolium repens*, none of n_p, h, and α changed much in elevated $[CO_2]_a$ (Ryle *et al.* 1992a), and enhanced shoot function was balanced by increased nitrogen uptake per unit of root mass. For *Lolium perenne*, much less nitrogen was distributed to leaves in elevated $[CO_2]_a$ (Ryle *et al.* 1992b), reducing the leaf function more than the functions of other parts of the plant.

Conceptual basis of the two root fraction models

The two models characterize two fundamentally different concepts concerning factors that might control the response of root fraction to elevated $[CO_2]_a$. The photosynthesis:growth model builds from the postulate that photosynthesis and growth are mechanistically linked, whereas the functional balance model is based on a linkage between allocation and physiological activity. The better fit of the observations to the photosynthesis:growth model does not invalidate the concept of functional balance, but it does highlight the importance of including relative growth rate in the assessment of plant responses to elevated $[CO_2]_a$.

The two formulations lead to both similar and contrasting predictions. Both predict that η_R should increase in response to increases in A_d/h. The two formulations, however, predict opposite effects of decreased n_p on η_R. The functional balance formulation (Eqn 5) predicts that decreased n_p should lead to decreased η_R, whereas the formulation based on photosynthesis:growth balance (Eqn 9) predicts the opposite. With the functional balance concept, whole-plant nitrogen demand is reduced when n_p decreases. As a consequence, the root fraction (η_R) should decrease to meet the reduced demand for nitrogen. In the photosynthesis:growth model, however, decreases in n_p lead to decreased R (Eqn 7) and increased η_R (Eqn 9) as long as α is fixed. However, α is not fixed in nature. Elevated $[CO_2]_a$ almost always leads to increased α and decreased n_p (Table 1). Without any change in growth, decreases in n_p caused by increased availability of carbohydrate should be completely compensated by increases in α. Growth stimulation in elevated $[CO_2]_a$ should appear as overcompensation, leading to an increase in the product n_p × α. One primary difference between the formulations based on photosynthesis:growth and functional balance is that only the former incorporates the interactive influences of n_p and α on η_R.

The two formulations are based on fundamentally different conceptual models. The photosynthesis:growth balance model represents a combination of two potentially independent approaches to calculating R, whereas the functional balance model is built on a single hypothesis that links function and allocation. The photosynthesis:growth model essentially postulates that R can be set by
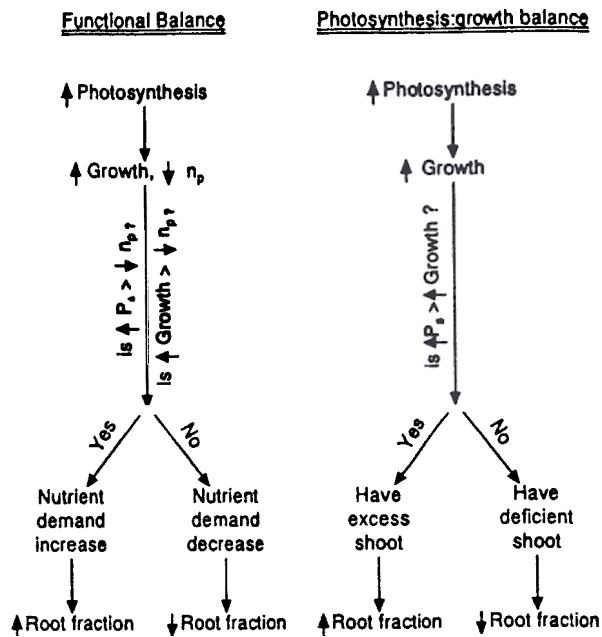
Figure 6. Schematic diagram illustrating the two kinds of regulatory paradigms that could lead to varying responses of root fraction to elevated $[CO_2]_a$.

either photosynthesis or nitrogen content and nitrogen productivity. In this model, any mismatch between the two is corrected by changes in shoot and root fractions. When elevated $[CO_2]_a$ leads to a growth increase that is smaller than the increase in photosynthesis, then photosynthate is produced in excess of the needs for growth and root fraction increases (Fig. 6).

