A trait-based ecosystem model suggests that long-term responsiveness to rising atmospheric CO$_2$ concentration is greater in slow-growing than fast-growing plants

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Summary

1. Atmospheric carbon dioxide concentration (C_a) has a direct and measurable effect on plant growth. However, it does not affect all plant species equally, which could lead to shifts in competitive dominance of species in ecosystems.

2. We used a dynamic plant carbon–nitrogen model to systematically examine how species traits affect the long-term C_a responsiveness of C$_3$ plants when growing as established monocultures in the field. The model was tested against responses of 7 C$_3$ herbaceous species growing in a free-air C_a enrichment (FACE) experiment (BioCON) in Minnesota, USA.

3. Model simulations showed that several species traits affected the C_a response strongly, giving rise to a number of testable hypotheses about interspecific differences in responsiveness to C_a. The largest responses to rising C_a were obtained for species with low carbon-use efficiency (net primary production: gross primary production ratio), low foliar carbon allocation, low stomatal conductance, low instantaneous photosynthetic nitrogen use efficiency and low specific leaf area.

4. In general, our model predicted that, for established plants growing in resource-limited field conditions, species with slow growth rates would be most responsive to elevated C_a. This prediction was supported by data from the BioCON experiment.

5. Our model also predicts that, for young plants growing in non-resource-limited conditions, species with high growth rates will be most responsive to elevated C_a. This difference in species ranking under different resource availabilities is largely explained by the indirect effects of C_a on leaf area. Leaf-area feedbacks favour fast-growing species the most during leaf-area expansion, but following stand maturation they favour slow-growing species the most.

6. These results imply that species that respond strongly to elevated C_a in short-term (non-resource-limited) glasshouse experiments are unlikely to also be the most responsive in resource-limited field conditions, and therefore that we cannot directly extrapolate from glasshouse experiments to predict which species will be most responsive to elevated C_a in the long term.

Key-words: carbon dioxide, nitrogen uptake, relative growth rate, species traits

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Introduction

The effect of rising atmospheric carbon dioxide concentration (C_a) on plants is, in general, a stimulation of photosynthetic rates (Curtis & Wang 1998; Long *et al.* 2004;

Ainsworth & Rogers 2007) and growth (Saxe, Ellsworth & Heath 1998; Körner 2006). However, the magnitude of the C_a effect varies among plant species (Campbell, Laing & Newton 1993; Joel *et al.* 2001; Belote, Weltzin & Norby 2003). Plant species that are more responsive to elevated C_a could become more abundant, due to improved competitive ability (Körner & Bazzaz 1996). Such shifts in species abundance have the potential to drive changes in plant community structure and function, which will also affect the organisms that rely on these communities. Therefore, to predict impacts of rising C_a on terrestrial ecosystems, it is important to determine which plant species are likely to be most responsive to elevated C_a. In this paper, we investigate theoretically the effect of species traits on responsiveness to C_a. Starting with simple assumptions about plant growth, we develop testable hypotheses for species traits that yield high responsiveness to C_a.

There are two special cases where the theory for differences among plant functional groups in responsiveness to C_a is relatively straightforward. Firstly, C_3 species are predicted to respond more to elevated C_a than C_4 species, because photosynthesis of C_3 species at current C_a is well below CO_2 saturation, unlike that of C_4 species, which have a CO_2-concentrating mechanism (Poorter 1993; Wand *et al.* 1999; Reich *et al.* 2001b). Secondly, nitrogen-fixing species are predicted to respond more to elevated C_a than non-nitrogen-fixing species, because nitrogen fixation leads to an accumulation of leaf nitrogen, which could alleviate potential nitrogen limitation of the C_a response (Ainsworth & Long 2005; Rogers, Ainsworth & Leakey 2009).

In this paper, we leave aside these special cases and focus on contrasts among non-nitrogen-fixing C_3 species, which comprise the bulk of plant species. There has been considerable debate in the literature regarding which C_3 species will be most responsive to elevated C_a. Several hypotheses have been put forward, based on differences among species in growth rate or in stoichiometric habitat. Experimental studies have generally found that plant species with high relative growth rate (RGR) respond more strongly to elevated C_a than plant species with low RGR (Hunt *et al.* 1993; Atkin *et al.* 1999; Poorter & Navas 2003; Körner 2006). For example, Atkin *et al.* (1999) tested a range of *Acacia* species and found that biomass of fast-growing species was more responsive to elevated C_a than that of slow-growing species. In a review paper, Poorter & Navas (2003) found a positive correlation between C_a responsiveness and RGR of a range of woody and herbaceous species. However, Poorter & Navas (2003) observed that these findings applied to plants growing in 'optimal' (non-resource-limited conditions) only and that prediction of species responses ought to consider growth analyses at the stand level.

An alternative hypothesis was put forward by Lloyd & Farquhar (1996), who argued on theoretical grounds that slower-growing plant species will have a larger C_a response than faster-growing plant species. They argued that plant growth rate is given by photosynthesis minus growth and maintenance respiration, where photosynthesis increases with rising C_a but maintenance respiration does not. For a given photosynthetic rate at ambient C_a, the higher the maintenance respiration rate, the larger the proportional response of growth rate to C_a. Also, given a fixed ambient photosynthetic rate, species with a high respiration rate will have a low RGR; therefore, Lloyd & Farquhar (1996) predicted species with a low RGR would show a stronger C_a response than those with a high RGR. However, these theoretical predictions were contradicted by the experimental results synthesized by Poorter & Navas (2003).

In addition, Lloyd & Farquhar (1996) suggested that species with low stomatal conductance should respond more to elevated C_a than species with high stomatal conductance. When the stomata are relatively closed, plants have low intercellular CO_2 concentration (C_i) in the leaves. At low C_i, the response of photosynthetic rate (A) to C_i is greater, resulting in a stronger response to elevated C_a. Niinemets, Flexas & Peñuelas (2011) extended this hypothesis by suggesting that plant species with low mesophyll conductance would have low chloroplastic CO_2 concentration and therefore should also be strongly responsive to elevated C_a.

