

Optimal nitrogen allocation controls tree responses to elevated CO₂

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Summary

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- Despite the abundance of experimental data, understanding of forest responses to elevated CO₂ is limited. Here I show that a key to previously unexplained production and leaf area responses lies in the interplay between whole-plant nitrogen (N) allocation and leaf photosynthesis.
- A simple tree growth model, controlled by net growth maximization through optimization of leaf area index (LAI) and plant N, is used to analyse CO₂ responses in both young, expanding and closed, steady-state canopies. The responses are sensitive to only two independent parameters, the photosynthetic capacity per leaf N (*a*) and the fine-root N : leaf N ratio.
- The model explains observed CO₂ responses of photosynthesis, production and LAI in four forest free air CO₂ enrichment (FACE) experiments. Insensitivity of LAI except at low LAI, increase in light-use efficiency, and photosynthetic down-regulation (as a result of reduced leaf N per area) at elevated CO₂ are all explained through the combined effects on *a* and leaf quantum efficiency.
- The model bridges the gap between the understanding of leaf-level and plant-level responses and provides a transparent framework for interpreting and linking structural (LAI) and functional (net primary production (NPP) : gross primary production (GPP) ratio, light-use efficiency, photosynthetic down-regulation) responses to elevated CO₂.

Key words: canopy nitrogen (N), elevated CO₂, forest, leaf area index (LAI), light-use efficiency, optimization, photosynthetic capacity, plant theory.

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Introduction

Modelling of forest responses to elevated CO₂ and environmental factors is a cornerstone of climate change research. In many models, light-use efficiency (ϵ_{GPP}) in combination with estimates of light absorption, often obtained from remote sensing methods, is used to estimate gross primary production (GPP). A maximum potential ϵ_{GPP} is reduced in response to environmental constraints and combined with a net primary production (NPP) : GPP ratio or a respiration function to obtain NPP. However, the assumptions and values used for these factors vary substantially. For the same forest type, maximum ϵ_{GPP} varies threefold between models (Xiao *et al.*, 2005), while others argue

that ϵ_{GPP} is conservative (Goetz & Prince, 1999). The common assumption that the NPP : GPP ratio is invariable (Waring *et al.*, 1998; Medlyn & Dewar, 1999) has also been challenged (Goetz & Prince, 1999). In summary, a general consensus on the appropriate assumptions for forest NPP modelling is lacking, which also carries over to the modelling of elevated CO₂ effects.

Experimental evidence of the effects of elevated CO₂ from free air CO₂ enrichment (FACE) and other investigations are accumulating. When all studies are compared, the range of observed responses in productivity and biomass is large. This large range is mostly the result of differences in the age of the studied stands; that is, if it is a young forest still increasing resource acquisition or if it has reached steady state in terms

of fine roots and LAI (Korner, 2006). For closed-canopy forests, NPP responses are conservative across species and sites (on average 23% higher at 550 than at 376 ppm CO₂) (Norby *et al.*, 2005). Nutrient additions strongly enhance the growth response to elevated CO₂ (Oren *et al.*, 2001; Reich *et al.*, 2006a). Light-use efficiency (ϵ_{NPP}) is increased while leaf area index (LAI) is usually little affected (Norby *et al.*, 2003), although at low LAI the CO₂ effect on LAI can be as large or larger than the effect on ϵ_{NPP} (Norby *et al.*, 2005). For the allocation to wood relative to fast turnover tissues (leaves and fine roots), both positive (Hamilton *et al.*, 2002; DeLucia *et al.*, 2005) and negative effects (Norby *et al.*, 2004) have been observed. Explanations for the above responses have been suggested mostly in qualitative terms. Nutrient limitation constrains the potential growth response, particularly for woody biomass increment (Korner, 2006), LAI is conservative because the gain in absorbed PAR per additional unit of LAI is small at higher LAI. To my knowledge, an explanation for the conservative NPP responses among closed-canopy forests (Norby *et al.*, 2005) is lacking. However, the question addressed here is as follows: can these different CO₂ responses be integrated and explained in a common framework?

In contrast to the variable responses of whole-plant properties to CO₂, the primary functional responses of leaves appear to be limited to increased photosynthesis and reduced stomatal conductance (Gifford, 2004). Observed down-regulation of photosynthetic capacity at elevated CO₂ can be attributed to reduced leaf nitrogen (N) (Ellsworth *et al.*, 2004), while photosynthetic capacity per leaf N per area (a) and quantum efficiency (initial slope of leaf photosynthesis vs PAR, ϕ) are consistently increased by elevated CO₂. This consistency suggest changes in a and ϕ as primary effects for up-scaling of elevated CO₂ responses. To scale up these leaf responses to the whole-plant level, they must be put into a framework that includes the effects of other limiting resources, such as nutrients and water. For water, however, the main response is stomatal regulation, which in this framework is included indirectly through a .

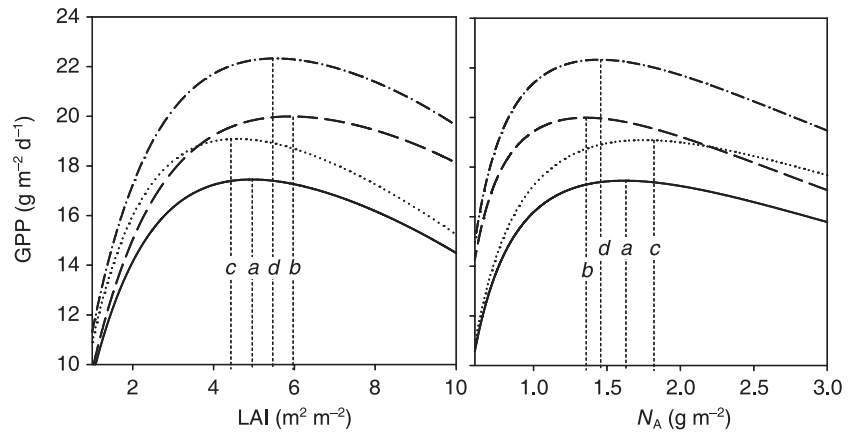
Nutrients, particularly N, commonly limit plant growth and its response to elevated CO₂ (Reich *et al.*, 2006a). The fact that N is very often a limiting and depletable resource for plant growth suggests that the plants should strive to optimize their use of N. Furthermore, for exponentially growing plants, growth rate is linearly related to plant N concentration and N supply (Ingestad, 1979), which is a strong indication of the close relation between plant N and plant growth. Because of self-shading, the linearity does not hold as the plants get larger, but this is no reason to question the link between N and plant functioning. On the contrary, because of its key role in the metabolic machinery, not only photosynthesis but also respiration scales with N (Vose & Ryan, 2002; Reich *et al.*, 2006b). Based on this dual role of plant N, it has been hypothesized that plant canopy N content is determined by optimizing NPP through a tradeoff between N-induced photosynthesis and whole-plant respiration (Dewar, 1996).

Here I extend Dewar's (1996) theory of optimal canopy N by including effects of shifts in foliage : root : sapwood ratios, to capture effects of changes in fine-root allocation in response to nutrient availability as well as the effect of sapwood accumulation. In this framework, leaf-level effects of CO₂ (on a and ϕ) are scaled up to the whole-tree level. The hypothesis is that this optimization at the whole-plant level can elucidate less well understood forest responses to elevated CO₂, such as the variation in NPP response among sites, the small responses in LAI (and absorbed PAR) relative to ϵ in most but not all cases, and the effects on wood : litter production ratio. The model should also provide insights into why and under what circumstances the NPP : GPP ratio is conserved in response to CO₂ and nutrient availability. Observations from four forest FACE experiments are used to evaluate the hypothesized model.

