

Why is plant-growth response to elevated CO₂ amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis

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Abstract. Experimental evidence indicates that the stomatal conductance and nitrogen concentration ([N]) of foliage decline under CO₂ enrichment, and that the percentage growth response to elevated CO₂ is amplified under water limitation, but reduced under nitrogen limitation. We advance simple explanations for these responses based on an optimisation hypothesis applied to a simple model of the annual carbon–nitrogen–water economy of trees growing at a CO₂-enrichment experiment at Oak Ridge, Tennessee, USA. The model is shown to have an optimum for leaf [N], stomatal conductance and leaf area index (LAI), where annual plant productivity is maximised. The optimisation is represented in terms of a trade-off between LAI and stomatal conductance, constrained by water supply, and between LAI and leaf [N], constrained by N supply. At elevated CO₂ the optimum shifts to reduced stomatal conductance and leaf [N] and enhanced LAI. The model is applied to years with contrasting rainfall and N uptake. The predicted growth response to elevated CO₂ is greatest in a dry, high-N year and is reduced in a wet, low-N year. The underlying physiological explanation for this contrast in the effects of water versus nitrogen limitation is that leaf photosynthesis is more sensitive to CO₂ concentration ([CO₂]) at lower stomatal conductance and is less sensitive to [CO₂] at lower leaf [N].

Additional keywords: carbon–nitrogen–water economy, climate change, CO₂ enrichment, forest model, leaf area index, stomatal conductance.

Introduction

It is clear from experimental data that the positive response of plant growth to elevated CO₂ is modified by water and nutrient limitations. Nutrient limitation is commonly shown to reduce the percentage CO₂ response. In a meta-analysis of CO₂ impacts on herbaceous and woody plants in free-air CO₂ enrichment (FACE) and open-top chamber experiments, nitrogen limitation was found to reduce the CO₂ response of aboveground biomass growth from +20.1% to +8.8% (de Graaff *et al.* 2006). An earlier meta-analysis of woody plants found that the CO₂ response of total biomass production was halved under nutrient limitation, from +30.9% to +15.5% (Curtis and Wang 1998). Similarly, a meta-analysis of CO₂ impacts on grasses found that nutrient stress reduced the CO₂ response of plant

biomass in C₃ grasses (Wand *et al.* 1999). A synthesis of the results from FACE experiments supports these conclusions (Nowak *et al.* 2004). The addition of nitrogen has been shown to increase plant CO₂ responses in FACE experiments on native grasses (Byrne and Jones 2002; Reich *et al.* 2006a), crops (Schneider *et al.* 2004) and tree species (Oren *et al.* 2001).

In contrast, water limitation is often shown to amplify the percentage response of plant growth to elevated CO₂, although this interaction is less consistently observed. In factorial CO₂ × water limitation experiments, the percentage growth response to CO₂ is generally found to be higher under water-stress conditions (e.g. Kimball and Mauney 1993; Field *et al.* 1997; Arp *et al.* 1998; Centritto *et al.* 1999), although in several

experiments there was no significant interaction (e.g. Guehl *et al.* 1994; Derner *et al.* 2003). Additional evidence comes from comparisons of CO₂ effects in dry and wet years. Morgan *et al.* (2004) reviewed this evidence for grassland and desert ecosystems and showed that the percentage stimulation of aboveground biomass by CO₂ was greater in dry years in the majority of these systems.

Plant–soil feedbacks are commonly invoked to explain these observations. It is widely argued that the reduced CO₂ response under nitrogen limitation is caused by increased nitrogen immobilisation in plant litter, biomass and soil (e.g. Comins and McMurtrie 1993; Diaz *et al.* 1993; Luo *et al.* 2004; Pepper *et al.* 2005, 2007). Similarly, it is thought that the amplification of the CO₂ response under low water availability is caused by reduced transpiration under elevated CO₂ leading to improved soil-water status (e.g. Field *et al.* 1996; Shaw *et al.* 2005).

It remains uncertain, however, whether soil feedbacks cause the observed interactions between elevated CO₂ and nitrogen and water limitations. Although litter carbon and nitrogen pools increase in size under elevated CO₂ (Luo *et al.* 2006), evidence is mixed for responses in microbial activity and nitrogen mineralisation under elevated CO₂ (Zak *et al.* 2000, 2003; Gill *et al.* 2002; Barnard *et al.* 2004; Reich *et al.* 2006a, 2006b). Equally, although stomatal conductance is consistently reduced under elevated CO₂ (Medlyn *et al.* 2001; Ainsworth and Long 2005), this reduction does not always translate to an equivalent reduction in transpiration or an improved soil-water status (e.g. Field *et al.* 1995; Baker *et al.* 1997; Wullschlegel and Norby 2001) because elevated CO₂ often increases leaf area index (LAI) (Ainsworth and Long 2005), which is a primary determinant of both productivity and water use (Wullschlegel *et al.* 2002).

In this paper we advance a growth-optimisation hypothesis for the interactions between elevated CO₂ and nitrogen and water limitations. This hypothesis, which is based on plant physiology alone, does not invoke potential soil–nitrogen feedbacks (although it is important to note that our analysis does not preclude the possibility that soil feedbacks induce or exacerbate nitrogen limitation). We explore this hypothesis using a simple model of plant carbon, nitrogen and water economy. The model is shown to have an optimum where annual plant productivity is maximised. The optimal stomatal conductance, leaf-nitrogen concentration ([N]) and canopy LAI are emergent outcomes of the model optimisation, rather than input parameters or submodels. The model is used to evaluate optimal productivity for monoculture stands of a deciduous hardwood tree, sweetgum (*Liquidambar styraciflua* L.) that have been growing for 10 years in a FACE experiment at Oak Ridge, Tennessee, USA. The model's optimum is determined for years with contrasting rainfall and nitrogen supply at current and elevated CO₂ concentrations. The model shows that the percentage CO₂ response of maximum plant productivity is greatest in low rainfall and high-N years.

To illustrate the optimisation hypothesis as clearly as possible, the plant model to which it is applied is kept very simple, and we

consider deciduous trees growing in environmental conditions that are constant throughout the growing season.

Materials and methods

The Oak Ridge FACE experiment

Monoculture stands of sweetgum (*Liquidambar styraciflua* L.) trees were planted in 1988 at a site in the Oak Ridge National Environment Research Park, Tennessee, USA (35°54'N, 84°20'W). The long-term mean annual temperature and rainfall are 13.9°C and 1371 mm, respectively. The annual rainfall between 1999 and 2006 ranged from 830 to 1576 mm, with an average of 1129 mm. A detailed site description is given by Norby *et al.* (2006). The FACE experiment commenced in 1997, when stands had achieved canopy closure, and treatments were initiated in 1998 with three plots at a [CO₂] of 375 and two plots at a [CO₂] of 550 p.p.m. Under elevated CO₂ the annual net primary productivity (NPP) increased by 22% on average over the first 9 years of the FACE experiment. The NPP response is dominated by fine-root production, which has doubled on average (Norby *et al.* 2004, 2006). Measured wood production has increased by only 10% on average and the peak annual LAI, which ranges between 5 and 6, has not responded to the high CO₂.

Model

The model, named MATEY (Model Any Terrestrial Ecosystem – Yearly), evaluates annual gross primary productivity (GPP) as the product of annual absorbed photosynthetically active radiation (APAR), which depends on LAI, and photosynthetic light-use efficiency (LUE), which depends on the biochemistry of photosynthesis and on the rate of CO₂ diffusion across the stomata. Plant respiration is incorporated via carbon-use efficiency (CUE = NPP/GPP). The model incorporates nitrogen and water limitations as constraints on productivity. We will first present equations for annual plant productivity, and then for limitations in nitrogen and water supply.

Annual plant productivity

We assume that GPP is proportional to APAR (cf. Medlyn *et al.* 2003). This relationship is commonly used for estimating regional and global NPP, often using remotely sensed measures of LAI and APAR (Potter *et al.* 1993; Ruimy *et al.* 1994; Myneni *et al.* 2002; Leuning *et al.* 2005). Annual APAR for a deciduous stand is calculated from the peak annual value of LAI using Beer's law:

$$\text{APAR} = \phi_0 (1 - \exp(-k f_L \text{LAI})), \quad (1)$$

where ϕ_0 is the growing-season incident PAR, k is a light-extinction coefficient and f_L is a factor that allows annual APAR of a deciduous tree stand to be evaluated from peak LAI. The symbols and parameter values estimated for sweetgum are defined in Table 1.