With the functional balance model, the critical relationship is not between photosynthesis and growth but between the supply of photosynthate and the supply of nitrogen. When an increase in photosynthate supply in elevated $[CO_2]_a$ is identical in magnitude to the proportional decrease in nitrogen concentration, then nitrogen supply matches photosynthate supply, and the root fraction is stable (Fig. 6). The root fraction should increase whenever the $[CO_2]_a$ response of photosynthesis is larger than the response of nitrogen concentration, implying increased nitrogen demands. The poor correspondence between the prediction based on functional balance and the data could be a result of several factors. Firstly, changes in the ratio of photosynthesis to growth, which may result from changes in respiration, exudation or tissue turnover, could alter the link between photosynthesis and shoot activity. Secondly, deviation from a linear relationship between A_d and n_p could alter the predictions. Thirdly, changes in nitrogen uptake per unit of root mass, assumed to be negligible in this analysis, are potentially important.

Overall, the better fit of the observations to predictions based on photosynthesis:growth balance than to predictions based on functional balance implies that the former is

more important in regulating biomass allocation under elevated $[CO_2]_a$. This evidence argues for increased focus in carbon partitioning studies on a paradigm based on relative responses of growth and photosynthesis to environmental forcing.

In summary, carbon and nitrogen relationships are altered at elevated $[CO_2]_a$ so that carbohydrate becomes relatively abundant and nitrogen becomes relatively scarce. As a result, specific leaf (n_m) and plant (n_p) nitrogen concentrations decreased in all the studies we examined. Leaf mass per unit area (h) and plant nitrogen productivity (α) increased in most studies. The responses of photosynthesis to elevated $[CO_2]_a$ were predicted well by the relative changes in n_m and h. When elevated $[CO_2]_a$ leads to increases in h that are larger than the decreases in n_m, such that nitrogen concentration per unit of leaf area increases, predicted photosynthesis is upregulated. Otherwise, predicted photosynthesis is downregulated or, if the decrease in n_m is much larger than the increase in h, depressed. The predicted root fraction increases whenever photosynthesis per unit of leaf mass (A_d/h) increases more than R in elevated $[CO_2]_a$. Otherwise, the predicted root fraction decreases.

ACKNOWLEDGMENTS

REFERENCES

Ågren G.I. (1985) Theory for growth of plants derived from the nitrogen productivity concept. *Physiologia Plantarum* 64, 17–28.

Ågren G.I. & Ingestad T. (1987) Root:shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant, Cell and Environment* 10, 579–586.

Brouwer R. (1962) Nutritive influences on the distribution of dry matter in the plant. *Netherlands Journal of Agricultural Sciences* 10, 399–408.

Brown K. & Higginbotham K.O. (1986) Effects of carbon dioxide enrichment and nitrogen supply on growth and boreal tree seedlings. *Tree physiology* 2, 223–232.

Bunce J.A. (1993) Effects of doubled atmospheric carbon dioxide concentration on responses of assimilation and conductance to humidity. *Plant, Cell and Environment* 16, 189–197.

Campbell W.J., Allen L.H. Jr & Bowes G. (1988) Effects of CO_2 concentration on Rubisco activity, amount and photosynthesis in soybean leaves. *Plant Physiology* 88, 1310–1316.

Chapin F.S. III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11, 233–260.

Chapin F.S. III (1991) Integrated responses of plants to stress. *BioScience* 41, 29–36.

Chu C.C., Coleman J.S. & Mooney H.A. (1992) Controls of biomass partitioning between roots and shoots: atmospheric CO_2 enrichment and the acquisition and allocation of carbon and nitrogen in wild radish. *Oecologia* 89, 580–587.

Coleman J.S. & Bazzaz F.A. (1992) Effects of CO_2 and tempera-

ture on growth and resource use of co-occurring C$_3$ and C$_4$ annuals. *Ecology* **73**, 1244–1259.

Coleman J.S., McConnaughay K.D.M. & Bazzaz F.A. (1993) Elevated CO$_2$ and plant nitrogen-use: Is reduced tissue nitrogen concentration size-dependent? *Oecologia* **93**, 195–200.

Conroy J.P. (1992) Influence of elevated atmospheric CO$_2$ concentrations on plant nutrition. *Australian Journal of Botany* **40**, 445–456.

Conroy J.P., Milham P.J. & Barlow E.W.R. (1992) Effect of nitrogen and phosphorus availability on the growth response of *Eucalyptus grandis* to high CO$_2$. *Plant, Cell and Environment* **15**, 843–847.