Theory and model description

Evolutionary principles state that optimization of fitness, determined by reproductive success, ultimately controls plant behaviour. But since fitness is difficult to measure and model, for tree modelling some measure of production is usually used as a substitute, for example NPP (Dewar, 1996) or canopy carbon export (Dewar *et al.*, 1998). However, here I assume that net biomass increment + reproductive production is more closely linked to fitness than either NPP or canopy carbon export. Looking at any instant in time, it seems logical that a plant maximizes its NPP, which is allocated according to the current demands of different organs. But in optimizing instantaneous NPP we are not accounting for the development over time, that is, that the amount and allocation of current NPP will affect NPP and survival the next year. Over its lifetime, growth and survival of a tree are determined by competitiveness and ability to acquire resources, for example, avoiding being overtopped by neighbouring trees, which is directly related to size (and often height). As size is equal to integrated biomass increment over time, size and hence fitness are likely to be maximized if biomass increment (net growth) is maximized at each moment in time. Furthermore, maximizing biomass increment at each instant in time can be seen as an approximate way of maximizing NPP over the lifetime, as NPP (per plant) generally increases with size. In addition to biomass increment, by definition, reproductive production should contribute to fitness. Therefore, net growth + reproductive production, that is, NPP less annual turnover (and any other carbon expenses) of leaves and fine roots, is the chosen target for optimization and is hereafter denoted as G . Turnover of woody structures, such as branches, are not deducted from G because of their long life span relative to leaves and fine roots. To obtain a framework for optimization of G , G must be formulated in terms of its components: canopy photosynthesis (gross primary production, GPP), respiration (R) and litter turnover (T).

Fig. 1 Gross primary production (GPP) as a function of leaf area index (LAI) and N_A (= canopy nitrogen/LAI) for a fixed canopy nitrogen (N_c). Solid line with optimum a , baseline values of photosynthetic capacity per leaf N (a) and leaf quantum efficiency ϕ . Dashed line with optimum b , 50% increase in a . Dotted line with optimum c , 17% increase in optimum ϕ . Dashed-dotted line with optimum d , combined 50 and 17% increase in a and ϕ , respectively (representative of an elevated CO_2 effect). Dotted vertical lines denote the optimal LAI and N_A values. Note that ϕ controls the initial slope of GPP while a controls GPP at higher LAI (Eqn 1a), causing the different shifts in the optimum. $N_c = 7.8 \text{ g m}^{-2}$. Parameter values for Oak Ridge (Supplementary Material, Table S1).



Upscaling from leaf to canopy photosynthesis

Leaf photosynthesis is described by the nonrectangular hyperbola model, which predicts leaf responses much more accurately than the rectangular hyperbola model (Thornley, 2002). In this model, light-saturated photosynthesis (A_{\max}) is a linear function of N content per unit area (N_A) and minimum N_A per leaf area (N_{\min}), $A_{\max} = a(N - N_{\min})$. The slope of the photosynthetic capacity vs leaf N (a) is central to the optimal plant behaviour and is related to the allocation of N to structural and photosynthetic uses in the leaf and to stomatal conductance (Hikosaka, 2004). a is increased by elevated CO_2 and reduced by water deficit (through stomatal regulation).

Using Beer's law of light extinction and optimal distribution of canopy N (N_c), as described in Franklin & Agren (2002), the total daily canopy photosynthesis (GPP, see Eqn 1a) can be derived as a function of N_c and absorbed PAR (I_a) through integration of leaf photosynthesis over the canopy (Supplementary Material, Eqns S1, S2). More complex canopy models, for example, differentiating sun and shade leaves, would probably be more accurate in absolute terms (dePury & Farquhar, 1997; Thornley, 2002). However, for the purpose of this paper, that is, to elucidate relative differences between CO_2 treatments, the increased complexity would mainly serve to obscure the results.

$$GPP = \frac{b}{2\theta}(\phi I_a + a(N_c - N_{\min}L)) - \frac{b}{2\theta} \sqrt{(\phi I_a + a(N_c - N_{\min}L))^2 - 4\phi I_a a(N_c - N_{\min}L)\theta}$$

Eqn 1a

(b , day length; ϕ , quantum efficiency; θ , a curvature parameter of leaf light response (parameter values and units are given in supplementary material Table S1)). I_a is related to radiation above the canopy (I_0), LAI (L) and the light extinction coefficient (k) according to:

$$I_a = I_0(1 - e^{-kL})$$

Eqn 1b

LAI (L) is determined by maximizing GPP (Eqn 1a) for a fixed N_c . Increasing LAI at small LAI increases GPP through increased light absorption. As LAI gets larger, light absorption saturates while the proportion of N that is nonphotosynthetic increases linearly with LAI (through the term $N_{\min}L$ in Eqn 1a), reducing GPP. Thus, for a fixed N_c , GPP has a maximum with respect to LAI (Fig. 1). This optimal LAI, for simplicity hereafter denoted just LAI or L , is approximately linearly related to N_c (Fig. 2), which means that mean canopy leaf N per area ($N_A = N_c/LAI$) is conservative during canopy development and among mature stands with differing N_c . However, N_A increases with photosynthetic capacity per N (a) and decreases with quantum efficiency (ϕ) (Fig. 1). These shifts in N_A happen because, for a fixed N_c , ϕ increases the initial slope of GPP vs LAI, while a increases GPP only at higher LAI (Eqn 1, Fig. 1). A combined increase in a and ϕ , where the increase in ϕ is one-third of the increase in a , as expected at elevated CO_2 (Cannell & Thornley, 1998), decreases N_A slightly for all N_c (Fig. 2). As GPP and LAI have been derived as functions of N_c , it is necessary to evaluate optimal N_c before they are fully defined.

Respiration and turnover

Respiration is modelled using the maintenance + growth respiration approach. Growth respiration (R_g) is a fraction of net assimilation, $R_g = (1 - \gamma)(GPP - R_m)$, where γ is the biosynthetic conversion efficiency, which is conservative; $\gamma = 0.7$ for whole-plant, woody species (Choudhury, 2001). Maintenance respiration (R_m) is proportional to N content across all living tissues, that is, canopy, sapwood and roots (Vose & Ryan, 2002), which can be explained through respiratory costs of protein turnover (Dewar *et al.*, 1998). A factor $q_f > 1$ accounts for the fact that fine roots have a higher respiration per N than other tissues (Ryan *et al.*, 1996):

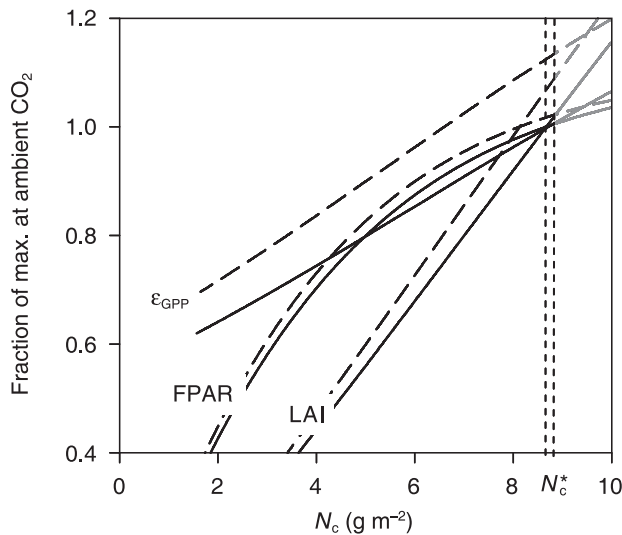


Fig. 2 Leaf area index (LAI), fraction light absorbed (FPAR) and light-use efficiency (ϵ_{GPP}) at variable canopy nitrogen (N_c). ϵ_{GPP} is more conservative than FPAR and LAI at changing N_c . ϵ_{GPP} is significantly increased by elevated CO_2 , while there is only a small increase in FPAR and LAI at a fixed N_c . Solid and dashed lines are for ambient and elevated CO_2 , respectively. The dotted vertical lines indicate optimal canopy N (N_c^*) for the ambient (leftmost line) and elevated CO_2 treatments.

$$R_m = r(1 + q_r f_r + f_s) N_c = r_w N_c \quad \text{Eqn 2a}$$

(r , basic respiration rate per unit nitrogen; f_s, f_r , ratios of N in sapwood and fine roots to N in canopy; r_w , whole-plant respiration per canopy nitrogen). Subscripts c, r and s , represent canopy, fine roots, and sapwood, respectively. The ratios f_s, f_r are restricted by the need for root and stem tissue to maintain the canopy (pipe theory; Shinozaki *et al.*, 1964), but changes in response to environmental and ontogenetic factors, such as soil nutrient availability (changes f_r) and tree height (changes f_s).