An alternative hypothesis was put forward by Berry & Roderick (2002). They argued that rising C_a would increase the availability of carbon relative to nitrogen, and that this decrease in relative nutrient availability would favour sclerophyll species that predominate in low-nutrient environments.

Thus, a number of trait-based hypotheses have been suggested for how C_a responsiveness might vary among species, but these ideas have not been fully explored. Our goal was to systematically evaluate, using a dynamic plant carbon–nitrogen model, which species traits lead to higher or lower responsiveness to elevated C_a. The model represents growth and nitrogen uptake of a plant monoculture growing in a natural environment with limiting light and nutrients. A plant species is characterized by a suite of traits. The traits that we consider are defined below and include photosynthetic traits, growth and respiration traits and root traits (Table 1).

We focus on plants growing as a monoculture in the field, as suggested by Poorter & Navas (2003). Resources are limiting in these conditions, as there is intraspecific competition for light and for nutrients. However, for simplicity, water limitation was not considered. We used a sensitivity analysis of the model to determine which species traits lead to high C_a responsiveness. The model was then used to examine the long-term responses to elevated C_a of prairie grassland C_3 species monocultures from the free-air CO_2 enrichment experiment Biodiversity, CO_2 and N (BioCON), in central Minnesota, USA (Reich *et al.* 2001a,b).

Table 1. Species traits used in the model, together with units and values used in model simulations. Trait values were taken from the C₃ grass and forb plant species at BioCON FACE experiment, Minnesota, USA (Table S1, Supporting Information). Mean trait values across the species were used as baseline values in the simulations. For the sensitivity analysis, the range of trait values was obtained by varying each trait by ±50%

| Trait	Definition	Baseline trait value [range]	Units
V_{cmax}/N	Maximum leaf carboxylation rate per unit leaf nitrogen	52 [26,78]	μmol g^{-1} N s^{-1}
J_{max}/V_{cmax}	Ratio of maximum electron transport to maximum carboxylation rate	1·86 [0·93,2·80]	Unitless
g_1	Stomatal conductance operating point	4·8 [2·4,7·2]	kPa$^{0.5}$
Y	Carbon-use efficiency	0·5 [0·25,0·75]	Unitless
R_f	Foliage respiration per unit N	43 [21·5,64·5]	g C g^{-1} N year^{-1}
R_r	Root respiration per unit N	50 [25,75]	g C g^{-1} N year^{-1}
k_s	Light extinction coefficient	0·6 [0·3,0·9]	m^2 ground m^{-2} leaf
SLA	Specific leaf area	14 [7,21]	m^2 leaf kg^{-1} DM
a_f	Fraction of C allocated to leaves	0·4 [0·2,0·6]	Unitless
a_r	Fraction of C allocated to roots (=1 − a_f)	0·6 [0·8, 0·4]	Unitless
S_r	Turnover rate of roots	0·75 [0·375,1·125]	year^{-1}
k_r	Nitrogen uptake parameter related to root biomass	0·0239 [0·01195,0·03585]	m^2 ground g^{-1} C
ρ	Ratio of root N : C to leaf N : C	0·6 [0·3,0·9]	Unitless
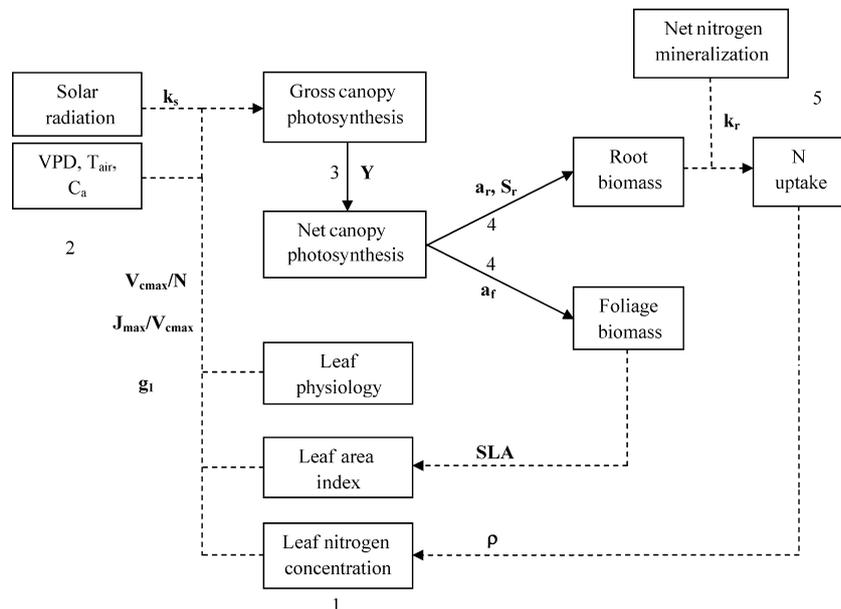
Fig. 1. Flowchart of the model used in this study, showing how species traits (abbreviations in bold; defined in Table 1) are linked. Dashed lines are the flows of information (parameters, conversion, etc.) and solid lines are flows of carbon. Numbers indicate processes as follows: (1) Scaling of leaf photosynthesis to the canopy, (2) Meteorological data as driving variables, (3) Subtraction of total respiration, (4) Annual allocation of new biomass growth to plant compartments, namely foliage and roots, and (5) Annual nitrogen uptake by the roots.

Materials and methods

INTRODUCTION

The model (Fig. 1) simulates plant growth as a result of dynamic physiological processes including photosynthesis, respiration, allocation, turnover and nitrogen uptake. Each process needs species-specific parameters to characterise the rate at which it occurs. These parameters, which describe species behaviour, are considered to be the species traits (Table 1). A plant species is represented by a vector of trait values. Although in reality some of these traits may be correlated, for simplicity we assume that any combination of traits is possible. In what follows, we describe the model and then describe how equilibrium sensitivity analyses were used to identify the species traits leading to the strongest responses to C_a.