The slope of the relationship between GPP and APAR is the LUE, which we model using the equations for canopy

Table 1. Symbol definitions, units and parameter values corresponding to the simulations in Fig. 4

Symbol	Definition	Value and units	Source
A_{\max}	Light-saturated photosynthetic rate at the top of the canopy	$\mu\text{mol CO}_2 \text{ m}^{-2}$ projected leaf area s^{-1}	Gunderson <i>et al.</i> (2002), Sholtis <i>et al.</i> (2004)
APAR	Absorbed photosynthetically active radiation for growing season	GJ PAR $\text{m}^{-2} \text{ year}^{-1}$	Norby and Iversen (2006)
C	Constant in equation for tree water use	$8.710 \text{ m}^3 \text{ mol}^{-1} \text{ kPa}^{-1}$	McMurtrie <i>et al.</i> (1990)
C_i	Inter-cellular CO ₂ concentration	p.p.m.	
C_f, C_w	Annual carbon production of leaves and wood	$\text{kg C m}^{-2} \text{ year}^{-1}$	Norby <i>et al.</i> (2006)
C_{exp}	Annual carbon export from the canopy to grow wood and fine roots	$\text{kg C m}^{-2} \text{ year}^{-1}$	Norby <i>et al.</i> (2006)
CUE	Carbon-use efficiency	0.5	Norby <i>et al.</i> (2006)
[CO ₂]	Atmospheric CO ₂ concentration	375, 550 p.p.m.	Norby <i>et al.</i> (2006)
f_L	Correction to LAI in calculation of APAR from peak LAI	0.94	From APAR and LAI data in Norby <i>et al.</i> (2003)
f_s	Growing-season length as a fraction of the year	0.58	Norby <i>et al.</i> (2006)
f_w	Annual plant water use as a fraction of the annual rainfall	0.8	Plausible value
g_s	Stomatal conductance to water vapour	$\text{mol m}^{-2} \text{ s}^{-1}$	Gunderson <i>et al.</i> (2002), Norby <i>et al.</i> (2006)
G_c	Canopy conductance	$\text{mol m}^{-2} \text{ s}^{-1}$	
J_{\max}	Maximum electron-transport rate at the top of the canopy at light-saturation	$\mu\text{mol m}^{-2} \text{ s}^{-1}$	Sholtis <i>et al.</i> (2004)
$J_{\max o}$	Slope of the relationship between J_{\max} and leaf-nitrogen content (g N m^{-2})	$70 \mu\text{mol g N}^{-1} \text{ s}^{-1}$	Estimated from data in Sholtis <i>et al.</i> (2004), Tissue <i>et al.</i> (2002)
k	Light extinction coefficient	0.41	Norby <i>et al.</i> (2003)
k_w	Light-extinction coefficient for understorey water use	1.0	Plausible value
LAI	Projected leaf area index	-	Norby <i>et al.</i> (2003)
LUE	Light-use efficiency	$\text{g C MJ}^{-1} \text{ PAR}$	Calculated from the model of Sands (1995, 1996). Also see Norby <i>et al.</i> (2003)
m	Leaf transmission coefficient	0	
N_{area}	Leaf-N content at the top of the canopy	g m^{-2}	Norby and Iversen (2006)
NPP	Net primary production of trees	$\text{kg C m}^{-2} \text{ year}^{-1}$	Norby <i>et al.</i> (2005, 2006)
[N] _f , [N] _w	Nitrogen concentration of leaves, wood	$\text{mg N g}^{-1} \text{ DW}$	Norby and Iversen (2006)
r	Fraction of N retranslocated at leaf senescence	0.5	Norby and Iversen (2006)
RF	Annual rainfall	800, 1200 mm	
SLA, SLA _o	Specific leaf area as canopy-average and at the top of the canopy	$11, 8 \text{ m}^2 \text{ kg}^{-1} \text{ DW}$	Norby and Iversen (2006)
t	Time	Year	
U	N uptake flux to aboveground biomass pools	$4, 6 \text{ g N m}^{-2} \text{ year}^{-1}$	From plant C and N content data
VPD	Growing-season average daylight vapour-pressure deficit	1.0 kPa	
α	Quantum yield of photosynthesis	-	Calculated from Eqn 3 (McMurtrie and Wang 1993)
λ	Average N : C ratio of new wood production relative to leaf N : C ratio multiplied by (C_w/C_{exp})	0.061	Calculated from wood and leaf-N data
Γ^*	CO ₂ compensation point for leaf photosynthesis	45 p.p.m.	McMurtrie and Wang (1993; Eqn 7) with temperature of 27°C)
ϕ_o	Incident photosynthetically active radiation for growing season	$1.41 \text{ GJ PAR m}^{-2} \text{ year}^{-1}$	Meteorological data
θ	Curvature of photosynthetic light response curve	0.95	
ω	C content of biomass	$0.46 \text{ g C g}^{-1} \text{ DW}$	Biomass data

photosynthesis derived by Sands (1995, 1996). In Sands' model, LUE is a function of the area-based photosynthetic rate at the top of the canopy (A_{\max}). We determine leaf-level A_{\max} by solving a pair of simultaneous equations for the rate of diffusion of CO₂ (CO₂ supply), which depends on stomatal conductance to water vapour (g_s):

$$A_{\max} = g_s ([\text{CO}_2] - C_i)/1.6, \quad (2a)$$

and for CO₂ demand, based on the biochemistry of leaf photosynthesis of C₃ plants (Farquhar and von Caemmerer 1982):

$$A_{\max} = \frac{(C_i - \Gamma^*) J_{\max}}{(C_i + 2\Gamma^*) 4}. \quad (2b)$$

In Eqns 2a and 2b, C_i and [CO₂] represent intercellular and atmospheric CO₂ concentrations, respectively, and Γ^* is the CO₂

compensation point. J_{\max} , which represents the maximum RuBP-regeneration rate for light-saturated leaves at the top of the canopy, is assumed to be proportional to leaf-N content: $J_{\max} = J_{\max 0} \times N_{\text{area}}$, where $J_{\max 0}$ is constant and N_{area} (g N m^{-2}) represents leaf-N content per unit leaf area at the top of the canopy. Eqns 2a and 2b, the so-called photosynthetic supply and demand curves, respectively, are illustrated in Fig. 1 for $[\text{CO}_2]$ of 375 and 550 p.p.m. The curves are shown in Fig. 1a for two values of N_{area} and in Fig. 1b for two values of g_s . Values of $[\text{CO}_2]$ and g_s affect the supply curve, whereas N_{area} affects the demand curve. A_{\max} , evaluated from the intersections of the supply and demand curves in Fig. 1a, b is an increasing function of both N_{area} and g_s , as

shown in Fig. 1c, d. However, there is an important difference in the CO_2 effect on these relationships, which is shown in Fig. 1e, f. The percentage response of A_{\max} to elevated $[\text{CO}_2]$ diminishes as N_{area} declines (Fig. 1e), but increases as g_s declines (Fig. 1f). These contrasting responses can be verified by calculating the ratio of A_{\max} at elevated and ambient CO_2 for high and low N_{area} from the curves in Fig. 1a, and for high and low stomatal conductance from the curves in Fig. 1b. This difference in the response of A_{\max} to N_{area} versus g_s is central to our conclusions in this paper.