Turnover (T) is expressed as a function of N_c , mean residence times of tissues (t), and N : C ratios (n) of canopy and roots:

$$T = \left(\frac{1}{t_c n_c} + \frac{f_r}{t_r n_r} \right) N_c = l_w N_c \quad \text{Eqn 2b}$$

(l_w , whole-plant litter production (turnover) per N_c).

To simplify the following expressions, an aggregated variable (w) of respiration and turnover per N_c is defined to represent total carbon costs per canopy nitrogen:

$$w = y r_w + l_w \quad \text{Eqn 2c}$$

f_r and f_s are the main controls of w and are ultimately increased by root allocation in response to reduced soil N availability and increased mass of living wood, respectively. Compared to f_r and f_s , changes in the N : C ratios (n) and turnover times (t)

have a smaller impact since they only enter the turnover function (Eqn 2b) and not the respiration function (Eqn 2a). Furthermore, they tend to be inversely correlated, for example, increased leaf N : C ratio (n_c) is correlated with shorter life span (t_c) (Wright *et al.*, 2004). Nevertheless, no such relation is imposed here and effects of changes in n_c at elevated CO_2 were evaluated.

It should be noted that, although N_c and n_c both occur in the expression for turnover, because leaf mass per area is not fixed, they are mathematically independent. Thus the derivation of optimal N_c (see following section) would not be invalidated by a changing n_c .

Production and efficiency of expanding and steady-state canopies

For expanding canopies, the development of GPP, R_m and T as functions of canopy N (N_c) can be derived directly from Eqns 1a and 2a,b. Here LAI is optimized for each N_c , as described above. NPP and G are then calculated according to Eqn 3a. As the canopy expands, N_c eventually reaches an optimal value where G is maximized and where no further expansion occurs (Fig. 3), unless there is a change in parameters. Optimal N_c is thus determined by the optimal tradeoff between the N-based carbon gain (GPP) and carbon losses ($R_m + R_g + T$). The state reached after full canopy expansion is hereafter referred to as steady state, which also includes any subsequent shifts in canopy optimal size resulting from changes in parameters, such as increasing sapwood (f_s) with height. Because all the terms of G are functions of N_c , the steady-state N_c (Eqn 3b) is readily derived by maximizing G (Eqn 3a) with respect to N_c (Supplementary Material). This optimal state of the system represents acclimation over timescales not shorter than the response time of the slowest relevant response mechanism. For example, in response to a change in CO_2 concentration, it may take a growing season for the root : foliage ratio and N_c to reach a new equilibrium; therefore, modelled optimal growth rate represents a growing season average and not shorter-term fluctuations.

By inserting N_c^* in the expressions for GPP and R_m , the properties GPP*, NPP*, and G^* of the steady-state canopy are obtained (Eqns 3b–f, where * denotes the optimized steady-state canopy). NPP and G , but not GPP, follow different paths in relation to N_c during canopy expansion and at steady state (Fig. 3).

$$G = \text{NPP} - T = y(\text{GPP} - R_m) - T = y\text{GPP} - wN_c \quad \text{Eqn 3a}$$

$$N_c^* = \frac{I_a \phi}{a} \left(\sqrt{\frac{1 - \theta}{aby} - \theta} \left(\frac{aby}{w} - 2\theta \right) + 2\theta - 1 \right) + N_{\min} L = \frac{I_a \epsilon_{\text{sat}}}{a} + N_{\min} L \quad \text{Eqn 3b}$$

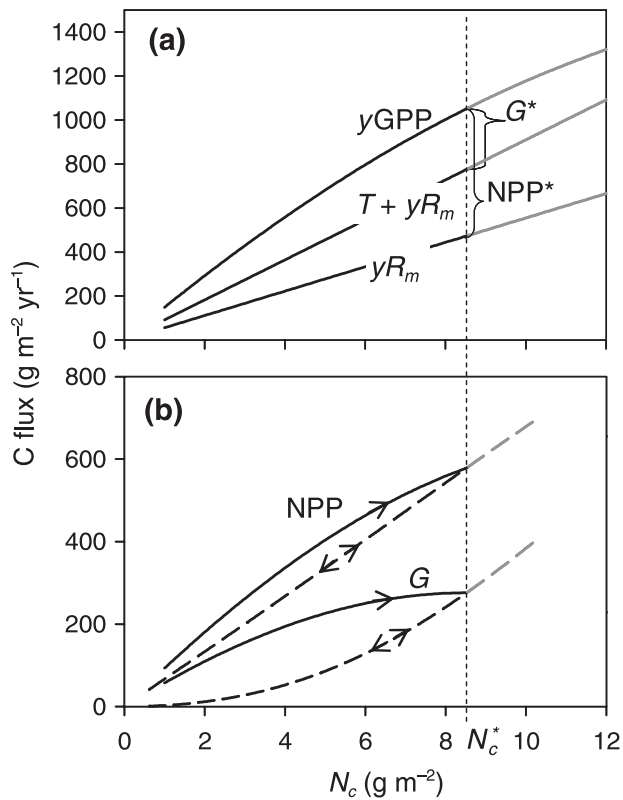


Fig. 3 Canopy expansion and optimal steady states. (a) For expanding canopies gross primary production (GPP), T (litter production) and R_m (maintenance respiration) are increasing with canopy nitrogen (N_c) up to N_c^* that maximizes net growth (G), where $yGPP$ and $T + yR_m$ are parallel (cf. Eqn 3a). (b) The paths of net primary production (NPP) and G of expanding canopies (solid lines) and steady-state canopies (dashed lines). For steady-state canopies, the curves of NPP and G are given by varying the slope of $T + yR_m$. This slope changes with age or soil fertility as a result of shifts in stem wood N: canopy N ratio (f_s) or root N: canopy N ratio (f_r). These changes in N partitioning move NPP* and G^* along the dashed lines; for example, increasing stem wood (f_s) with age causes a decrease.

($\epsilon_{sat} = a(N_c^* - N_{min}L)/I_a$, light-saturated photosynthetic light-use efficiency, that is, if all leaves operate at A_{max}).

$$GPP^* = hI_a \epsilon_{GPP} \quad \text{Eqn 3c}$$

where

$$\epsilon_{GPP} = \phi \left(1 - \frac{1 - \theta}{\sqrt{\frac{aby}{w} - \theta}} \right) \quad \text{Eqn 3d}$$

The light-use efficiency of GPP (ϵ_{GPP}) has an upper theoretical limit of ϕ ($2.73 \mu\text{g C J}^{-1}$, Wong *et al.*, 1979).

G^* and NPP^* are given by

$$G^* = hI_a \left(y\epsilon_{GPP} - \frac{w}{ab}\epsilon_{sat} \right) - N_{min}Lw = hI_a \epsilon_G - N_{min}Lw \quad \text{Eqn 3e}$$

$$NPP^* = G^* + N_c^* t_w \quad \text{Eqn 3f}$$

(ϵ_G , slope of the light-use efficiency of G).

GPP^* , NPP^* , G^* and N_c^* are all approximately linear functions of absorbed PAR where the light-use efficiencies (the slopes) are controlled by the leaf quantum efficiency (ϕ) and the ratio aby/w . The factors in this ratio thus strongly regulate the system; the numerator reflects responses in photosynthetic capacity (a) and day length (b) and the denominator, total carbon costs per canopy N (w), responds to the relative allocation to nonphotosynthetic parts, that is, roots (f_r) and sapwood (f_s). While GPP^* , NPP^* , G^* all monotonically increase with the ratio aby/w , the effect on N_c^* is more complex. N_c^* is increased by the ratio aby/w but at the same time it decreases with a (denominator in the first factor in Eqn 3b), which makes the N_c^* response to a small. An important consequence of this is that N_c^* is much less sensitive to changes in photosynthetic capacity (a) than to changes in root and sapwood allocation (through w). The response to a is also variable, that is, positive at small N_c^* and negative at larger N_c^* . As N_c^* occurs where the slopes of GPP and $yR_m + T$ vs N_c are parallel (cf. Fig. 4), the response of N_c^* to a is determined by the change in slope of GPP vs N_c in response to a ($= (\partial/\partial a) (\partial GPP/\partial N_c)$). This change of slope is positive at small N_c^* and negative at larger N_c^* .