PHOTOSYNTHESIS

At the leaf scale, photosynthesis is represented using the standard biochemical model of leaf photosynthesis (Farquhar & von Caem-

merer 1982). The species traits for photosynthesis required for this model are V_{cmax}/N (μmol CO₂ g^{-1} N s^{-1}), the maximum carboxylation rate per unit leaf nitrogen, which indicates the potential photosynthetic nitrogen use efficiency; and J_{max}/V_{cmax} (unitless), the ratio of the maximum light-driven electron flow rate to the maximum carboxylation rate, which indicates the relative resource allocation to each of these photosynthetic processes. The intercellular CO₂ concentration, C_i, is calculated from the optimal stomatal conductance model of Medlyn *et al.* (2011) as follows:

$$\frac{C_i}{C_a} = \frac{g_1}{g_1 + \sqrt{D}}, \qquad \text{eqn 1}$$

where g_1 is the stomatal operating point (kPa$^{0.5}$), D is the vapour pressure deficit (kPa) and C_a is the atmospheric carbon dioxide concentration at the leaf surface (μmol mol^{-1}). The species trait g_1 indicates the plant's water use strategy – plants with high g_1 have high stomatal conductance per unit photosynthesis, and a low water use efficiency.

Instantaneous leaf photosynthesis is scaled to daily canopy photosynthesis using the method of Sands (1995), which makes

the following assumptions: (i) the canopy is horizontally homogenous and vertically heterogenous; (ii) the PAR distribution within the canopy follows Beer's law; (iii) at any point in the canopy the light-saturated photosynthetic rate per unit leaf area is proportional to the ratio of PAR at that point to the full-sun PAR; (iv) and diurnal variation of PAR is sinusoidal. The resulting canopy photosynthesis model expresses daily canopy photosynthesis (GPP, g C m^{-2} day^{-1}) of the plant as the product of photosynthetic light-use efficiency (LUE, g C MJ^{-1}) and daily absorbed photosynthetically active radiation (APAR, MJ m^{-2} day^{-1}). LUE is the efficiency with which absorbed or intercepted light energy is converted to carbon, and it depends on the traits determining leaf photosynthetic rate, namely V_{cmax}/N, J_{max}/V_{cmax} and g_1. APAR depends on the light extinction coefficient k_s and the leaf-area index (LAI), which is calculated from foliage biomass and specific leaf area (SLA, m^2 kg^{-1} DM). Thus, the species traits used in determining APAR are k_s and SLA. The light extinction coefficient k_s is the ratio of shadow area of leaves to actual leaf area, while SLA is the ratio of leaf area to leaf mass.

RESPIRATION

Since the representation of respiration in models is an ongoing subject of debate (King *et al.* 2006), we tested two alternative models of plant respiration. In the first model, total annual plant respiration (R_{tot}) is assumed to be a constant fraction of gross canopy photosynthesis. Under this assumption, annual plant respiration is given by

$$R_{tot} = (1 - Y)GPP,\qquad\qquad \text{eqn 2}$$

where GPP is the total annual canopy photosynthesis and Y is the carbon-use efficiency, which represents plant biomass production per unit gross carbon fixation. The species trait Y is assumed to be constant, independent of temperature and C_a for a given species (Waring, Landsberg & Williams 1998; Dewar, Medlyn & McMurtrie 1999; Litton, Raich & Ryan 2007).

The alternative formulation is to express plant respiration proportional to plant nitrogen content (Reich *et al.* 1998, 2008; Tjoelker *et al.* 2005). In this case, leaf and root respiration rates are linearly related to the corresponding mass-based nitrogen concentrations. Hence, the total annual respiration of the plant is

$$R_{tot} = R_f N_f + R_r N_r,\qquad\qquad \text{eqn 3}$$

where R_f (g C g^{-1} N year^{-1}) and R_r (g C g^{-1} N year^{-1}) are traits which characterize the species respiration rate, and N_f and N_r are the total foliage and root N contents, respectively (g N m^{-2}). We obtain annual net primary production (NPP, g C m^{-2} year^{-1}) as

$$NPP = GPP - R_{tot}.\qquad\qquad \text{eqn 4}$$

ALLOCATION AND TURNOVER

Growth of foliage and roots is calculated on an annual time step and is calculated using fixed allocation fractions and turnover rates. Following the study by McMurtrie (1991), we assume biomass in each year is equal to the biomass of the previous year plus new growth and less turnover. Thus, annual foliage and root biomass are

$$B_f(t + 1) = B_f(t) + a_f NPP(t) - B_f(t)S_f,\qquad \text{eqn 5}$$

$$B_r(t + 1) = B_r(t) + a_r NPP(t) - B_r(t)S_r,\qquad \text{eqn 6}$$

where $B_f(t)$ and $B_r(t)$ are foliage and root biomass at time t (g C m^{-2}), respectively, a_f and a_r are the allocation fractions to foliage and root biomass (dimensionless), respectively, and S_f and S_r are the senescence rates of foliage and roots (year^{-1}), respectively (McMurtrie 1991). The species trait characterizing the allocation process is a_f; note that

$$a_f + a_r = 1.\qquad\qquad \text{eqn 7}$$

Senescence traits are S_f and S_r. S_f was set to 1 year^{-1} for this paper because species considered were from a prairie grassland and shed all functioning leaves in every winter (Reich *et al.* 2001b; Tjoelker *et al.* 2005).

NITROGEN UPTAKE AND ALLOCATION

Nitrogen uptake (N_{uptake}) is represented as a saturating function of root biomass, following the study by Ju & DeAngelis (2009). The saturation level is the net soil nitrogen mineralization rate, N_{min} (g N m^{-2} year^{-1}), which is an input to the model. N_{uptake} is calculated on an annual time step as

$$N_{uptake}(t) = N_{min}(1 - \exp(-k_r B_r(t))),\qquad \text{eqn 8}$$

where k_r (m^2 g^{-1} C) is a species trait that describes root N uptake efficiency (analogous to the light extinction coefficient). An increase in the value of k_r increases the N_{uptake} per unit root biomass (Zerihun & Bassirirad 2001; Schulze, Härtling & Stange 2011).