Curtis P.S., Drake B.G. & Whigham D.F. (1989) Nitrogen and carbon dynamics in C$_3$ and C$_4$ estuarine marsh plants grown under elevated CO$_2$ in situ. *Oecologia* **78**, 297–301.

Davidson R.L. (1969) Effect of root:leaf temperature differentials on root:shoot ratios in some pasture grasses and clover. *Annals of Botany* **33**, 561–569.

Delucia E.H., Sasek T.W. & Strain B.R. (1985) Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. *Photosynthesis Research* **7**, 175–184.

Eamus D. & Jarvis P.G. (1989) The direct effects of increase in the global atmospheric CO$_2$ concentration on natural and commercial temperate trees and forests. *Advances in Ecological Research* **19**, 1–55.

Farquhar G.D., von Caemmerer S. & Berry J.A. (1980) A biochemical model of photosynthetic CO$_2$ assimilation in leaves of C$_3$ species. *Planta* **149**, 79–90.

Farrar J.F. & Williams M.L. (1991) The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. *Plant, Cell and Environment* **14**, 819–830.

Field C.B. (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* **56**, 341–347.

Field C.B., Chapin F.S. III, Matson P.A. & Mooney H.A. (1992) Responses of terrestrial ecosystems to the changing atmosphere: A resource-based approach. *Annual Review of Ecology and Systematics* **23**, 201–235.

Harley P.C., Thomas R.B., Reynolds J.F. & Strain B.R. (1992) Modelling photosynthesis of cotton grown in elevated CO$_2$. *Plant, Cell and Environment* **15**, 271–282.

Hilbert D.W., Larigauderie A. & Reynolds J.F. (1991) The influence of carbon dioxide and daily photon-flux density on optimal leaf nitrogen concentration and root:shoot ratio. *Annals of Botany* **68**, 365–376.

Hirose T. & Werger M.J.A. (1987) Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* **72**, 520–526.

Hocking P.J. & Meyer C.P. (1991a) Effects of CO$_2$ enrichment and nitrogen stress on growth, and partitioning of dry matter and nitrogen in wheat and maize. *Australian Journal of Plant Physiology* **18**, 339–356.

Hocking P.J. & Meyer C.P. (1991b) Carbon dioxide enrichment decreases critical nitrate and nitrogen concentrations in wheat. *Journal of Plant Nutrition* **14**, 571–584.

Johnson R.H. & Lincoln D.E. (1991) Sagebrush carbon allocation patterns and grasshopper nutrition: the influence of CO$_2$ enrichment and soil mineral limitation. *Oecologia* **87**, 127–134.

Lambers H. & Poorter H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* **23**, 187–261.

Luo Y. & Nobel P.S. (1993) Growth characteristics of *Opuntia ficus-indica* as affected by light, water, and CO$_2$. *Physiologia Plantarum* **87**, 467–474.

Miao S.L., Wayne P.M. & Bazzaz F.A. (1992) Elevated CO$_2$ differentially alters the responses of coocurring birch and maple seedlings to a moisture gradient. *Oecologia* **90**, 300–304.

Mooney H.A. & Chiariello N.R. (1984) The study of plant function – the plant as a balanced system. In *Perspectives on plant population ecology* (eds R. Dirzo and J. Sarukhan), pp. 305–323. Sinauer Associates Inc., Sunderland, MA.

Norby R.J., Gunderson C.A., Wullschleger S.D., O'Neill E.G. & McCracken M.K. (1992) Productivity and compensatory response of yellow-poplar trees in elevated CO$_2$. *Nature* **357**, 322–324.

Norby R.J., O'Neill E.G. & Luxmoore R.J. (1986) Effects of atmospheric CO$_2$ enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. *Plant Physiology* **82**, 83–89.

Pettersson R. & McDonald A.J.S. (1992) Effects of elevated carbon dioxide concentration on photosynthesis and growth of small birch plants (*Betula pendula* Roth.) at optimal nutrition. *Plant, Cell and Environment* **15**, 911–919.

Radoglou K.M., Aphalo P. & Jarvis P.G. (1992) Response of photosynthesis, stomatal conductance and water use efficiency to elevated CO$_2$ and nutrient supply in acclimated seedlings of *Phaseolus vulgaris* L. *Annals of Botany* **70**, 257–264.

Reynolds J.F. & Thornley J.H.M. (1982) A shoot:root partitioning model. *Annals of Botany* **49**, 585–597.