Effects of elevated CO_2 enter the system through a combined increase in a and ϕ (Cannell & Thornley, 1998). These parameters directly affect GPP and, as shown in Eqn 1a, elevated CO_2 raises both the initial slope (through a) and the maximum (through ϕ) of GPP as a function of N_c . The increase in ϕ has a positive effect on N_c^* , while, as discussed above, the effect of a on N_c^* is negative unless N_c^* is very small. The combined increases in ϕ and a cause a small positive net effect of elevated CO_2 on N_c^* , although the effect increases at decreasing N_c^* (Fig. 4). However, if at the same time carbon costs per N_c (w) increases, for example because of increased fine-root allocation, the total effect may be reduced N_c^* at elevated CO_2 (Fig. 4).

The carbon use efficiency = NPP/GPP ratio can be expressed and, for steady-state canopies, approximated by:

$$\begin{aligned} \frac{NPP^*}{GPP} &= \frac{y(GPP - R_m)}{GPP} = y \left(1 - \frac{R_m}{GPP} \right) \\ &\approx y \left(1 - \left(\frac{r}{ab} \right)^{2/3} \sqrt{1 + q_r f_r + f_s Q} \right) \end{aligned} \quad \text{Eqn 3g}$$

where the function Q is insensitive to variation of its parameters ($Q \approx 1.3$ for all realistic parameter values; Supplementary Material, Eqn S7). The NPP/GPP^* ratio has an upper limit of y (≈ 0.7) and is rather insensitive to changes in relative root and stem allocation (f_r and f_s) and associated changes in N_c^* . This invariance is not surprising since both GPP and R_m are increasing functions of N_c (Eqns 1a, 2a). The NPP/GPP^*

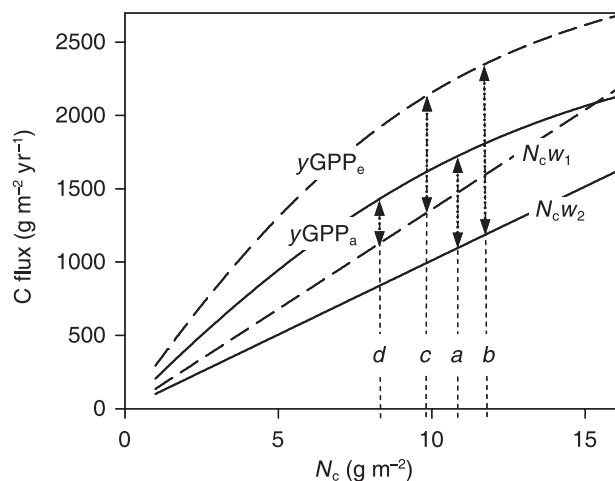


Fig. 4 Optimal canopy state and effects of elevated CO_2 and root nitrogen : leaf nitrogen ratio (f_r). Net growth ($G^* = y\text{GPP} - N_c w$, arrows; cf. Eqn 3a) and optimal canopy nitrogen (N_c^* ; dotted vertical lines) resulting from photosynthesis at ambient vs elevated CO_2 (GPP_a and GPP_e , respectively) and from different w_1, w_2 (= slopes of $yR_m + T$, respiration and litter production) because of shifts in f_r (cf. Fig. 3). The position of N_c^* is shown for control conditions (a); elevated CO_2 only (b); elevated CO_2 + increased w (c); ambient CO_2 + increased w (d). Shifting conditions from a to b, compared with shifting from d to c, illustrates the effect of elevated CO_2 at high vs low N_c^* . Shifting from a to c compared with from a to b represents the difference between a CO_2 response restricted by increased root allocation and an unrestricted response. Applied leaf CO_2 effect; 50% increase in a and 16.7% increase in ϕ .

ratio is increased by elevated CO_2 through the effect on a (Eqn 3g) and decreases during canopy expansion (Fig. 5). The effect of canopy expansion is the result of the saturating response of GPP combined with the linear increase in R_m (Fig. 3).

Optimal LAI of the expanding canopy (L) and the steady-state canopy (L^*) are identical for a fixed N_c (Fig. 1). However, for the steady-state canopy an analytical expression for L^* , including the effect of optimal N_c , can be obtained by inserting I_a (Eqn 1b) in G^* (Eqn 3e) and maximizing with respect to L , which gives:

$$L^* = \frac{1}{k} \ln \left(\frac{kbI_0\epsilon_G}{N_{\min}w} \right) \quad \text{Eqn 3h}$$

The PAR absorption of the optimized canopy (I_a) is then obtained through its direct link to L (Eqn 1b) as

$$I_a^* = I_0 \left(1 - \frac{N_{\min}w}{kbI_0\epsilon_G} \right) \quad \text{Eqn 3i}$$

PAR absorption saturates earlier with increasing canopy size than light-use efficiency because of its exponential nature (Fig. 2).

As shown above, LAI vs N_c (N_A) increases slightly with CO_2 for a fixed N_c . Here Eqn 3h shows that also when including

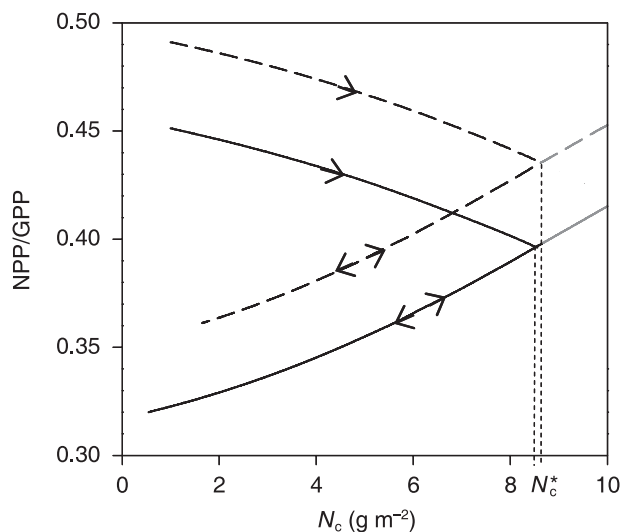


Fig. 5 Net primary production (NPP) : gross primary production (GPP) ratio vs canopy nitrogen (N_c). NPP : GPP ratios for an expanding canopy (upper lines) and for a steady-state canopy (lower lines) at ambient CO_2 (solid lines) and elevated CO_2 (dashed lines). Arrows indicate possible directions of canopy development. NPP : GPP decreases with N_c for an expanding canopy, while for steady-state canopies NPP : GPP is positively related to N_c^* .

the effect of CO_2 on N_c for steady-state canopies, L^* (at constant w) is slightly increased by elevated CO_2 through the increased light-use efficiency (ϵ_G). However, the L^* response to CO_2 is always smaller than the response of ϵ_G , since L^* is a logarithmic function of ϵ_G .

Modelling the CO_2 effects in FACE experiments

To evaluate the hypothesized model, published observations from four forest FACE sites (whole stand elevated CO_2 experiments) representing closed-canopy stands (meaning canopies horizontally filling the growing space) were used. The sites are: Oak Ridge (sweet gum, steady-state canopies), Duke forest (Loblolly pines, steady-state canopies), POPFACE (poplars, expanding canopies) and Aspen FACE (mixed aspen dominated, expanding canopies). The observations used here all represent elevated and ambient CO_2 treatments where no other treatments were applied. Further information about the sites and relevant references are given in Table 1.