The quantum yield (α) of photosynthesis can be obtained from the model of Farquhar and von Caemmerer (1982) in the

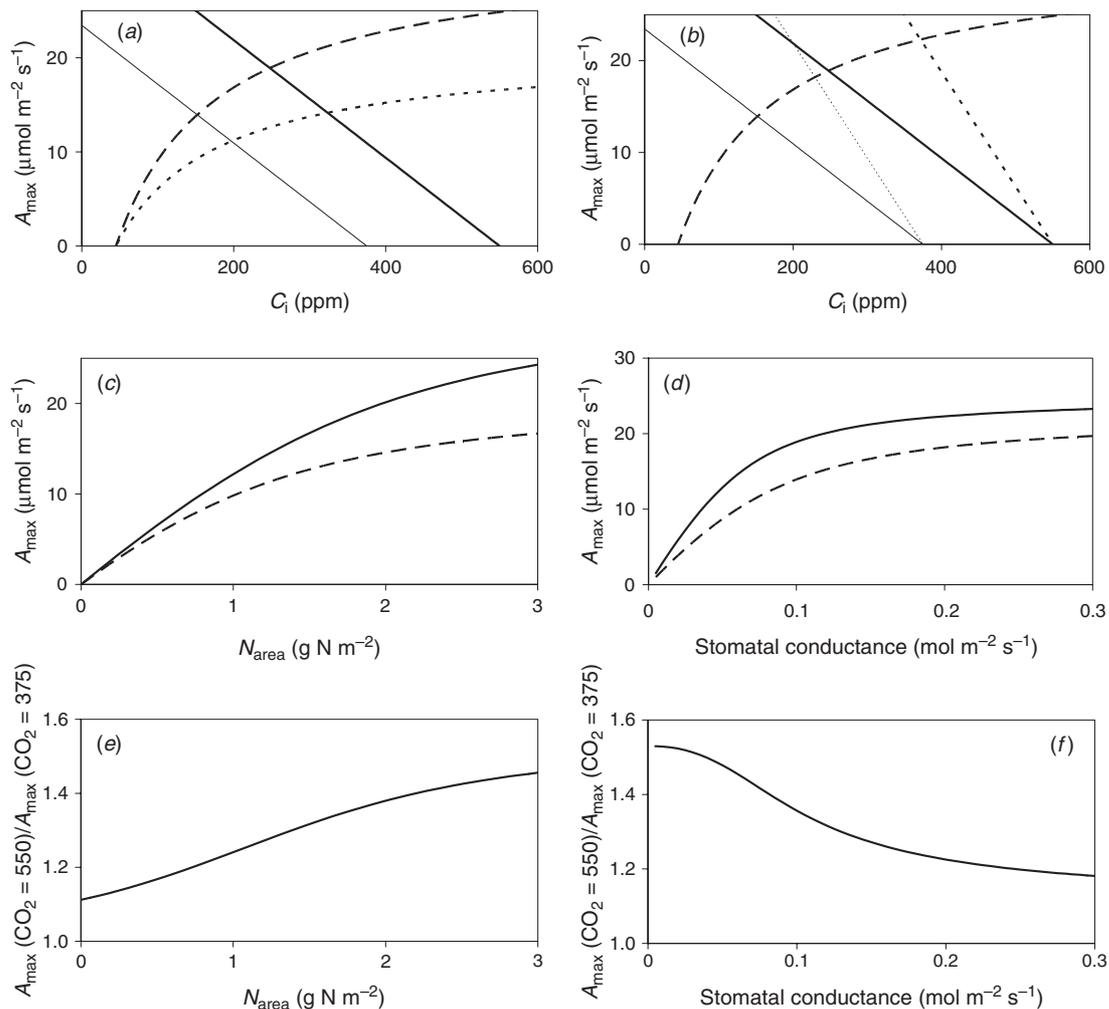


Fig. 1. (a) Photosynthetic supply curves (Eqn 2a) for a CO_2 concentration ($[\text{CO}_2]$) of 375 (thin solid line) and 550 p.p.m. (thick solid line) with stomatal conductance (g_s) = $0.1 \text{ mol m}^{-2} \text{ s}^{-1}$, and demand curves for leaf-nitrogen content (N_{area}) = 1.2 and 1.8 g N m^{-2} (dots and dashes, respectively). (b) Supply curves for $[\text{CO}_2]$ of 375 (thin lines) and 550 p.p.m. (thick lines) with g_s = 0.1 (solid) and 0.2 (dots) $\text{mol m}^{-2} \text{ s}^{-1}$ and demand curves for $N_{\text{area}} = 1.8 \text{ g N m}^{-2}$ (dashes), which is the measured value of N_{area} at top of the sweetgum canopy (Norby and Iverson 2006). (c) The dependence of light-saturated photosynthetic rate A_{\max} on N_{area} with a fixed g_s of $0.1 \text{ mol m}^{-2} \text{ s}^{-1}$ and (d) on g_s when $N_{\text{area}} = 1.8 \text{ g N m}^{-2}$ for $[\text{CO}_2]$ of 375 (dashed lines) and 550 p.p.m. (solid lines) under the assumption that J_{\max} is proportional to leaf-N content. (e) The proportional response of A_{\max} to elevated $[\text{CO}_2]$ with increasing leaf-N content. (f) The proportional response of A_{\max} to elevated $[\text{CO}_2]$ with increasing g_s .

limit as C_i approaches ambient [CO₂] (cf. McMurtrie and Wang 1993):

$$\alpha = 0.07 \frac{([\text{CO}_2] - \Gamma^*)}{([\text{CO}_2] + 2\Gamma^*)}, \quad (3)$$

which gives α values of 0.050 and 0.055 for [CO₂] of 375 and 550 p.p.m., respectively.

Sands (1995, 1996) evaluates daily canopy photosynthesis under the following assumptions: (1) the photosynthetic light response is a non-rectangular hyperbolic function of photon-flux density with a light-saturated photosynthetic rate (A_{\max}), quantum yield (α) and curvature (θ), (2) the canopy is horizontally uniform, (3) PAR distribution within the canopy obeys Beer's law (Eqn 1), (4) light-saturated photosynthetic rate declines with canopy depth in proportion to the vertical decline of PAR, (5) α and θ do not vary within the canopy, and (6) diurnal variation of incident PAR is sinusoidal. The model makes no explicit assumption about N distribution within the canopy. Sands (1995, 1996) derives an equation for daily canopy photosynthesis as the product of APAR, given by Eqn 1, and LUE, expressed as an integral over-canopy depth and over the diurnal cycle. For simplicity we ignore the temperature dependences of J_{\max} , α and Γ^* , and we assume that incident PAR is constant over the growing season. Annual GPP takes the form:

$$\text{GPP} = \text{LUE} \times \text{APAR}. \quad (4)$$

Like A_{\max} , the canopy-scale variable LUE is an increasing function of both leaf-N content (N_{area}) and stomatal conductance

(g_s) (Fig. 2*a, b*). The upper limit to LUE is set by the quantum yield. The N-dependence of LUE (Fig. 2*a*) is weaker than the N-dependence of light-saturated photosynthesis (A_{\max} , Fig. 1*c*) because a substantial portion of the leaf canopy is below light saturation. LUE increases with [CO₂] at all levels of N_{area} and g_s , but there is a qualitative difference between the CO₂ dependences, as shown in Fig. 2*c, d*. The percentage response of LUE to increased [CO₂] decreases as N_{area} declines, provided N_{area} is less than $\sim 1.8 \text{ g N m}^{-2}$ (Fig. 2*c*), whereas the percentage response of LUE to increased [CO₂] increases as g_s declines (Fig. 2*d*). This contrast is a direct consequence of the dependences of A_{\max} on leaf-N content and g_s (Fig. 1).