Rochefort L. & Bazzaz F.A. (1992) Growth response to elevated CO$_2$ in seedlings of four co-occurring birch species. *Canadian Journal of Forest Research* **22**, 1583–1587.

Ryle G.J.A., Powell C.E. & Davidson I.A. (1992a) Growth of white clover, dependent on N$_2$ fixation, in elevated CO$_2$ and temperature. *Annals of Botany* **70**, 221–228.

Ryle G.J.A., Powell C.E. & Tewson V. (1992b) Effect of elevated CO$_2$ on the photosynthesis, respiration, and growth of perennial ryegrass. *Journal of Experimental Botany* **43**, 811–818.

Ryle G.J.A., Woledge J., Tewson V. & Powell C.E. (1992c) Influence of elevated CO$_2$ and temperature on the photosynthesis and respiration of white clover dependent on N$_2$ fixation. *Annals of Botany* **70**, 213–220.

Sage R.F. (1990) A model describing the regulation of ribulose-1,5-bisphosphate carboxylase, electron transport and triosephosphate use in response to light intensity and CO$_2$ in C$_3$ plants. *Plant Physiology* **94**, 1728–1734.

Sage R.F., Sharkey T.D. & Seemann J.R. (1989) Acclimation of photosynthesis to elevated CO$_2$ in five C$_3$ species. *Plant Physiology* **89**, 590–596.

Sharkey T.D. (1985) Photosynthesis in intact leaves of C$_3$ plants: physics, physiology, and rate limitations. *Botanical Review* **51**, 53–105.

Silvola J. & Ahlholm U. (1992) Photosynthesis in willows (*Salix* x *dasyclados*) grown at different CO$_2$ concentrations and fertilization levels. *Oecologia* **91**, 208–213.

Stitt M. (1991) Rising CO$_2$ levels and their potential significance for carbon flow in photosynthetic cell. *Plant, Cell and Environment* **14**, 741–762.

Teramura A.H., Sullivan, J.H. & Ziska L.H. (1990) Interaction of elevated ultraviolet-B radiation and CO$_2$ on productivity and photosynthetic characteristics in wheat, rice and soybean. *Plant Physiology* **94**, 470–475.

Thomas R.B., Richter D.D., Ye H., Heine P.R. & Strain B.R. (1991) Nitrogen dynamics and growth of seedlings of an N-fixing tree (*Gliricidia sepium* (Jacq.) Walp.) exposed to elevated atmospheric carbon dioxide. *Oecologia* **88**, 415–421.

Vu J.C.V., Allen L.H. Jr & Bowes G. (1989) Leaf ultrastructure, carbohydrates and protein of soybeans grown under CO$_2$ enrichment. *Environmental and Experimental Botany* **29**, 141–147.

Wong S.C. (1990) Elevated atmospheric partial pressure of CO$_2$

and plant growth. II. Non-structural carbohydrate content in cotton plants and its effect on growth parameters. *Photosynthesis Research* **23**, 171–180.

Wong S.C., Kriedemann P.E. & Farquhar G.D. (1992) $CO_2 \times$ nitrogen interaction on seedling growth of four species of eucalypt. *Australian Journal of Botany* **40**, 457–472.

Woodin S., Graham B., Killick A., Skiba U. & Cresser M. (1992) Nutrient limitation of the long term response of heather [*Calluna vulgaris* (L.) Hull] to CO_2 enrichment. *New Phytologist* **122**, 635–642.

APPENDIX 1: THE PHOTOSYNTHESIS MODEL AND PARAMETER VALUES

The model

$$A = \min \{A_1, A_2, A_3\} \tag{A1}$$

$$A_1 = V_{cmax} \frac{C_i - \Gamma}{C_i + k_c(1 + O/k_o)} - \rho \tag{A2}$$

$$A_2 = J \frac{C_i - \Gamma}{4.5 C_i + 10.5 \Gamma} - \rho \tag{A3}$$

$$J = \frac{J_{max} I}{I + 2.1 J_{max}} \tag{A4}$$

$$A_3 = 3 TPU - \rho \tag{A5}$$

$$V_{cmax} = k_1 n_a + k_2 \tag{A6}$$

$$J_{max} = k_3 n_a + k_4 \tag{A7}$$

$$TPU = k_5 n_a + k_6 \tag{A8}$$

$$\rho = k_7 n_a + k_8 \tag{A9}$$

$$C_i = C_a - A/g_{s, co_2} \tag{A10}$$

$$g_{s, co_2} = k_9 - k_{10} C_a \tag{A11}$$

Parameter values

I = $1000 \mu mol\ m^{-2}\ s^{-1}$
Γ = $31.0 \mu mol\ mol^{-1}$
K = $k_c(1 + O/k_o) = 827$
k_1 = 35.7
k_2 = 12.4
k_3 = 92.55
k_4 = 13.85
k_5 = 5.13
k_6 = 0.63
k_7 = 0.775
k_8 = -0.238
k_9 = $0.324*$
k_{10} = 1.64×10^{-4}