Parameters for the control plots of the FACE stands were collected from publications, except for a, f_r and r , which were determined by fitting of observed data (GPP, G , NPP, LAI) (supplementary material, Tables S1 and S2), using length of growing season to derive annual numbers from the daily values given by the equations. The modelling of the elevated CO_2 stands was then done with the same parameter values as for the control stands, except for the leaf photosynthetic capacity per N (a) and the root N : canopy N ratio (f_r), which were multiplied by the observed relative changes (in percentage) in these

Table 1 Site data and primary CO₂ effects (Δa , $\Delta\phi$, Δf_r) applied for modelling of the forest free air CO₂ enrichment (FACE) sites*

Site name	Location	Mean temp (°C)	Species	Planting year	Canopy state ^a	<i>n</i> ^b	Δa (%) ^c	$\Delta\phi$ (= $\Delta a/3$)	Δf_r (%) ^d
POPFACE	Italy: 42°22'-N, 11°48'-E	14.1	Three poplar species	1999	Expanding	3	53 ¹	17.7	49.8 ^{2,3}
Aspen FACE	USA: 45°36'-N, 89°42'-W	4.9	Aspen, birch	1997	Expanding	8	21 ⁴	7	4.1 ⁵
Duke forest	USA: 35°59'-N, 79°6'-W	15.5	Loblolly pine	1983	Steady state	1	38 ⁶	12.7	52.2 ^{7,8}
Oak Ridge	USA: 35°54'-N, 84°20'-W	14.2	Sweetgum	1988	Steady state	1	58 ⁶	19.3	105.3 ⁹

*Further details of the sites available in King *et al.* (2004). Superscripted numbers represent the following: 1, Calfapietra *et al.* (2005); 2, Gielen *et al.* (2005); 3, Lukac *et al.* (2003); 4, Takeuchi *et al.* (2001); 5, King *et al.* (2005); 6, Springer *et al.* (2005); 7, Finzi *et al.* (2002); 8, Finzi *et al.* (2006); 9, Norby & Iversen (2006).

^aExpanding canopies have not yet reached their optimal state (steady state).

^bNumber of pairs of plots (elevated and ambient CO₂) used for each site (only observations from years when the canopy was closed were included).

^cObserved CO₂ effect on leaf photosynthetic capacity per N (*a*).

^dObserved CO₂ effect on fine-root : leaf N ratio (*f_r*).

parameters caused by the elevated CO₂ treatment for each site (Table 1). In addition, an *a*-dependent increase in quantum efficiency (ϕ) was applied, equal to one-third of the increase in *a* (Cannell & Thornley, 1998; Long *et al.*, 2004). By fitting the parameters *a* and *f_r* for control stands and then applying observed relative changes to model the changes caused by elevated CO₂, the influence of potential errors in the measured absolute values in these highly spatially and temporally variable parameters is removed. In this way focus is kept on the changes caused by elevated CO₂ while minimizing potential effects of problems in baseline predictions or observations.

The observed CO₂-induced increase in *a* (Δa) was obtained by fitting observed leaf $A_{\max} - N_A$ data for ambient and elevated CO₂ treatments to separate slopes and a common N_{\min} , since estimated N_{\min} was not significantly different between treatments. The effects on *f_r* (Δf_r) were calculated from observed data on differences between elevated and ambient CO₂ treatments in amounts and nitrogen concentrations of fine roots and leaves. For Duke forest, Δf_r was partly estimated by extrapolation in time because of missing data for the main part of the investigated period. For the poplar sites (POPFACE and Aspen FACE), despite slight differences among the species within each site, one value of Δf_r per site was used because Δa was available for one species per site only.

Small changes in physiological parameters resulting from CO₂ treatment were also observed for leaf and fine-root N : C ratios and turnover rates. These effects only marginally affected the results (slightly improving the fit in Fig. 7) and were excluded from the further modelling in order to keep focus on the more important factors. The reasons for the small effects of changes in N : C ratios in this framework are that photosynthesis (within a species) is much more strongly linked to N_A , which is used in this model, than to N : C ratio (Meir *et al.*, 2002), while for respiration, the effects of N : C ratio are indirectly included through changes in total N.

Because the poplar stands were in a phase of expanding canopy, the preoptimal production equations as functions of canopy N were used, while for Oak Ridge and Duke forest the

optimized equations were used since these stands had reached steady-state canopies.

Results and Discussion

Neglecting seasonal and daily variations in environmental variables, the presented model is clearly focused on mechanistic understanding rather than predictive ability. Nevertheless, the predicted CO₂ responses (the relative differences between elevated CO₂ and control treatments) are in reasonable agreement with observations (Figs 6–8). Furthermore, given the inherent variation and uncertainty in estimates of forest production, the value of further improved matching between model and observations is questionable.

Variation in NPP responses

Looking at the NPP responses to CO₂, they are large for the POPFACE compared with the other sites, which is also true for the LAI responses (Fig. 7). These large responses are the result of the well known effect of accelerated development in young stands, where not only biomass but also production increases faster over time at elevated than at ambient CO₂ (Fig. 6). Disregarding the effects of accelerated development, the CO₂ responses of NPP are similar among sites, as has been pointed out by Norby *et al.* (2005). In light of this theory, the similarity of NPP responses is a product of dissimilar photosynthetic (Δa , $\Delta\phi$) and allocation (Δf_r) effects, adding up to similar total effects. The stronger the photosynthetic response, the stronger the increase in *f_r* (Table 1), causing down-regulation of production because of increased root respiration and turnover. This balance of effects is probably the result of the fact that enhanced photosynthesis, caused by increased Δa , increases nutrient demand, which is followed by augmented root allocation. Consequently, increased nutrient availability (fertilization) should substantially increase the CO₂ response of wood and leaf production, especially at infertile sites, as has been observed (Oren *et al.*, 2001). The leaf-level mechanisms

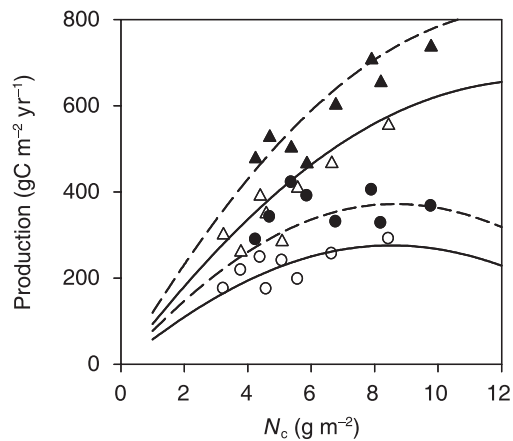


Fig. 6 Development of poplar stands (Aspen FACE) in relation to their canopy nitrogen (N_c). Modelled (lines) and observed (points) G (net growth; lower lines, circles) and NPP (net primary production; upper lines, triangles) of developing poplar stands (Aspen FACE) in ambient CO_2 (solid lines, open symbols) and elevated CO_2 (dashed lines, closed symbols). In modelling the ambient CO_2 treatment, the model has been fitted to measured data by adjusting f_r (root nitrogen : leaf nitrogen ratio) and a (of photosynthetic capacity per leaf N). For modelling the elevated CO_2 treatments, observed changes in f_r and a at elevated CO_2 have been applied without refitting any parameters. $r^2 = 0.68, 0.81$ for modelled vs measured CO_2 effects on NPP and G , respectively.