Net primary production is obtained by subtracting plant respiration, which we assume to be a fixed fraction of GPP:

$$\text{NPP} = \text{GPP} \times \text{CUE}, \quad (5)$$

where CUE, the so-called carbon-use efficiency, represents plant biomass production per unit gross carbon fixation. We assume constant CUE, which is supported by data from the Oak Ridge experiment and other sites (Norby *et al.* 2002, 2006; DeLucia *et al.* 2005, 2007), as well as by modelling studies (Dewar *et al.* 1998, 1999). This approach for evaluating NPP is favoured over the alternative of determining NPP from explicit equations for autotrophic respiration because our model does not simulate the carbon and nitrogen contents of the roots and stems, which would be needed to evaluate whole-stand maintenance and growth respirations. We use the model to

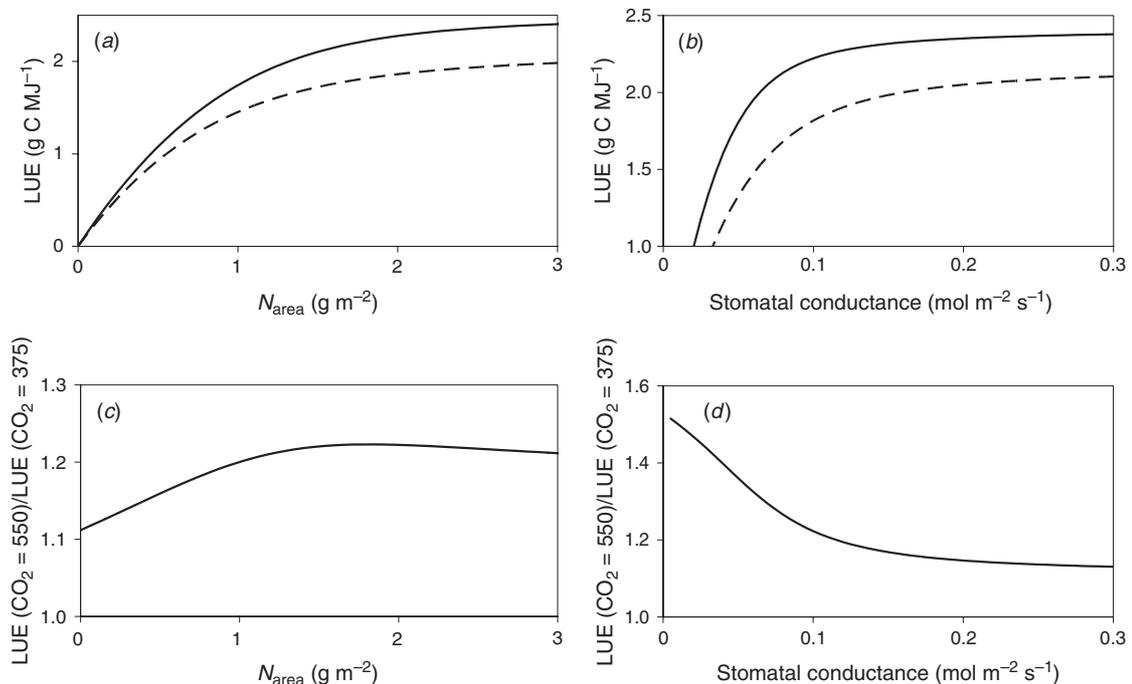


Fig. 2. (a) The dependence of light-use efficiency (LUE; g C MJ⁻¹ photosynthetically active radiation) on leaf-nitrogen content at the top of the sweetgum canopy (N_{area} ; g m⁻²) with fixed stomatal conductance (g_s) (= 0.1 mol m⁻² s⁻¹), and (b) on g_s (mol m⁻² s⁻¹) for fixed N_{area} (= 1.8 g N m⁻²) for a CO₂ concentration ([CO₂]) of 375 (dashed lines) and 550 p.p.m. (solid lines). Proportional responses of LUE to elevated [CO₂] as functions of (c) N_{area} and (d) g_s .

evaluate the 'canopy carbon export' (C_{exp}), that is, the net carbon available to grow wood and fine roots after accounting for plant respiration. C_{exp} is equal to NPP minus the carbon used for annual leaf growth:

$$C_{\text{exp}} = \text{NPP} - C_f = \text{NPP} - \frac{\text{LAI} \omega}{\text{SLA}}, \quad (6)$$

where C_f is the annual foliar carbon production, SLA is the canopy-average specific leaf area (leaf surface area per unit dry weight) and ω is the carbon content of the biomass.

Thus, our expressions for GPP, NPP and C_{exp} (Eqns 4, 5 and 6) all depend on the canopy variables N_{area} , g_s and LAI, and on $[\text{CO}_2]$.

Annual nitrogen balance

Annual N balance requires that annual N flux to aboveground pools (U , $\text{g N m}^{-2} \text{ year}^{-1}$) is equal to annual N allocation to grow new wood and leaves (cf. McMurtrie 1991):

$$U = \frac{(1-r) [N]_f C_f + [N]_w C_w}{\omega}, \quad (7)$$

where C_f and C_w are the annual C production of leaves and wood, $[N]_f$ is the canopy-average foliar N concentration, $[N]_w$ is the N concentration of new wood, and r is the fraction of canopy N derived through internal recycling (i.e. from N retranslocated at leaf senescence). At the Oak Ridge experiment, annual N flux to aboveground pools (U), estimated from biomass C and N data, varied between 4 and $7 \text{ g N m}^{-2} \text{ year}^{-1}$ among five plots over the first 9 years of the FACE experiment, and did not differ significantly between CO_2 treatments (cf. Norby and Iversen 2006). Furthermore, the measured values of the expression $([N]_w C_w / C_{\text{exp}})$ are proportional to $[N]_f$ with $[N]_w C_w / C_{\text{exp}} = \lambda [N]_f$, where $\lambda = 0.061$ at both current and elevated $[\text{CO}_2]$. Eqn 7 then gives an equation relating C_{exp} to annual N uptake (U):

$$C_{\text{exp}} = \frac{U - (1-r)[N]_f \text{LAI} / \text{SLA}}{\lambda [N]_f / \omega} \quad (8)$$

Annual water balance

Stomatal conductance is evaluated from an equation for annual water balance at a level of simplicity that is comparable to the above N-balance model. We assume that annual plant water use is a fixed fraction (f_w) of the annual rainfall (RF). The fraction $1-f_w$ represents water lost through evaporation of rainwater intercepted by the canopy or drainage below the rooting zone or runoff. The value of f_w typically ranges from 0.7 to 0.9 depending on the frequency and intensity of rainfall events and on rooting depth (Eamus *et al.* 2006). For a tree canopy well coupled to the atmosphere, tree water use is proportional to $\text{VPD} \times G_c$, where VPD represents the daylight vapour-pressure deficit averaged over the growing season, and G_c is the canopy conductance represented by $G_c = g_s \times \text{LAI}$ (Jarvis and McNaughton 1986), where g_s is assumed to be constant with canopy depth. For

simplicity we assume that VPD is constant. Annual water use for a tree-only system with no understorey is:

$$f_w \text{RF} = C \text{VPD} g_s \text{LAI} f_L f_S, \quad (9)$$

where C is a product of the physical constants in the Penman-Monteith equation and f_S represents growing-season length as fraction of the year. We assume that, when trees are absent, the annual water use by the understorey, including ground evaporation, is equal to $f_w \times \text{RF}$ and, when trees are present, it is reduced from this by a factor $\exp(-k_w f_L \text{LAI})$, where k_w is a water-flux extinction coefficient that characterises the attenuation of understorey evapo-transpiration as a function of overstorey LAI. For instance, for ground vegetation that is weakly coupled to the atmosphere, k_w would represent the attenuation of net radiation. If both trees and understorey are present, the equation for annual water balance is:

$$f_w \text{RF} = C \text{VPD} g_s \text{LAI} f_L f_S + f_w \text{RF} \exp(-k_w f_L \text{LAI}), \quad (10)$$

or rearranging terms:

$$C \text{VPD} g_s \text{LAI} f_L f_S = f_w \text{RF} (1 - \exp(-k_w f_L \text{LAI})). \quad (11)$$

This leads to an inverse relationship between stomatal conductance and LAI:

$$g_s = \frac{f_w \text{RF} (1 - \exp(-k_w f_L \text{LAI}))}{C \text{VPD} f_L f_S \text{LAI}}. \quad (12)$$

Water and nitrogen constraints

Annual water balance places a constraint on the relationship between LAI and tree stomatal conductance given by Eqn 12. The water-balance constraint is shown in Fig. 3a for years with annual rainfall of 800, 1200 and 1600 mm. The values of g_s and LAI must lie somewhere on this constraint line. In other words, for a given annual rainfall, the canopy can 'opt' for a low LAI with high g_s or for a high LAI with low g_s , or for an intermediate LAI with intermediate g_s .