Nitrogen taken up is allocated to leaves and roots following carbon allocation to leaves and roots, as follows:

$$\begin{aligned} \text{new N to leaves} &= a_f NPP[N_f]_{new} \\ \text{new N to roots} &= a_r NPP[N_r]_{new} \end{aligned},\qquad \text{eqn 9}$$

where $[N_f]_{new}$ and $[N_r]_{new}$ are the N/C ratios of newly constructed foliage and roots, respectively. The nitrogen concentration in roots is assumed to be proportional to the concentration in foliage (Newman & Hart 2006):

$$[N_r]_{new} = \rho[N_f]_{new}.\qquad\qquad \text{eqn 10}$$

The ratio of root to foliage N/C ratio, ρ, is the trait that characterizes the plant species. Given values of N_{uptake} and ρ, values of $[N_f]_{new}$ and $[N_r]_{new}$ can be calculated from eqns 8 to 10.

Since we are interested in the C_a response following stand maturation, equilibrium analysis was applied to the model. The model reaches equilibrium values for plant carbon and nitrogen contents. The derivation of the equilibrium values is shown in the Supporting Information. Following the study by Comins & McMurtrie (1993), the equilibrium is obtained as the intersection of a photosynthetic constraint on production and a nitrogen availability constraint on production, both of which can be expressed as relationships between net primary productivity (NPP) and leaf N/C ratio ($[N_f]$) (Fig. S1, Supporting Information). Our model differs from that of Comins & McMurtrie (1993), in that we consider a fixed soil N mineralization rate, and only short-term plant pools, rather stem and soil carbon and nitrogen pools with long turnover times, and thus can obtain the true equilibrium of the model rather than a quasi-equilibrium as in the study by Comins & McMurtrie (1993). Effects of plant-soil feedbacks will be considered in future work (A.A. Ali, B.E. Medlyn, P.D. Smith, K.Y. Crous & P.B. Reich, unpublished).

MODEL SIMULATIONS

The model was used to examine the long-term responses to elevated C_a of prairie grassland plant species monocultures at the BioCON free-air C_a enrichment (FACE) experiment located in

central Minnesota (45°24′13·5″N, 93°11′08″W). Species monocultures grow in sandy soil and were manually weeded to maintain species composition. More climate and site description information can be found in the studies by Reich *et al.* (2001a,b) and Crous *et al.* (2010). Model simulations were carried out for ambient C_a (360 ppm) and elevated C_a (550 ppm) conditions. Model simulations were carried out for low nitrogen availability conditions. The net nitrogen mineralization rate (N_{min}) was assumed constant and equal to 3 g N m^{-2} year^{-1}, which is the rate observed for native grassland patches at the BioCON field site (Reich *et al.* 2001c). The growing season of all of the plant species ranges from mid-May to mid-September. Leaf-area development of the plant species over the growing season was assumed to follow a 'stepped' curve to mimic the time course of leaf-area index.

The model was applied to four C$_3$ grasses (*Agropyron repens, Bromus inermis, Koeleria cristata, Poa pratensis*) and three nonleguminous C$_3$ forbs (*Achillea millefolium, Anemone cylindrica, Solidago rigida*). These species are native or naturalized to the local area and have a range of growth and allocation strategies, with estimated foliar allocation ranging from 0·2 to 0·68 (Table S1, Supporting Information). Trait values represent species averages over 4 years and were obtained from CO$_2$ response curves measured at the BioCON site (see Crous *et al.* 2010), or from other information (Table S1, Supporting Information). The model was validated against biomass data for these seven species from the BioCON experiment.

We then carried out sensitivity analysis of the model to species trait values, in order to investigate the responsiveness of different species to elevated C_a. The model was first run with baseline trait values, which were calculated as the average trait values of this set of species. In the main sensitivity analysis, each trait value was perturbed, one at a time, by ±50%. In each case, responsiveness to C_a was calculated as the effect on net primary productivity of an increase in C_a from 360 to 550 ppm. The analysis was conducted in this way in order to identify which species traits have the most effect on the plant response to C_a. We also carried out a

second sensitivity analysis in which the trait values were perturbed to the minimum and maximum values observed across the suite of BioCON species. This second sensitivity analysis indicates which traits were most likely to drive differences in species response among the BioCON species. Finally, using the measurements and the model outcomes, the seven species' responsiveness to elevated C_a in monoculture was explored.

Results

The model was first validated against biomass data for seven species growing in the BioCON FACE experiment. Modelled biomass was estimated as equilibrium biomass calculated for each species using species trait values given in Table S1 (Supporting Information) and meteorological data measured on-site during the year 2002. For these simulations, respiration was assumed to equal 50% of photosynthesis (carbon-use efficiency $Y = 0.5$). Measured biomass was the average biomass measured on monoculture plots during the years 2003–2006 (5–8 years after experiment establishment). Figure 2 compares the modelled and measured biomass of the seven species under ambient and elevated C_a. The general trends across species are captured. Moreover, the relationship between measured and modelled biomass was near to the 1 : 1 line, suggesting no tendency to under- or over-predict at either high or low biomass levels.