$*k_9$ and k_{10} were derived from data for *Phaseolus vulgaris* measured at a temperature of 24–25 °C, a vapour pressure deficit in the leaf chamber of approximately 1.0 KPa, and an air circulation velocity of approximately 1 m s^{-1} (Radoglou *et al.* 1992).

APPENDIX 2. SYMBOLS, UNITS AND DEFINITIONS

Symbol	Unit	Definition
A	$\mu mol\ m^{-2}\ s^{-1}$	Photosynthetic rate
A_1	$\mu mol\ m^{-2}\ s^{-1}$	Photosynthetic rate with Rubisco limited
A_2	$\mu mol\ m^{-2}\ s^{-1}$	Photosynthetic rate with RuBP limited
A_3	$\mu mol\ m^{-2}\ s^-$	Photosynthetic rate with phosphate limited
$A_d^{\bullet}$	$g\ m^{-2}\ d^{-1}$	Daily net assimilation rate
A_{max}	$\mu mol\ m^{-2}\ s^{-1}$	Photosynthetic capacity
C_a	$\mu mol\ mol^{-1}$	Ambient CO_2 concentration
C_i	$\mu mol\ mol^{-1}$	Intercellular CO_2 concentration
$[CO_2]_a$	$\mu mol\ mol^{-1}$	Atmospheric CO_2 concentration
g_{s, co_2}	$\mu mol\ m^{-2}\ s^{-1}$	Stomatal conductance
$h^{\bullet}$	$g\ m^{-2}$	Leaf mass per unit area
I	$\mu mol\ m^{-2}\ s^{-1}$	Instantaneous photon flux density
I_0	$\mu mol\ m^{-2}\ s^{-1}$	Maximum photon flux density
J	$\mu mol\ m^{-2}\ s^{-1}$	Rate of electron transport
J_{max}	$\mu mol\ m^{-2}\ s^{-1}$	Light-saturated rate of electron transport
$k_1 - k_{10}$		Coefficients
k_c	$\mu mol\ mol^{-1}$	Michaelis–Menton constants for CO_2
k_o	$\mu mol\ mol^{-1}$	Michaelis–Menton constants for oxygen
n_a	$g\ m^{-2}$	Area-based leaf nitrogen concentration
n_m	$g\ g^{-1}$	Mass-based leaf nitrogen concentration
$n_p^{\bullet}$	$g\ g^{-1}$	Plant nitrogen concentration
N_u	$g\ g^{-1}\ d^{-1}$	Nutrient uptake rate
O	$mol\ mol^{-1}$	Partial pressure of oxygen
$R^{\bullet}$	$g\ g^{-1}\ d^{-1}$	Relative growth rate
t	h	Time
TPU	$\mu mol\ m^{-2}\ s^{-1}$	Phosphate release rate in triose phosphate utilization
V_{cmax}	$\mu mol\ m^{-2}\ s^{-1}$	Maximum RuBP carboxylase activity
$\alpha^{\bullet}$	$g\ g^{-1}\ d^{-1}$	Plant nitrogen productivity
η_L	$g\ g^{-1}$	Leaf fraction
η_R	$g\ g^{-1}$	Root fraction
η_S	$g\ g^{-1}$	Shoot fraction
Γ	$\mu mol\ mol^{-1}$	CO_2 compensation point without dark respiration
ρ	$\mu mol\ m^{-2}\ s^{-1}$	Dark respiration
σ_R	$g\ g^{-1}\ d^{-1}$	Root activity
σ_S	$g\ g^{-1}\ d^{-1}$	Shoot activity

$^{\bullet}$Subscripts a and e on these variables in the text refer to plants grown at ambient ($350 \mu mol\ mol^{-1}$) and elevated ($700 \mu mol\ mol^{-1}$) $[CO_2]_a$, respectively.