Similarly, the annual nitrogen balance imposes a constraint between LAI and leaf $[\text{N}]$, which can be derived by equating Eqns 6 and 8, by assuming leaf $[\text{N}]$ is constant with canopy depth (Norby and Iversen 2006), and by calculating leaf-N content at the top of the canopy from the canopy-average N concentration: $N_{\text{area}} = [N]_f / \text{SLA}_o$, where SLA_o is the specific leaf area at the top of the canopy. The relationship between LAI and leaf $[\text{N}]$ is shown in Fig. 3b for $g_s = 0.1 \text{ mol m}^{-2} \text{ s}^{-1}$ and for N-uptake rates of 2, 4 and $6 \text{ g N m}^{-2} \text{ year}^{-1}$. The values of leaf $[\text{N}]$ and LAI must lie somewhere on this constraint line. Thus, for a given annual N uptake, the canopy can 'opt' for a low LAI with high $[\text{N}]$ or for a high LAI with low $[\text{N}]$, or for an intermediate LAI with intermediate $[\text{N}]$.

Taken together, these constraint lines (Fig. 3a, b) impose two relationships between g_s , LAI and leaf $[\text{N}]$ so that only one out of these three canopy variables can be varied independently. In the next section we will examine how forest productivity varies with g_s , LAI and leaf $[\text{N}]$, taking into account the constraints between

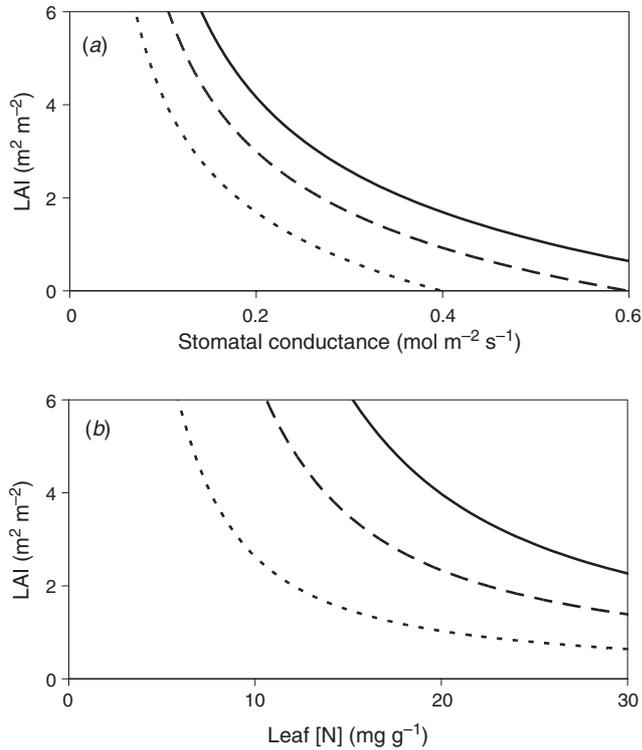


Fig. 3. (a) The relationship between leaf area index (LAI) and stomatal conductance (g_s) derived from annual the water balance (Eqn 10) for forest stands with contrasting water supply (annual rainfall = 800, 1200 and 1600 mm year⁻¹; dotted, dashed and solid lines, respectively). (b) The relationship between LAI and leaf-nitrogen concentration derived from the nitrogen balance for forest stands with contrasting fertility (N uptake = 2, 4 and 6 g N m⁻² year⁻¹; dotted, dashed and solid lines, respectively) for fixed g_s (= 0.1 mol m⁻² s⁻¹).

these three variables imposed by annual water and nitrogen balances.

Modelling questions

Our primary aim is to use the model to investigate plant responses to elevated CO₂ under nitrogen and water limitation and to examine the qualitative relationship between productivity and nitrogen and water supplies. We applied the model to two related issues:

- (1) How does annual NPP depend on leaf [N], stomatal conductance (g_s) and LAI? This question will be addressed for a year with relatively high annual rainfall (RF = 1200 mm) and relatively high N uptake to aboveground pools ($U = 6$ g N m⁻² year⁻¹). We will show that there are optimal leaf [N], g_s and seasonal peak LAI that maximise annual NPP.
- (2) How does maximum NPP depend on [CO₂] for years with contrasting annual rainfall (RF = 800 and 1200 mm) and contrasting N uptake ($U = 4$ and 6 g N m⁻² year⁻¹)? How do the optimal values of leaf [N], g_s and LAI shift at high [CO₂]?

We evaluated NPP as a function of leaf [N], g_s and LAI. Because these three variables are related through water and nitrogen balances, as illustrated in Fig. 3 and discussed above, C_{exp} can be evaluated as a function of leaf [N] or g_s or LAI alone. NPP can then be calculated from C_{exp} using Eqn 6.

We parameterised the MATEY model for deciduous sweetgum trees growing at the Oak Ridge FACE experiment at [CO₂] of 375 and 550 p.p.m. During each growing season the deciduous tree canopy expands until it reaches peak LAI, following seasonal patterns described by Norby *et al.* (2003). The model predicts annual NPP as a function of peak LAI achieved once the canopy is fully expanded, annual rainfall (RF), growing-season incident PAR (ϕ_0), average growing-season VPD and annual N uptake (U) to aboveground pools, all of which vary from year to year at the Oak Ridge site. Although we will compare the model output with the experimental results, it is not our aim to develop a model that closely fits the experimental data. Parameter values for the model are listed in Table 1.

Results

How does NPP depend on leaf [N], g_s and LAI?

Curves for NPP at current CO₂ are shown in Fig. 4 as functions of leaf [N] or g_s or LAI for a year with N uptake $U = 6$ g N m⁻² year⁻¹ and RF = 1200 mm, and for years with the same RF, but with reduced N uptake ($U = 4$ g N m⁻² year⁻¹, RF = 1200 mm), and with the same U , but with reduced RF ($U = 6$ g N m⁻² year⁻¹, RF = 800 mm). All three curves have peaks with respect to leaf [N] (Fig. 4a), g_s (Fig. 4b) and LAI (Fig. 4c). The existence of a peak in NPP with respect to LAI (Fig. 4c) can be understood as the result of a trade-off between APAR and LUE. As LAI increases, APAR increases asymptotically (Eqn 1), but g_s and leaf [N] both decline because of water and N limitations (Fig. 3), so that LUE declines steadily (Fig. 2a, b). Thus, at low values of LAI, APAR is low, but g_s and leaf [N] and LUE are high. Conversely, at high values of LAI, APAR is high, but g_s and leaf [N] and LUE are low. At either extreme of LAI, NPP (= CUE × LUE × APAR) is low, so that NPP is maximised at some intermediate value of LAI. The existence of the peaks in NPP with respect to leaf [N] (Fig. 4a) and g_s (Fig. 4b) then follows from the water- and nitrogen-balance constraints depicted in Fig. 3.

When U is reduced by 33%, the maximum NPP declines by 10% (Fig. 4), and the peak shifts to reduced leaf [N] and LAI, but increased g_s . When rainfall is reduced by 33%, the maximum NPP again declines by 10% (Fig. 4), but the peak shifts to reduced g_s and LAI, and increased leaf [N]. Table 2 shows that as the rainfall increases at fixed [CO₂], the optimum shifts to higher g_s and LAI and to lower leaf [N], whereas when N supply increases at fixed CO₂ the optimum shifts to higher leaf [N] and LAI and to lower g_s . The predicted shift towards reduced leaf [N] with increasing rainfall is consistent with field observations of lower leaf [N] at higher rainfall and of higher leaf [N] at any given SLA in drier than wetter regions (Reich *et al.* 1999; Wright *et al.* 2003). The shift towards higher leaf [N] at lower rainfall has in the past been associated with a greater drawdown of inter-cellular [CO₂], such that low-rainfall species achieve higher photosynthetic