In the main sensitivity analysis, species traits were perturbed one at a time by ±50%. This analysis demonstrated that species traits have a clear effect on C_a responsiveness (Table 2). The sensitivity analysis was carried out using
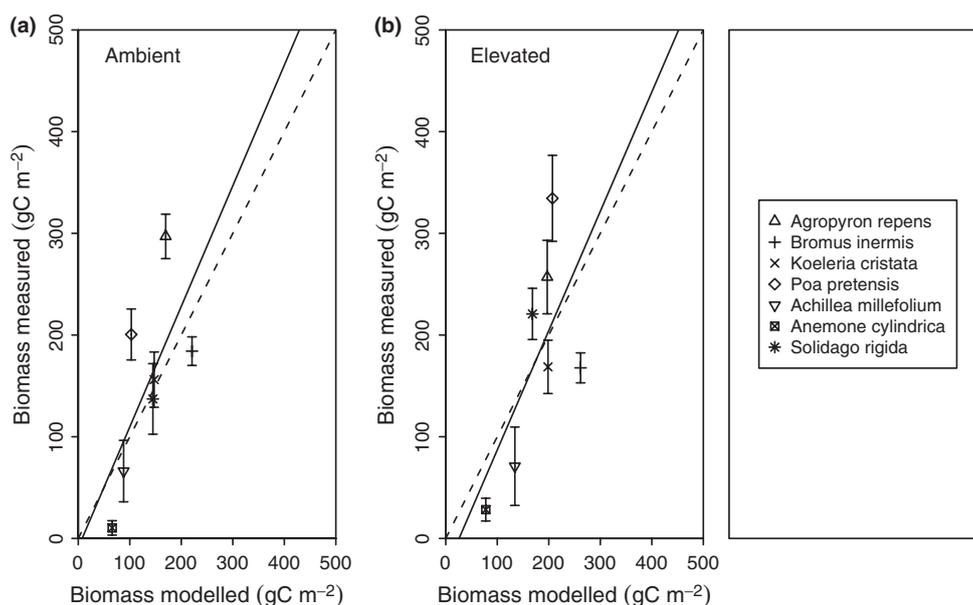

Fig. 2. Model validation against measured biomass data from the Biodiversity, CO$_2$ and N (BioCON) experiment. Modelled and measured total biomass of seven species (four C$_3$ grasses and three C$_3$ forbs) under ambient C_a in panel (a) or at elevated C_a in panel (b). Measured biomass data are average June biomass of species monoculture plots over the period 2003 to 2006. The modelled biomasses are the equilibrium biomass values of the model when parameterized with the species traits for the seven BioCON species (Table S1, Supporting Information). The solid line is the regression line while the dashed line is the 1 : 1 line. The R^2 values for modelled vs. measured biomass under ambient and elevated C_a are 0·45 and 0·43, respectively.

two different assumptions of respiration (eqns 2 and 3). When whole-plant respiration was assumed to be proportional to GPP, the traits Y (carbon-use efficiency), a_f (fraction of carbon allocated to foliage), g_1 (stomatal conductance operating point) and k_s (light extinction coefficient) (in that order) had the strongest effects on the C_a response. Positive responses to C_a were obtained for species with low Y, low a_f, low g_1 and low k_s. In contrast, the traits S_r (root turnover rate) and ρ (root to leaf nitrogen ratio) had relatively little effect on the C_a response. A second sensitivity analysis was also carried out using the observed ranges in species traits at the BioCON experiment (data not shown). In this analysis, the traits Y and k_s were not considered as we did not have observed ranges for these traits. For the BioCON species, the traits a_f (fraction of carbon allocated to foliage), k_r (root nitrogen uptake parameter) and SLA (specific leaf area) had the strongest effect on the C_a response. The ranking of the g_1 parameter was reduced because there was relatively little difference in the g_1 parameter among this group of species, while the ranking of the k_r parameter was increased because of the large variation in this parameter across species (Table S1, Supporting Information).

The choice of respiration assumption had relatively little effect on the modelled sensitivities: when whole-plant respiration was assumed to be proportional to whole-plant nitrogen content, the directional effects of species traits on the C_a response were largely similar to those assuming respiration was a fixed proportion of GPP, although the ranking of traits changed slightly. Under this assumption, the most positive responses to C_a occurred for species with

low a_f, low V_{cmax}/N, low g_1, low S_r and low SLA. The respiration parameters (R_f and R_r) had less effect on the response than the carbon-use efficiency (Y), but in both cases, the response was the highest for the species with highest respiration rate. The chief difference between the models run using two different respiration assumptions lay in the effect of the root turnover (S_r): when respiration was assumed proportional to photosynthesis, S_r had a small positive effect on the C_a response, whereas when respiration was assumed proportional to nitrogen content, S_r had a large negative effect on the C_a response. In what follows, we focus on the case where respiration is assumed proportional to photosynthesis. However, we discuss the difference between the assumptions when we consider the effect of the trait S_r.

Table S2 (Supporting Information) gives more detail of the modelled responses, for the case where respiration is assumed proportional to photosynthesis. Net primary productivity (NPP) is broken down into its components, LUE and the APAR. Corresponding values of LAI and N : C ratios of foliage ([N]$_f$) are also given. We use this information to explain the modelled effects of species traits on the C_a response, considering each species trait in turn.

RESPIRATION TRAITS (Y, R_f, R_r)

Under both respiration assumptions, plant species with a high respiration rate were most responsive to elevated C_a (Table 2). Under the assumption that respiration is proportional to photosynthesis, plant species with a low carbon-use efficiency (Y) had a stronger response (+35%) than species with a high Y (+19%). Similarly, plant species with high respiration rates per unit leaf nitrogen (R_r, R_f) had stronger responses (+24–25%) than species with low respiration rates (+19–20%). The effect of respiration on the C_a response can be understood through its effect on LAI. All else being equal (given the assumptions of the model), plant species with high respiration rates have relatively low NPP, which leads to low LAI (Fig. 3). At low LAI, C_a responses are relatively high, because of the saturating response of APAR to LAI. For species with low LAI, a small increase in LAI leads to a large increase in APAR and thus a large increase in NPP. In contrast, when plants already have higher LAI, a small change in LAI does not change APAR, or NPP, by as much. Thus, species with low LAI (such as species with low Y or high R_r and R_f) tend to be more responsive to elevated C_a than species with high LAI (such as species with high Y or low R_r and R_f).

As we show in the following sections, this feedback through LAI can be used to explain the effect of the traits V_{cmax}/N, SLA, a_f and ρ on the C_a response. The trait k_s has a similar effect but acts directly on APAR rather than on LAI. However, the traits J_{max}/V_{cmax}, g_1, S_r and k_r also affect the C_a response in other ways, which are described below.