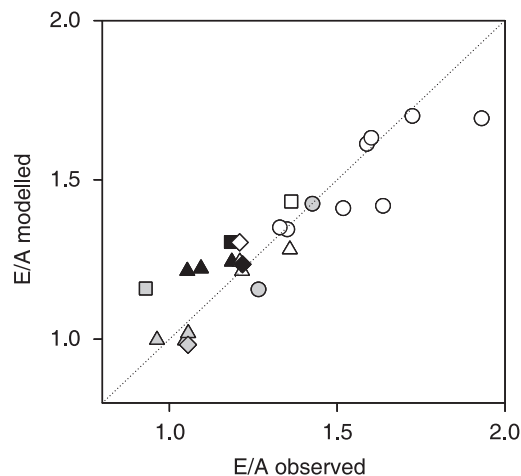


Fig. 7 Modelled vs observed properties in free air CO_2 enrichment (FACE) sites. Elevated/ambient CO_2 (E/A) values for net primary production (NPP; open symbols), gross primary production (GPP; black symbols) and leaf area index (LAI; grey symbols) for the FACE sites, POPFACE (circles), Aspen FACE (triangles), Oak ridge (diamonds) and Duke forest (squares). $r^2 = 0.83$ for all modelled vs observed data. Modelling of CO_2 effects done as in Fig. 6. Data sources are in Supplementary Material, Table S2. Note that for Duke forest LAI, apparently other data exist than those shown here, since in another study $E/A > 1$ for LAI (Norby *et al.*, 2005). This indicates a potential explanation for the discrepancy between model and observation, where $E/A < 1$, used here for LAI in Duke forest.

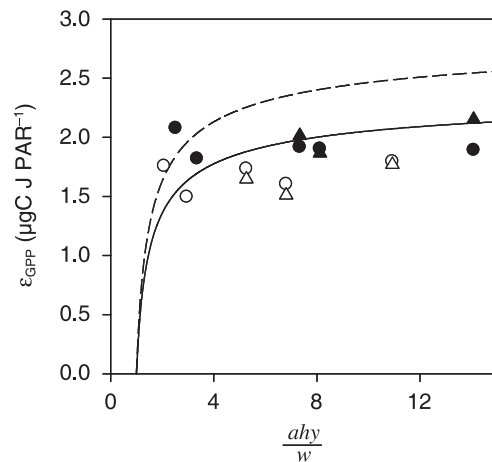


Fig. 8 Observed vs modelled and potential light-use efficiency of gross primary production (ϵ_{GPP}). ϵ_{GPP} modelled for steady-state (lines) and expanding canopies (triangles), and ϵ_{GPP} observed (circles) at ambient CO_2 (open symbols, solid line) and elevated CO_2 (closed symbols, dashed line) vs the ratio ahy/w . The steady-state canopies (Duke forest and Oak ridge; the four leftmost points) are already at their steady-state ϵ_{GPP} (cf. Eqn 3d). The expanding canopies (POPFACE) ϵ_{GPP} are expected to increase vertically towards the lines representing steady-state canopies. Modelling of expanding canopies at ambient and elevated CO_2 is done as in Fig. 6, using one set of parameters and CO_2 effects for each site. $r^2 = 0.90$ for the modelled vs measured CO_2 effect. The ratio ahy/w controls photosynthetic capacity vs respiration + litter production per canopy N.

behind the differences in Δa among the sites (Table 1) are not within the scope of this paper but a possible explanation has to do with temperature differences, which strongly affect the response of a (Long *et al.*, 2004). Indeed, temperature effects could explain the small Δa in Aspen FACE, which has a significantly lower mean temperature than the other sites (Table 1).

Light-use efficiency, LAI and light absorption

An interesting aspect of the CO_2 effect, especially in relation to remote sensing-based modelling approaches, is the response in light-use efficiency relative to light absorption (APAR). Here APAR responses are mediated solely through changes in LAI, although APAR also depends on light extinction k because, to my knowledge, significant CO_2 effects on k have not been observed in the modelled sites. Large CO_2 effects on LAI are only seen in the poplar sites and can mainly be attributed to an accelerated development effect (as discussed earlier). The small observed CO_2 effects on LAI of the steady-state canopies of Duke forest and Oak Ridge and in other experiments have previously mainly been interpreted as a consequence of saturation of APAR. Here I suggest a new interpretation of the general insensitivity of LAI to CO_2 as well as of the observed increased sensitivity at low LAI (Norby *et al.*, 2005).

Through leaf photosynthetic capacity per N (a) and quantum efficiency (ϕ), elevated CO_2 increases both the initial slope and the maximum of GPP as a function of canopy N (N_c) (Eqn 1a). As illustrated in Fig. 4, unless N_c is very low, this lifts the GPP vs N_c curve without much change in its slope and therefore only marginally increases N_c^* . Together with the simultaneous small effect of elevated CO_2 on optimal LAI for a given N_c (Figs 1, 2), the small effect on N_c^* accounts for the small effects of CO_2 on LAI. Furthermore, the photosynthetic effects of CO_2 are often followed by an increase in fine-root allocation that increases carbon costs per $N_c(w)$. This allocation effect further reduces the LAI response and can even lead to decreased LAI through down-regulation of N_c^* (Fig. 4), as, at the same time, the LAI : N_c ratio remains largely unchanged (Fig. 2).

Furthermore, the larger increase in LAI caused by elevated CO_2 at smaller than at larger LAI can be attributed to the shape of the GPP– N_c curves. Despite the generally low sensitivity of the shape of the GPP– N_c curves to CO_2 , the larger CO_2 effect on a (increasing initial slope) than on ϕ (increasing maximum GPP; increase in ϕ is equal to one-third of the increase in a) does cause the curves for ambient and elevated CO_2 to become less parallel at low N_c . For a fixed w this leads to a larger effect of elevated CO_2 on N_c^* at low than at high N_c^* (Fig. 4). This effect on N_c^* then carries over to LAI, as discussed above.

As predicted by the model and as expected from leaf responses, light-use efficiency of GPP (ϵ_{GPP}) is significantly increased by elevated CO_2 (Figs 2, 8). However, contrary to assumptions in some studies (Goetz & Prince, 1999), ϵ_{GPP} is here predicted to increase with N_c and LAI, both during canopy development and if caused by changes in w at steady-state conditions (Fig. 2). In agreement with this, observed and predicted ϵ_{GPP} for a site with expanding canopies (POP-FACE) are lower than the theoretical prediction for steady-state conditions, while for the steady-state FACE sites they are on average slightly higher than the theoretical steady-state prediction (Fig. 8). In further agreement with the model predictions, a positive correlation between N_c and light-use efficiency during canopy expansion and in response to fertilization has been observed for loblolly pine stands (Martin & Jokela, 2004).

Leaf responses

In agreement with the observations, the model predicts that canopy average leaf N per area $N_A (= N_c/\text{LAI})$ is slightly reduced by elevated CO_2 , -8.1 and -9.7% for observed and modelled data, respectively. In line with the results by Ellsworth *et al.* (2004), the reduction in N_A causes a down-regulation of leaf photosynthetic capacity (A_{max}) without changing the basic relations among leaf photosynthesis, leaf N and CO_2 concentration. Previous explanations for the down-regulation have focused on leaf internal mechanisms or N

dilution in response to source and sink changes (Ellsworth *et al.*, 2004). However, here a fundamentally new interpretation is suggested for the ultimate reason behind the more proximate effects of leaf-level changes. The reduction in N_A and associated photosynthetic down-regulation follow from whole-plant optimization of LAI and canopy N rather than as a secondary consequence of primary leaf internal effects.

In the presented framework, mass-based leaf N concentration or N : C ratio does not directly influence photosynthesis (which is controlled by N_A) and plays a small role in controlling the CO_2 and N responses discussed in this paper (with the possible exception of litter : wood production ratio as discussed below). It should be noted that the within-species acclimation responses discussed here should not be confused with the sometimes strong leaf N : C ratio–photosynthesis correlations observed among species. Furthermore, because no relation is imposed between leaf mass per area and N_A , effects on N : C ratio cannot be predicted here. Thus, it is implicitly assumed that mechanisms not included in the present framework control leaf N : C ratio. These mechanisms can be revealed by adding a nutrient uptake model to the present framework, to predict N : C ratio responses from optimized mass balance, as will be shown in future work.

NPP : GPP ratio

The model predicts NPP : GPP ratio to increase by elevated CO_2 , to decrease during canopy expansion, but to increase with N_c^* for steady-state canopies (Fig. 5). Because of the small number of observations available here ($n = 5$) combined with the small effects, the measured and modelled CO_2 effects here (11 and 4%, respectively) are not significant.