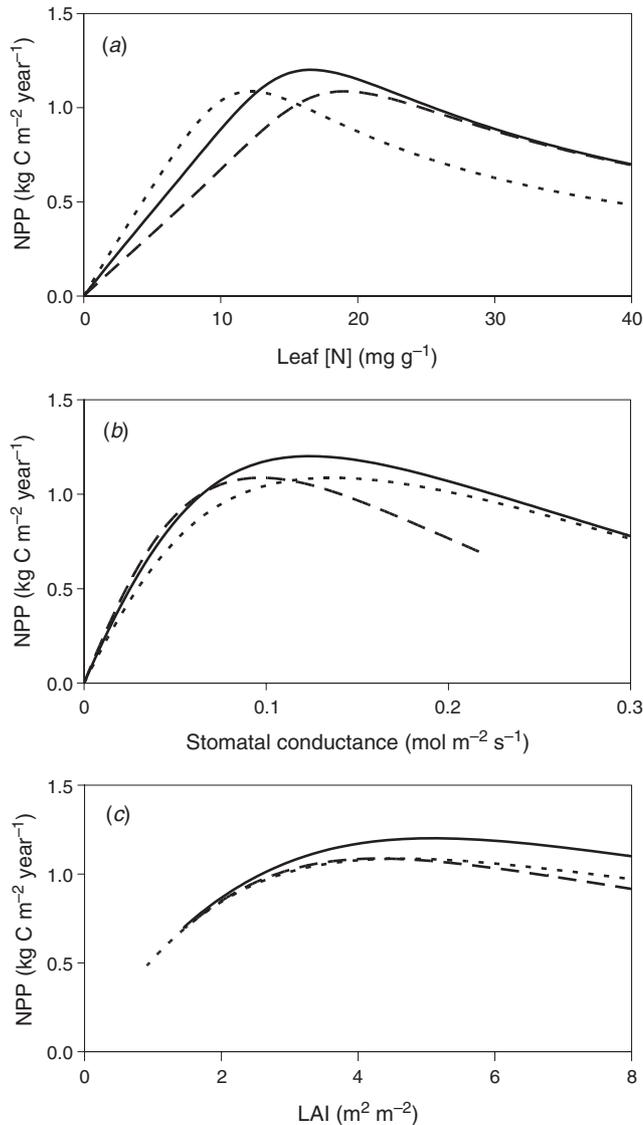


Fig. 4. Simulated net primary production (NPP; Eqn 5) as a function of (a) average leaf-N concentration, (b) stomatal conductance (g_s) and (c) leaf area index (LAI) for a stand with N uptake $U = 6 \text{ g N m}^{-2} \text{ year}^{-1}$ and annual rainfall RF = 1200 mm (solid lines), $U = 4 \text{ g N m}^{-2} \text{ year}^{-1}$ and RF = 1200 mm (dotted lines) and $U = 6 \text{ g N m}^{-2} \text{ year}^{-1}$ and RF = 800 mm (dashed lines).

Table 2. Model optima at ambient and elevated CO₂ concentration ([CO₂])

The optima at [CO₂] of 375 and 550 p.p.m., respectively, followed by the percentage CO₂ response (given in parentheses) for plant parameters (stomatal conductance, leaf [N], light-use efficiency (LUE), leaf area index (LAI), absorbed photosynthetically active radiation (APAR), net primary production (NPP) and carbon export (C_{exp})), where NPP is maximised. Results are given for stands with low and high N uptake to aboveground pools ($U = 4$ and $6 \text{ g N m}^{-2} \text{ year}^{-1}$) and low and high annual rainfall (RF = 800 and 1200 mm)

Year	Stomatal conductance (mol m ⁻² s ⁻¹)	Leaf [N] (mg N g ⁻¹ DW)	LUE (g C MJ ⁻¹ PAR)	LAI	APAR (GJ m ⁻² year ⁻¹)	NPP (kg C m ⁻² year ⁻¹)	C_{exp} (kg C m ⁻² year ⁻¹)
Low N, Low RF	0.102, 0.090 (-12)	13.5, 11.6 (-14)	1.80, 2.04 (+14)	4.1, 4.7 (+14)	1.12, 1.18 (+5)	1.00, 1.20 (+20)	0.83, 1.01 (+21)
Low N, High RF	0.135, 0.124 (-9)	12.2, 10.9 (-11)	1.85, 2.07 (+12)	4.6, 5.1 (+10)	1.17, 1.21 (+3)	1.09, 1.26 (+16)	0.89, 1.04 (+17)
High N, Low RF	0.097, 0.083 (-14)	19.0, 15.9 (-16)	1.90, 2.20 (+15)	4.3, 5.1 (+18)	1.14, 1.21 (+6)	1.09, 1.33 (+22)	0.91, 1.12 (+23)
High N, High RF	0.124, 0.109 (-12)	16.6, 14.3 (-14)	1.98, 2.25 (+13)	5.1, 5.8 (+14)	1.21, 1.26 (+4)	1.20, 1.42 (+18)	0.99, 1.17 (+19)

rates at a given stomatal conductance (Reich *et al.* 1999; Wright *et al.* 2003).

How does maximum NPP depend on [CO₂]?

We evaluated the optima where NPP is maximised at current and elevated CO₂. Fig. 5 illustrates the effects of elevated CO₂ on NPP as a function of leaf [N], g_s and LAI for a year with high N uptake ($U = 6 \text{ g N m}^{-2} \text{ year}^{-1}$) and high annual rainfall (RF = 1200 mm). The peak value of NPP is higher at elevated CO₂ than current CO₂, but the optimum shifts to lower values of leaf [N] and g_s and higher values of LAI. These CO₂ responses are summarised in Table 2. The model predicts an 18% increase in maximum NPP at elevated CO₂.

To examine the interactive effects of CO₂, rainfall and N supply, we evaluated the CO₂ response for years with low and high N uptake ($U = 4$ and $6 \text{ g N m}^{-2} \text{ year}^{-1}$) and low and high annual rainfall (RF = 800 and 1200 mm). Optimal g_s and leaf [N] decline under increased [CO₂], while LAI and NPP increase. These changes are greatest in the dry, high-N year and lowest in the wet, low-N year. The [CO₂] responses in the wet, high-N and dry, low-N years are intermediate between these two extremes. The percentage changes are shown in parentheses in Table 2.

Discussion

Comparison with experimental data from the Oak Ridge site

In view of the model's simplicity, we do not expect it to closely match the experimental data. Nevertheless, the modelled variables shown in the Figures and in Table 2 have all been measured at the Oak Ridge FACE experiment, and it is instructive to compare the model outputs with field data. Simulated values of A_{max} at current and elevated CO₂ (Fig. 1c) are comparable with the values measured for upper-canopy leaves in 1999–2000, when N_{area} ranged from 1.6 to 2.2 g N m⁻² (Gunderson *et al.* 2002; Tissue *et al.* 2002; Sholtis *et al.* 2004). Our conclusion that the ratio A_{max} at elevated [CO₂] to A_{max} at current [CO₂] increases as g_s declines is confirmed by data in Norby *et al.* (2006; fig. 13.2). Modelled values of stomatal conductance in Table 2 cannot be compared with measured values (Gunderson *et al.* 2002) because modelled values of g_s represent seasonal, whole-canopy averages. It should be noted, however, that modelled g_s declines by 9–14% at elevated CO₂ compared with current CO₂, whereas the