Table 2. Effects of species traits on predicted net primary production (NPP) responses to C_a. Each species trait was varied one at a time by $\pm 50\%$. Values are given as ratios of NPP at elevated C_a to ambient C_a. Column (a) gives values when whole-plant respiration is assumed proportional to GPP (eqn 2); column (b) gives values when whole-plant respiration is assumed proportional to plant nitrogen content (eqn 3). Bold values indicate which trait value (-50% or $+50\%$) yielded the largest CO_2 response

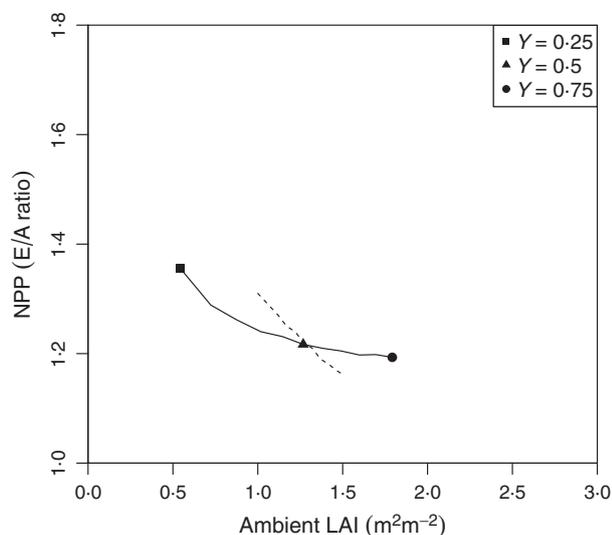| (a) Respiration proportional to GPP (eqn 2) Baseline response = 1·22			(b) Respiration proportional to plant nitrogen content (eqn 3) Baseline response = 1·22		
Species Trait	Trait −50%	Trait +50%	Species Trait	Trait −50%	Trait +50%
V_{cmax}/N	**1·28**	1·20	V_{cmax}/N	**1·33**	1·24
J_{max}/V_{cmax}	1·14	**1·26**	J_{max}/V_{cmax}	1·16	**1·30**
g_1	**1·29**	1·20	g_1	**1·31**	1·21
Y	**1·35**	1·19	R_f	1·20	**1·24**
			R_r	1·19	**1·25**
k_s	**1·29**	1·19	k_s	**1·25**	1·20
SLA	**1·28**	1·20	SLA	**1·30**	1·20
a_f	**1·32**	1·19	a_f	**1·37**	1·19
S_r	1·21	**1·23**	S_r	**1·30**	1·20
k_r	**1·26**	1·21	k_r	**1·24**	1·21
ρ	1·20	**1·23**	ρ	1·20	**1·24**

Fig. 3. Enhancement ratio of NPP (equilibrium NPP at elevated C_a divided by that at ambient C_a) as a function of equilibrium leaf-area index (LAI) at ambient C_a, illustrating sensitivity to respiration rates using both respiration assumptions. The solid curve is generated by varying the carbon-use efficiency (Y) from its baseline value (0·5) by ±50%. The highest NPP enhancement ratio and lowest ambient LAI are obtained for the lowest Y. The dashed curve is obtained by varying species respiration rates (R_f, R_r) by ±50%. Similarly, the highest C_a responsiveness and lowest ambient LAI are obtained for the highest respiration rates.

MAXIMUM LEAF PHOTOSYNTHETIC RATE (V_{CMAX}/N), SPECIFIC LEAF AREA (SLA), FRACTION OF CARBON ALLOCATED TO FOLIAGE (a_f) AND NITROGEN COVARIANCE BETWEEN FOLIAGE AND ROOTS (ρ)

From Table 2, plant species with low V_{cmax}/N, low SLA, low a_f or high ρ values were more responsive to elevated C_a than species with high V_{cmax}/N, high SLA, high a_f or low ρ values. These traits affect the C_a response by changing equilibrium NPP and hence changing equilibrium LAI (Table S2, Supporting Information). This effect on LAI fully explains the NPP response, as is demonstrated in Fig. 4, which shows the C_a response as a function of LAI for different trait values. Panels (a), (e), (f) and (i) show the effects of the traits V_{cmax}/N, SLA, a_f and ρ, respectively, and it can be seen that the C_a response does not depend on the trait value. Thus, these traits affect the C_a response only through their effect on ambient LAI.

LIGHT EXTINCTION COEFFICIENT (k_s)

The trait k_s affects the C_a response by changing equilibrium NPP, as a consequence of changing equilibrium APAR, rather than changing LAI. This is shown in Fig. 4d: the C_a response increases with decreasing APAR, but the value of k_s does not change this relationship. Plant species with lower k_s have more vertical leaves. With high sun angles, light penetrates further into the canopy (Jones 1992) and a smaller proportion of incident PAR is

absorbed. Thus, for a given LAI, species with low k_s will have a steeper response of APAR to LAI than species with high k_s. Increasing C_a will thus have a larger effect on APAR when k_s is low and consequently will also have a larger effect on productivity.

RATIO OF MAXIMUM ELECTRON TRANSPORT TO MAXIMUM CARBOXYLATION VELOCITY (J_{MAX}/V_{CMAX})

The trait J_{max}/V_{cmax} affects the C_a response not only by changing equilibrium LAI. Figure 4b shows that, although the biomass enhancement ratio decreases with increasing LAI, the relationship differs for different values of J_{max}/V_{cmax}. The reason for this shift in the C_a response curve is as follows. When Rubisco activity (V_{cmax}) is limiting, photosynthesis is more responsive to C_a than when electron transport (J_{max}) is limiting (Farquhar & von Caemmerer 1982). When J_{max}/V_{cmax} is increased, electron transport rates become relatively high, so photosynthesis becomes more frequently limited by Rubisco activity. Thus, the C_a response increases. In contrast, when J_{max}/V_{cmax} is decreased, electron transport rates become relatively low, so photosynthesis becomes more frequently limited by electron transport, and the C_a response decreases.