The theory lends support to the common assumption that the NPP : GPP ratio can be conservative under different conditions. Under a range of soil fertility (change in root : canopy N ratio, f_r) or age (increase in sap wood : canopy N ratio, f_s), there are only small differences in NPP : GPP (Eqn 3g) although, in agreement with observations (Mäkelä & Valentine, 2001), a slight decrease at increasing f_s is predicted. The mechanistic background for the commonly observed invariance in NPP : GPP ratio has previously been elucidated in relation to temperature and short-term fluctuations in photosynthesis (Dewar *et al.*, 1998, 1999). The presented theory expands the theoretical support for these findings to include effects of longer-term shifts in leaf : root : stem ratios (f_r, f_s).

Litter vs wood production

An important question for the sustainability of potential CO_2 -induced carbon accumulation is the allocation of production to fast turnover litter (foliage and fine-root production, T) vs allocation to wood (wood : litter ratio). The wood : litter ratio can be approximated by

$$\frac{\text{NPP} - T}{T} = \frac{\text{NPP}}{T} - 1 = \frac{\text{NPP}}{N_c} \frac{1}{l_w} - 1$$

(l_w , litter production per canopy N (N_c)). NPP/N_c is increased by elevated CO_2 but otherwise conservative in relation to N_c^* for steady-state canopies (Fig. 3). Thus, the wood : litter ratio is increased by elevated CO_2 (through NPP/N_c) and decreases with the litter production per N_c (through l_w), where l_w is sensitive to f_r (the root N : foliage N ratio), as discussed in the theory section. Since f_r is controlled by soil N availability, this explains why the wood allocation response to elevated CO_2 is sensitive to N availability. However, the FACE plots analysed here either are not steady-state canopies (POPFACE, Aspen FACE), where NPP/N_c is decreasing with N_c (Fig. 3), or show a substantial increase in f_r (Duke forest, Oak ridge), counteracting the elevated CO_2 effect on wood : litter ratio. Thus, as expected, the CO_2 effects on wood : litter ratio in the sites presented here are small, on average 10 and 1% for modelled and measured responses, respectively. Because the wood : litter ratio is largely controlled by l_w (Eqn 2b), the generally negligible influences of N : C ratios and life spans of leaf and roots (see section on 'Modelling the CO_2 effects in FACE experiments') may be more important for this particular response. Indeed, including measured effects on N : C ratios and life spans lowers the modelled CO_2 effect on wood : litter ratio to, on average, 2% (SD = 4.0%), not significantly different from the 1% (SD = 4.3%) measured response. CO_2 -induced lowering of N : C ratios reduces the wood : litter ratio mainly through increased litter carbon losses per N_c at elevated CO_2 (cf. Eqn 2b), as at the same time N_c^* is largely unaffected.

Rationale and limitations of the approach

In ecophysiological optimality models, there is usually very little discussion of the choice of target for optimization, although it is fundamental. The rationale for the chosen optimization criterion of NPP minus root and leaf litter production (G) has been explained above. Supporting the principle, experiments on stands of spruce and beech have shown that competitiveness is determined by the standing foliage mass and the annual branch volume increment rather than annual investments in foliage (Reiter *et al.*, 2005). Providing support for the inclusion of reproductive production in G , reproductive enhancement by elevated CO_2 has been observed (Ladeau & Clark, 2006). However, to evaluate the effect of optimizing G vs NPP in this framework, a version of the model based on optimization of NPP was analysed. In general this modification did not significantly alter the results, except that higher N contents were predicted and that NPP as a function of N_c (canopy N productivity) assumed a more curved upwards shape than the almost straight (for steady-state canopies) or slightly curved down (for expanding canopies) relation predicted by the original model (Fig. 3). The canopy

N productivity curve of the original G maximizing model corresponds better to observations (Smith *et al.*, 2002).

Scaling up CO_2 responses from observed leaf responses, not describing the effects within the leaves, makes the suggested model incomplete from some practical perspectives. However, the approach taken serves to focus the analysis on the consequences of the leaf effects in a whole-plant perspective, rather than probing into the leaf internal CO_2 responses, which are already well understood (Gifford, 2004). A natural extension of the presented framework is the addition of a soil nutrient uptake model. This addition would make it possible to analyze effects of changes in soil nutrient availability on forests production explicitly, rather than the currently used implicit effects through root allocation. However, the restriction of the system boundaries to explicitly include only plant properties (and not soil) in the analysis presented here serves to minimize the amount of uncertainty, in terms of both model assumptions and measurements, and to maximize the significance of the current conclusions.

Conclusions

The framework presented offers a transparent whole-tree optimality perspective on forest responses to CO_2 and nitrogen. It is used to show how primary leaf photosynthesis and fine-root allocation responses scale up to control whole-system behaviour, explaining the range of NPP responses observed in forest FACE experiments. It shows how production (GPP and NPP) and structure (LAI and canopy N) are linked in response to N availability (through the fine-root : leaf N ratio). It suggests a novel interpretation of the small and variable CO_2 responses on LAI, based on the change in slope of the GPP–canopy N relation shifting the optimal canopy N only slightly. It predicts that there is a consistent increase, although small, in optimal LAI vs canopy N at elevated CO_2 , that is, a reduction in N_A , thus suggesting a new ultimate explanation for the CO_2 -induced leaf photosynthetic down-regulation, as leaf photosynthesis is largely controlled by N_A .

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Supplementary Material

The following supplementary material is available for this article online:

Appendix S1

- A Leaf and canopy photosynthesis
- B Derivation of optimal N_c (Eqn 3b)
- C Derivation of NPP/GPP
- D Derivation of LAI (L^*) of the steady-state canopy

Table S1 Parameters and symbols

Table S2 Origins of measured data

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Appendix S1.

A. Leaf and canopy photosynthesis

Canopy photosynthesis (GPP) is calculated by integration of leaf photosynthesis (GPP_{leaf}) over canopy depth (z). A_{max} (Eqn 1a) is a function of N per leaf area (N_A), assuming an optimal nitrogen distribution (Eqn S2) as described in (Franklin & Agren, 2002). PAR absorbed by a leaf is related to canopy depth according to $I(z) = I_0 k e^{-kz}$, where k is the light extinction coefficient and I_0 is incident PAR above the canopy. The integral (A1) is easily calculated by first separating out the z dependence through the factor $k e^{-kz}$, which occur in all terms of the integrand.

$$GPP = \int_0^L GPP_{leaf} dz = \int_0^L \frac{\phi I(z) + A_{max}(z) - \sqrt{(\phi I(z) + A_{max}(z))^2 - 4\phi I(z) A_{max}(z)\theta}}{2\theta} dz \quad \text{Eqn S1}$$

$$N_A(z) = \frac{(N_c - N_{min}L)k e^{-kz}}{1 - e^{-kL}} + N_{min} \quad \text{Eqn S2}$$

B. Derivation of optimal N_c (Eqn 3b)

Optimal N_c is derived through maximization of G with respect to N_c . To simplify calculations, the substitution $N_p = N_c - N_{min}L$ is made, so that optimal N_c is given by

$$\frac{dG}{dN_c} = \frac{dG}{dN_p} \frac{dN_p}{dN_c} = \frac{dG}{dN_p} = 0 \quad \text{Eqn S3}$$

Using the last expression in Eqn 3a ($G = y GPP - w N_c$)

$$\frac{d}{dN_p} G = y \frac{d}{dN_p} GPP - w = \frac{h y a}{2\theta} \left(1 - \frac{\phi I_a + a N_p - 2\phi I_a \theta}{\sqrt{(\phi I_a + a N_p)^2 - 4\phi I_a a N_p \theta}} \right) - w \quad \text{Eqn S4}$$

Solving Eqn S4 = 0 for N_p gives two solutions where one is negative and the other is

$$N_p = \frac{I_a}{a} \phi \left(\sqrt{\frac{1-\theta}{a h y - \theta}} \left(\frac{a h y}{w} - 2\theta \right) + 2\theta - 1 \right) \quad \text{Eqn S5}$$