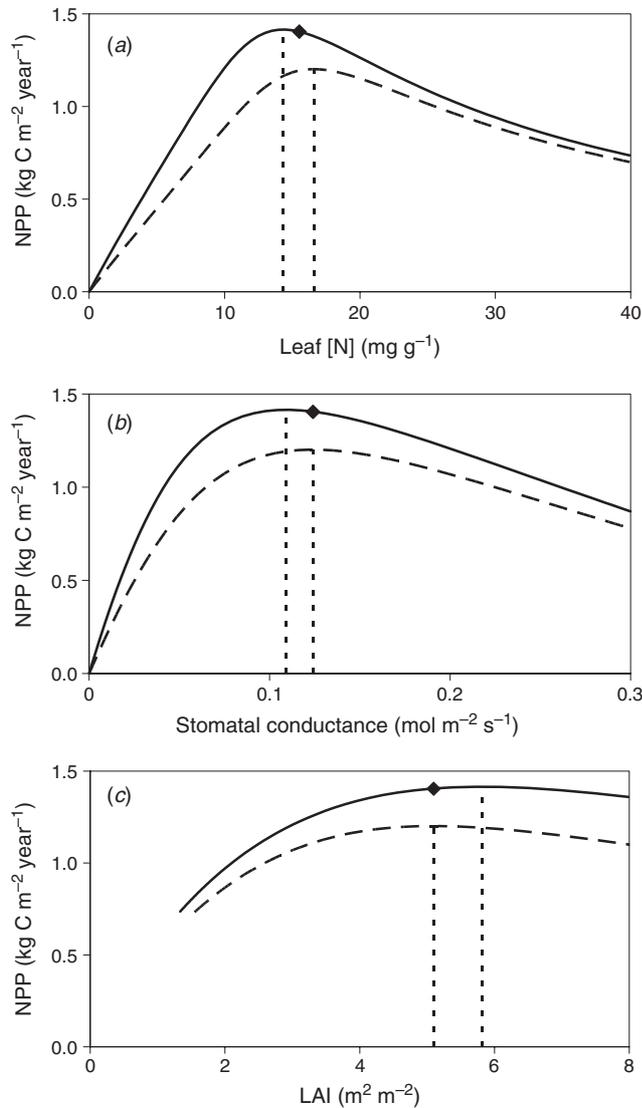


Fig. 5. Values of net primary production (NPP; Eqn 5) at a CO₂ concentration ([CO₂]) of 375 (dashed lines) and 550 p.p.m. (solid lines) as functions of (a) average leaf-N concentration, (b) stomatal conductance (g_s) and (c) leaf area index (LAI) for a stand with N uptake $U = 6 \text{ g N m}^{-2} \text{ year}^{-1}$ and annual rainfall $RF = 1200 \text{ mm}$. The optima at current and elevated CO₂ are indicated by dashed vertical lines. Diamonds indicate the effect if g_s is the same at current and elevated CO₂.

measured g_s was 24% lower at elevated CO₂ in the upper canopy, but did not differ significantly from current CO₂ in the mid-canopy (Gunderson *et al.* 2002). The modelled values of leaf [N] in Table 2 are consistent with the range of measured leaf [N] (13–19 mg g^{-1} at current CO₂ and 11–17 mg g^{-1} at elevated CO₂) reported by Norby and Iversen (2006). The modelled decline of leaf [N] at elevated CO₂ (11–16%) is larger than the average measured decline of 10% (Norby and Iversen 2006; Norby *et al.* 2006). The modelled values of LUE and APAR in Table 2 agree broadly with the measured values (Norby *et al.* 2003, 2006). The model underestimates seasonal peak LAI, with optimal values

ranging from 4.1 to 5.8 (Table 2) compared with measured LAI values of 5 to 6 (Norby *et al.* 2003). The NPP at current and elevated CO₂ (Table 2) is slightly overestimated by the model, while modelled percentage increases in NPP (ranging from 16 to 22%; Table 2) are similar to the measured increases (13–27% with an average increase of 21%; Norby *et al.* 2006). The model predicts that increased NPP at elevated CO₂ is achieved predominantly through an increase in LUE rather than APAR, which is consistent with the conclusions from the measurements (Norby *et al.* 2005; McCarthy *et al.* 2006; Table 2).

Why are plant-growth responses to elevated CO₂ amplified when water is limiting, but reduced when nitrogen is limiting?

The answer to this question lies in the leaf-scale photosynthetic responses illustrated in Fig. 1. As noted earlier, A_{max} is an increasing function of both leaf [N] (Fig. 1c) and stomatal conductance (Fig. 1d), and both functions increase as [CO₂] increases. However, there is one important difference: the ratio of A_{max} at elevated [CO₂] to A_{max} at current [CO₂] decreases with decreasing leaf [N] (Fig. 1e), but increases with decreasing stomatal conductance (Fig. 1f).

These leaf-scale trends manifest themselves at the canopy scale in the relative responses of LUE to [CO₂] (Fig. 2). This means that, as leaf [N] declines under N limitation (Table 2), LUE becomes less sensitive to [CO₂]. In contrast, as stomatal conductance declines under water limitation (Table 2), LUE becomes more sensitive to [CO₂]. In turn, NPP (which is proportional to LUE) becomes less sensitive to [CO₂] under N limitation and more sensitive to [CO₂] under water limitation, as shown in Table 2. These model results are in accord with the findings from high-CO₂ experiments summarised in the Introduction. The model's prediction of an enhanced CO₂ response at low stomatal conductance is in accord with an observation at the Duke Forest FACE experiment that annual stem-growth response to high CO₂ is greatest in years with high VPD (Moore *et al.* 2006). A more direct test of the model's predictions of amplified CO₂ response at low stomatal conductance and at high leaf [N] is possible from high CO₂ experiments that provide hourly or daily CO₂-exchange data (e.g. Medhurst *et al.* 2006). The above physiological explanation for the interactive effects of CO₂, water and nitrogen does not invoke any potential soil feedbacks, although the model does not exclude the possibility that soil feedbacks will operate and may be responsible for reduced N uptake under elevated CO₂, as proposed by Comins and McMurtrie (1993).

Are the CO₂ responses predicted by MATEY relevant to systems other than water- and N-limited deciduous trees? The estimates of NPP and the CO₂ responses presented in Table 2 follow as consequences of the results in Figs 1 to 3. The equations for photosynthesis represented in Fig. 1 are applicable to all C₃ plants. Calculations of LUE (Fig. 2) are applicable to any canopy satisfying the above six assumptions made by Sands (1995). The calculations shown in Fig. 3b depict a trade-off between LAI and leaf [N] that will generally occur in N-limited systems. Fig. 3b will not apply, however, when growth is limited by an element other than nitrogen, such as phosphorus.

If growth is P limited, then Fig. 3*b* should be replaced by a curve expressing a trade-off between LAI and P concentration, and LUE should be expressed as a function of [P]. The N-balance constraint, represented by Eqn 7, assumes a deciduous canopy that is replaced annually. The model can be extended to non-deciduous canopies if we make the further assumption that LAI and canopy N are in a steady-state. The water-balance constraint depicted in Fig. 3*a* as a trade-off between LAI and g_s will apply to any water-limited system for which plant water use is proportional to canopy conductance $G_c (= LAI \times g_s)$.

Fig. 1*e* indicates that A_{max} is more sensitive to $[CO_2]$ at high N_{area} than at low N_{area} . Does that imply that the percentage increase of A_{max} at high CO_2 should be larger under high-N conditions than under low-N conditions? The evidence from FACE experiments is that stimulation of A_{max} at elevated CO_2 is 23% lower under low-N conditions (Ainsworth and Long 2005; Ainsworth and Rogers 2007). Based on the above photosynthesis model (Eqn 2), however, the answer to this question will not necessarily be yes because realised values of A_{max} at high $[CO_2]$ are net of any changes in both leaf [N] and stomatal conductance (Ellsworth *et al.* 2004; Reich *et al.* 2006*b*). If reductions in leaf [N] and stomatal conductance at high CO_2 are both greater in high-N conditions than in low-N conditions, as indicated in Table 2, then our model may be consistent with two particular experiments, which found that measured A_{max} is equally sensitive to $[CO_2]$ under low- and high-N conditions (Reich *et al.* 2006*b*). To address this issue properly it would be necessary to extend our photosynthesis model (Eqn 2*b*) to include the N dependence of the maximum carboxylation rate (McMurtrie and Wang 1993; Ainsworth and Rogers 2007).

Interpreting variations in leaf [N] and stomatal conductance as optimal responses

Table 2 shows that with increasing rainfall, the optimal operating point shifts to higher stomatal conductance and lower leaf [N], whereas the opposite response occurs with increasing N supply. LAI increases in both cases. Thus, there is a strong interaction between nitrogen and water for maximisation of productivity, reflecting the fact that the annual water- and nitrogen-balance constraints operate simultaneously in the model, so that a change in one constraint modifies the effect of the other (cf. Farquhar *et al.* 2002; Wright *et al.* 2003).