STOMATAL CONDUCTANCE OPERATING POINT (g_1)

Species with lower g_1 values were more responsive to elevated C_a than plant species with high g_1 values (Table 2). This outcome holds under both respiration assumptions. The trait g_1 affects the C_a response through its effect on equilibrium LAI, as with other traits, but also affects the C_a response by a second mechanism (Fig. 4c). This effect on the C_a response is mediated through the intercellular CO$_2$ concentration, C_i. Plant species with lower g_1 have lower C_i. At low C_i, photosynthesis is more CO$_2$-limited, so the response of photosynthesis to increasing C_a is greater.

NITROGEN UPTAKE PARAMETER RELATED TO ROOT BIOMASS (k_r)

The root nitrogen uptake parameter k_r also has a second effect on the C_a response, in addition to the effect via the equilibrium LAI (Fig. 4h). The second effect is mediated by nitrogen uptake. Nitrogen uptake is a nonlinear function of root biomass, similar to the nonlinear relationship of APAR with LAI. Thus, an increase in root biomass in plants with low root biomass will have a larger effect on nutrient uptake than a similar increase in root biomass in plants with a high root biomass. Species with low k_r values have low nutrient uptake per unit root biomass. At ambient C_a, such species will have both low equilibrium LAI and low equilibrium root biomass. Thus, high C_a benefits such species by increasing their nutrient uptake as well as their absorbed PAR, more than it does for species with high values of k_r. Hence, the plant species with lower k_r
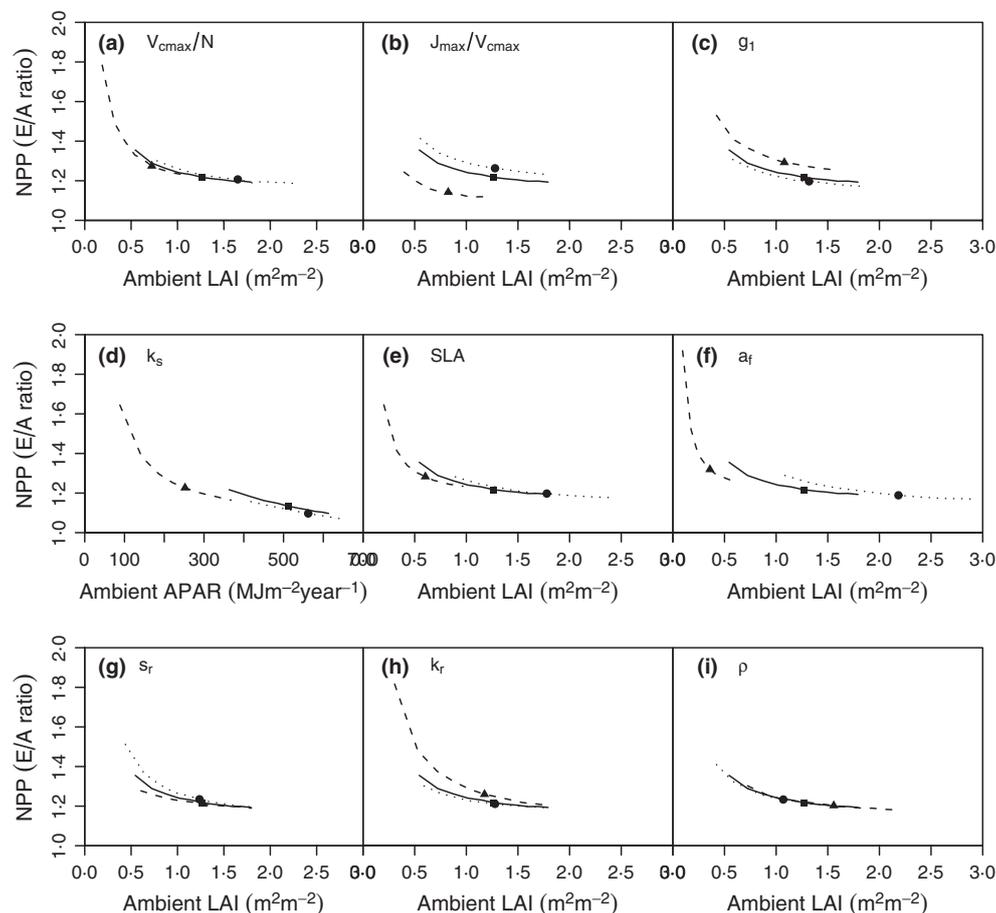
Fig. 4. Enhancement ratio of NPP, as a function of equilibrium leaf-area index (LAI) of a monoculture at ambient C_a. Each panel shows the effect of a different trait (indicated on the panel). The three curves in each panel correspond to species with three different values for that trait (base, low and high trait values). The line corresponds to the base value, the dashed line corresponds to the low value, and the dotted line corresponds to the high trait value. Each curve was generated by varying carbon-use efficiency (Y). The point on each curve indicates where $Y = 0.5$. Note: the graph for the trait k_s (d) has ambient absorbed photosynthetically active radiation (APAR), rather than ambient LAI, on the x-axis (see text).

values are predicted to be more responsive to elevated C_a than plant species with higher k_r values.

ROOT TURNOVER RATE (S_r)

For most traits, the effect of the trait on the C_a response is similar whether respiration is assumed to be proportional to photosynthesis or to nitrogen content (Table 2). The exception is the root turnover rate (S_r). Under the assumption that respiration is proportional to photosynthesis, S_r affects the C_a response through its effects on equilibrium LAI and root biomass, similar to the effect of the trait k_r. Plant species with higher S_r values have lower equilibrium root biomass than plant species with lower S_r values. Thus, they operate on the steepest part of the nitrogen uptake vs. root biomass curve. They also have low nutrient uptake, which reduces NPP, resulting in low equilibrium LAI. Thus, both nutrient uptake and absorbed PAR are increased fairly strongly by high C_a for species with low S_r values.