Substituting again $N_p = N_c - N_{min}L$ gives optimal N_c (N_c^*)

$$N_c^* = \frac{I_a}{a} \phi \left(\sqrt{\frac{1-\theta}{a h y - \theta}} \left(\frac{a h y}{w} - 2\theta \right) + 2\theta - 1 \right) + N_{min}L = \frac{I_a \varepsilon_{max}}{a} + N_{min}L \quad \text{Eqns S6, 3b}$$

$$\text{, where } \varepsilon_{max} = \phi \left(\sqrt{\frac{1-\theta}{a h y - \theta}} \left(\frac{a h y}{w} - 2\theta \right) + 2\theta - 1 \right)$$

C. Derivation of NPP/GPP

Using Eqns 3a–3f, NPP/GPP is derived according to:

$$\frac{NPP}{GPP} = \frac{y(GPP - R_m)}{GPP} = y \left(1 - \frac{R_m}{GPP}\right) \quad \text{Eqn S7}$$

$$\text{, where } \frac{R_m}{GPP} = \frac{r_w N_c}{GPP} = \frac{r_w \frac{I_a \varepsilon_{\max}}{a}}{h I_a \varepsilon_{GPP}} \left(1 + \frac{N_{\min} L}{N_c}\right) = \frac{r_w \varepsilon_{\max}}{a h \varepsilon_{GPP}} \left(1 + \frac{N_{\min} L}{N_c}\right) \quad \text{Eqn S8}$$

$$\text{and } \frac{\varepsilon_{\max}}{\varepsilon_{GPP}} = \sqrt{\left(\frac{a h y}{w} - \theta\right)(1 - \theta) + \theta} \quad \text{Eqn S9}$$

Inserting S9 in S8 and then in S7 gives

$$\frac{R_m}{GPP} = \left(\frac{r}{a h}\right)^{2/3} \sqrt{1 + q_r f_r + f_s} Q \quad \text{Eqn S10}$$

, where

$$Q = \left(\frac{r}{a h}\right)^{1/3} \sqrt{1 + q_r f_r + f_s} \left(\sqrt{\left(\frac{a h y}{r_w y + t_w} - \theta\right)(1 - \theta) + \theta}\right) \left(1 + \frac{N_{\min} L}{N_c}\right) \quad \text{Eqn S11}$$

This equation for Q was chosen because it remains approximately constant when the parameters are varied over relevant ranges. Measured and estimated parameters values (Supplementary material Table S1) for two of the studied FACE sites (Oak Ridge and Duke forest) was inserted in Eqn S11 to get a baseline value of Q (= 1.23 for Oak ridge and 1.3 for Duke forest). For the parameters a , f_r , f_s , n_c and r their values were then varied through a range from 0.6 times the original value to double the original value. In no case did Q deviate more than 10% from the baseline value. Furthermore, the approximation used in Eqns S10 and 3g is used only for illustration, while the full equations of NPP and GPP are used for calculations.

D. Derivation of LAI (L^*) of the steady-state canopy

According to Eqn 3e $G^* = h I_a \varepsilon_G - N_{\min} L w$. Inserting $I_a = I_0(1 - e^{-kL})$ (Eqn 1b) in Eqn 3e gives

$$G^* = h I_0(1 - e^{-kL}) \varepsilon_G - N_{\min} L w \quad \text{Eqn S12}$$

, which is maximized with respect to L ($dG^*/dL = 0$) to obtain

$$L^* = \frac{1}{k} \ln \left(\frac{k h I_0 \varepsilon_G}{N_{\min} w} \right)$$

Eqns S13, 3h

Table S1 Parameters and symbols

Symbol	Parameter	Unit	Parameter values [#]				Reference / Estimate
			Site				
			POP-FACE	Aspen FACE	Oak Ridge	Duke forest	
a	Slope of $N_A - A_{max}$ relation	$\mu\text{gC gN}^{-1} \text{s}^{-1}$	52	42	77	39	*
n_c	Leaf N:C ratio	mgN gC^{-1}	51 ¹	35 ²	33 ³	17 ³	
n_r	Fine-root N:C ratio	mgN gC^{-1}	34	23	24 ⁴	23 ⁴	POPFACE & Aspen FACE: $n_r = 2/3 n_c$
f_r	$N_{fineroot} : N_{canopy}$ ratio	-	0.24	0.08	0.59	0.42	*
f_s	$N_{sapwood} : N_{canopy}$ ratio	-	0.2 ⁵	0.2 ⁶	1 ⁷	1 ⁸	
k	Canopy light extinction factor	-	0.4	0.4	0.5	0.5	typical values
N_{min}	x-axis intercept of $N_A - A_{max}$ relation	gN m^{-2}	0.4	0.4	0.4	0.4	typical value
ϕ	Photosynthetic quantum efficiency	$\mu\text{gC J}^{-1}$	2.73 ⁹	2.73 ⁹	2.73 ⁹	2.73 ⁹	Same for all sites
r	maintenance respiration per N	$\text{gC gN}^{-1} \text{d}^{-1}$	0.048	0.41	0.30	0.20	*
t_c	Leaf mean residence time	d	160 ¹⁰	140 ¹¹	187 ¹²	404 ¹³	
t_r	Fine-root mean residence time	d	80	70	142 ¹⁴	641 ⁴	POPFACE & Aspen FACE $t_r = t_c/2$
y	Biosynthetic conversion efficiency	-	0.72 ¹⁵	0.72 ¹⁵	0.72 ¹⁵	0.72 ¹⁵	average of woody species
θ	Convexity of leaf photosynthesis – I_0 relation	-	0.75	0.75	0.75	0.75	typical value
h	Day length	s d^{-1}	14 ¹⁰	14 ¹¹	12 ¹⁶	14 ¹²	growing season average values
I_0	Incident PAR above the canopy	$\text{J s}^{-1} \text{m}^{-2}$	207 ¹⁰	168 ¹¹	211 ¹⁶	184 ¹²	

¹(Calfapietra *et al.*, 2005), ²(Karnosky *et al.*, 2003), ³(Springer *et al.*, 2005), ⁴(George *et al.*, 2003), ⁵(Gielen *et al.*, 2005), ⁶(King *et al.*, 2005), ⁷(Norby *et al.*, 2002), ⁸(Finzi *et al.*, 2002), ⁹(Wong *et al.*, 1979), ¹⁰(Wittig *et al.*, 2005), ¹¹(Takeuchi *et al.*, 2001), ¹²(Norby *et al.*, 2003), ¹³(Hamilton *et al.*, 2002), ¹⁴(Norby *et al.*, 2004), ¹⁵(Choudhury, 2001), ¹⁶(Delucia *et al.*, 2002). * Estimated by fitting model to measured data on GPP, NPP, G , L , N_c (Table S2) for ambient CO_2 treatments. [#] Values are for ambient CO_2 concentration

Table S2 Origins of measured data

Symbol	Parameter	Unit	Reference			
			Site			
			POP- FACE	Aspen FACE	Oak Ridge	Duke forest
G	NPP – litter production	gC m ⁻² y ⁻¹	1	2	3	4
L	Leaf area index (LAI)	m ² m ⁻²	5	6	7	8
GPP	Canopy photosynthesis	gC m ⁻² y ⁻¹	1	-	9	9
NPP	Net primary production	gC m ⁻² y ⁻¹	1	2	3	4
N _c	Canopy nitrogen	gN m ⁻²	1,10	6	7, 11	4

¹(Gielen *et al.*, 2005), ²(King *et al.*, 2005), ³(Norby *et al.*, 2002), ⁴(Finzi *et al.*, 2002), ⁵(Gielen *et al.*, 2003), ⁶(Karnosky *et al.*, 2003), ⁷(Norby *et al.*, 2003), ⁸(DeLucia *et al.*, 2002), ⁹(DeLucia *et al.*, 2005), ¹⁰(Calfapietra *et al.*, 2005), ¹¹(Springer *et al.*, 2005)

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