Optimal leaf [N] and stomatal conductance both decline at elevated CO_2 for all four simulations presented in Table 2, in agreement with the results of CO_2 enrichment experiments (e.g. Ainsworth and Long 2005). Reduced leaf [N] and g_s are not detrimental to the NPP of high- CO_2 plants because photosynthesis is more efficient at high CO_2 . Therefore, the plant can reduce its leaf [N] and can partially close its stomata, enabling it to maintain a higher LAI and a slightly enhanced NPP. In terms of the above Figures, optimal leaf [N] and g_s decline because as $[CO_2]$ increases, LUE increases and approaches its asymptotic value at reduced leaf [N] and g_s , as illustrated in Fig. 2*a, b*. Reductions in both leaf [N] and stomatal conductance at the optimum are greatest in the dry, high-N year, and lowest in the wet, low-N year. This difference occurs because LUE is most sensitive to $[CO_2]$ under water limitation and least sensitive under nitrogen limitation. Thus, the percentage

reductions in leaf [N] and g_s depend on the relative steepness of the LUE functions in Fig. 2 at current and elevated CO_2 .

Numerous experiments have shown that elevated CO_2 stimulates leaf photosynthesis of C_3 plants and lowers stomatal conductance (Medlyn *et al.* 1999, 2001; Ainsworth and Long 2005). These two responses are normally portrayed in the literature as having dissimilar and unrelated effects on productivity, with increased photosynthesis having a direct effect and reduced g_s having an indirect effect through water savings and a lengthened growing season (e.g. Shaw *et al.* 2005). This view has led to concerted efforts to quantify water savings in field CO_2 -enrichment experiments, often concluding that such savings are modest (Wullschlegel *et al.* 2002). In contrast to that view, our physiology-based model assumes no water savings at elevated CO_2 on an annual timescale. The model puts reduced leaf [N] and reduced stomatal conductance on an equal footing as optimal acclimation responses that enhance productivity at elevated CO_2 . This notion of integration of C, N and water relations is consistent with evidence that decreased stomatal conductance at elevated CO_2 can actually contribute to photosynthetic down-regulation, usually attributed only to declining leaf [N] (Lee *et al.* 2001).

What can we conclude about species that show little or no stomatal closure at elevated CO_2 ? According to our model the optimal response is for stomata to close with increasing CO_2 . Non-optimal responses may be expected, however, if the modelled NPP is relatively insensitive to g_s . Thus, there will be little benefit in closing stomata at high CO_2 if the graph of NPP versus g_s is relatively flat, which is the case for Fig. 5*b*. If stomata do not close at elevated CO_2 then we infer from the water-balance constraint (Eqn 12) that LAI will not change at high CO_2 and from Fig. 5*a* that the reduction in leaf [N] at high CO_2 will be smaller than that predicted at the optimum (see the diamond symbols in Fig. 5).

The objective of maximising canopy photosynthesis or NPP is common in the plant-modelling literature (e.g. Ackerly 1999; Anten 2005; Hikosaka 2005). Some previous models based on the maximisation of NPP have predicted optimal LAIs that exceed observed LAIs (Anten *et al.* 1995). However, in most of these studies the objective was to maximise the carbon gain for fixed-canopy N content. One model whose optimum does closely match the observed LAIs is that of Franklin and Ågren (2002) and Franklin (2007), who credited their model's success to its inclusion of leaf senescence and leaf-N retranslocation. Both processes are incorporated in the above model (Eqn 7).

Future model development

By assuming constant nitrogen uptake to aboveground pools, we are ignoring the role of roots in nitrogen acquisition, a dominant aspect of the CO_2 response at the Oak Ridge FACE experiment (Norby *et al.* 2004), and soil decomposition processes, which may immobilise nitrogen at high CO_2 (e.g. Luo *et al.* 2004) and may even override plant physiological responses to high CO_2 (Medlyn *et al.* 2000). Existing equilibrium-based approaches for evaluating N uptake from models incorporating biogeochemistry and N losses as a result of forest management practices (e.g. Comins and McMurtrie 1993; Dewar and

McMurtrie 1996; McMurtrie and Comins 1996) could be integrated with our plant model. The N-cycling constraints described in these models would replace the N-balance model above (Eqn 7). Thus, while our main aim here has been to show that a model based on leaf physiology alone can explain many features of the observed CO₂ responses, we acknowledge the importance of including roots and soil feedbacks in models of plants at high CO₂.

Our assumption that tree water use is proportional to canopy conductance is strictly appropriate only for low LAI canopies that are tightly coupled to atmospheric conditions. In canopies with high LAI, and on regional scales, transpiration may be more weakly related to canopy conductance. Moreover, our assumption of constant stomatal conductance is a gross simplification of a highly dynamic process. Because LUE is a non-linear, saturating function of stomatal conductance (Fig. 2), our use of a time-averaged stomatal conductance will overestimate GPP. Another over-simplification is the assumption that a constant proportion of annual rainfall is transpired. Notwithstanding these shortcomings, the model does provide qualitative insights into the interplay between CO₂-induced stomatal closure and increased leaf area. The above shortcomings could be dealt with in a more detailed, daily time-step carbon–water–nitrogen cycling model incorporating a relationship between canopy interception of precipitation and LAI. One attraction of retaining an optimisation approach, however, is that variables such as stomatal conductance, leaf [N], water- and nitrogen-use efficiency are emergent properties predicted by the model, rather than model inputs or submodels.

Once roots and stems are incorporated into the MATEY model it will be possible to evaluate whole-stand maintenance respiration, which scales with total plant N content (Ryan 1991; Reich *et al.* 2006c) and is temperature dependent, and growth respiration, which is proportional to the carbon used for growing new biomass. This will represent an advance over the less mechanistic approach of assuming constant CUE. It is known for instance that CUE is variable and tends to be higher in young stands and possibly under wet or fertile conditions (e.g. Mäkelä and Valentine 2001; DeLucia *et al.* 2007). Another potential model application is to simulate the impacts of greenhouse warming on plant productivity. Several parameters in Table 1 are temperature dependent, in particular J_{\max} , α , Γ^* , CUE, VPD and N uptake (Medlyn *et al.* 2000).

The optimisation approach developed in this paper provides a tool for determining the upper limit to plant productivity as a function of site nitrogen and water supplies that should prove useful for evaluating carbon-storage potential. It is not clear, however, that plants will adapt to maximise NPP. Our stand-scale optimisation hypothesis may be viewed as only an approximation to natural selection at the scale of the individual. Optimisation at the individual scale, for example, using game-theory approaches, may predict that stand productivity will be slightly suboptimal because each individual must compete with its neighbours for resources, and so it may be in each individual's interest to maintain its resource capture of light, nitrogen or water above the stand-scale optimum (e.g. King 1993; Schieving and Poorter 1999; Anten 2002). As

noted above, however, our stand-scale optimisation hypothesis is consistent with global trends in the variations in leaf traits of numerous species across sites varying in rainfall (Reich *et al.* 1999; Wright *et al.* 2003), where the traits of the individual species probably do reflect natural selection at the individual scale.

The optimisation approach illustrated here for a simple forest model might in principle be applied to more detailed physiology-based simulation models incorporating seasonal variation in weather and model parameters. A more detailed model may incorporate more realistic assumptions than the simple model presented here. In particular, this approach could be applied to models incorporating a site water-balance model driven by daily weather data with g_s related to soil moisture and VPD, and a nitrogen-cycling model incorporating soil feedbacks, which may affect nitrogen uptake under high CO₂ and altered climatic conditions. It is likely that models that are more detailed than MATEY will also possess optima for NPP, leaf [N], g_s and LAI on appropriate timescales.

Conclusions

Our simple model for the annual carbon, nitrogen and water economy of a plant stand is based on accepted understanding of leaf physiology. By maximising NPP, we predict optimum values of g_s , leaf [N], LAI and NPP. Despite the omission of root and soil feedbacks, the model captures many responses observed in the Oak Ridge FACE experiment and other high-CO₂ experiments, including reduction in leaf [N] and g_s . The sensitivity of leaf photosynthesis to [CO₂] is reduced with decreasing leaf [N], but increases with decreasing g_s . As a result of these physiological responses, the predicted plant growth response to elevated [CO₂] is reduced under nitrogen limitation, but amplified under water limitation, which is consistent with a great deal of the experimental evidence. The model represents a plausible hypothesis based on optimal plant-physiological function for differences in CO₂ responses observed at sites with contrasting fertility and water status.

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