However, when respiration is assumed proportional to plant nitrogen content, plant species with lower S_r values

are predicted to be more responsive to elevated C_a than plant species with higher S_r values (Table 2). The reason for this difference is that plant species with lower S_r values have higher root biomass. Under the assumption that respiration is proportional to plant nitrogen content, plants with high root biomass have high respiration rates, reducing NPP and resulting in low LAI. As for plant species with low Y values, this means the plant species with lower S_r values are predicted to be more responsive to elevated C_a than plant species with higher S_r values.

COMPARISON WITH BIOCON DATA

The key point demonstrated in Fig. 4 is that the strongest relative responses to elevated C_a are predicted for the least-productive, lowest-LAI species. We tested this conclusion against data from the monoculture plots in the BioCON experiment. Figure 5 shows the measured long-term effect of elevated C_a on NPP as a function of ambient LAI of the seven monoculture species and compares this with model predictions for these species. The model
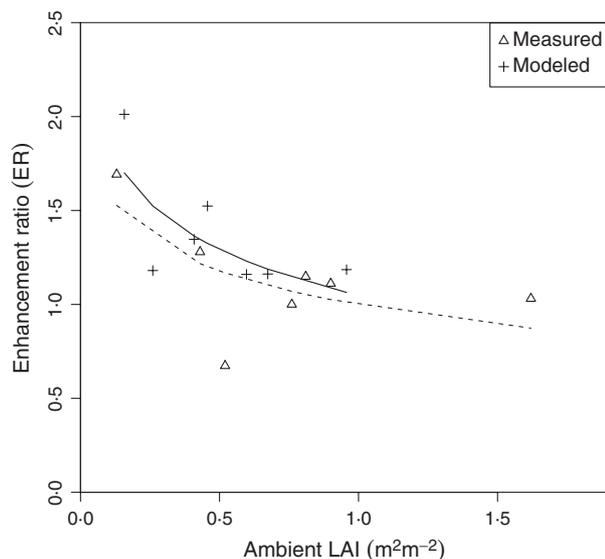
Fig. 5. Comparison of predicted NPP enhancement ratio to measurements for seven species growing in the Biodiversity, CO_2 and N free-air C_a enrichment (BioCON FACE) experiment. Measured data are shown as average CO_2 enhancement ratio of NPP over the period 2003–2006 as a function of measured leaf-area index (LAI) at ambient C_a. Model predictions are shown as equilibrium NPP enhancement as a function of equilibrium LAI at ambient C_a. The solid curve is a best-fit regression of model output, while the dashed curve is the best-fit regression to measured data.

Fig. 6. Predicted time course of the NPP enhancement ratio, using the non-equilibrium version of the model. Two species with values of V_{cmax}/N yielding differing growth rates (dashed line: high $A_{cmax}N$ = fast growth rate, solid line: low V_{cmax}/N = slow growth rate) are compared. Initially, the C_a response is highest for the fast-growing species, due to a rapid leaf-area feedback. However, as the species approach equilibrium, the C_a response is highest for the slow-growing species, as the leaf-area feedback is highest for this species. The relative responsiveness to C_a of the two species thus depends on the time at which they are compared.

predicts that species that have a lower LAI under ambient C_a would have the highest relative response to elevated C_a. The measured data support this prediction (Fig. 5). There is one species which is an 'outlier'; the correspondence between modelled and measured data still holds even if this species is removed from the comparison.

Discussion

Using a plant C/N model, we have shown that there are considerable differences among both real species and hypothetical trait-simulated species in responsiveness to rising C_a under resource-limited conditions. In particular, species with low carbon-use efficiency (Y), low carbon allocation to foliage (a_f), low stomatal conductance operating point (g_1), low maximum carboxylation rate per unit leaf nitrogen (V_{cmax}/N) and low SLA are predicted to be most responsive to C_a under resource-limited conditions (Table 2). This is, to our knowledge, the first systematic modelling study exploring how plant species are likely to vary in C_a responsiveness based on the suite of traits they possess.

FAST-GROWING AND SLOW-GROWING PLANT SPECIES

There is considerable experimental evidence showing that in young plants growing individually, species with high RGR are most responsive to elevated C_a (Hunt *et al.* 1993; Atkin *et al.* 1999; Poorter & Navas 2003; Körner 2006). Poorter & Navas (2003), in a meta-analysis of 80 research articles on elevated C_a effects on both herbaceous
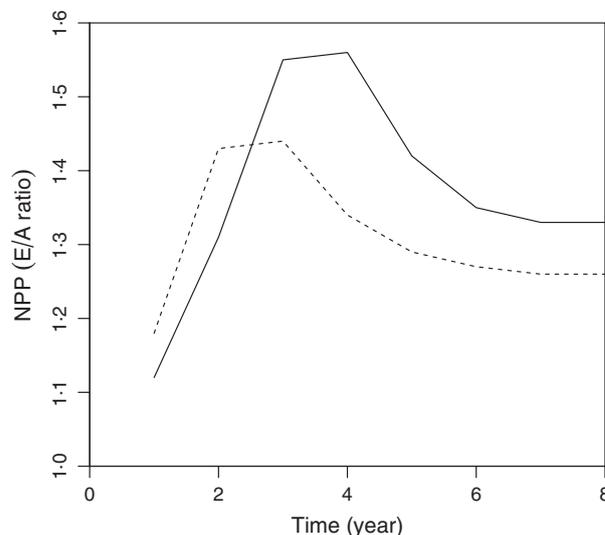
and woody plant species, found that the biomass enhancement ratio was highest for species with high RGRs. Similarly, in a study carried out by Atkin *et al.* (1999) on *Acacia* species, fast-growing species were reported to respond more strongly to elevated C_a than slow-growing *Acacia* species. The non-equilibrium version of our model agrees with these results (Fig. 6). Plants, as seedlings, initially grow quasi-exponentially. Increased plant dry mass is generated by the stimulation of RGR during early exposure to elevated C_a (Masle, Hudson & Badger 1993). During this period, plants with high RGR are likely to be most responsive to elevated C_a, because their rapid increase in leaf area provides a positive feedback to the direct C_a response of photosynthesis.

However, we also demonstrate that this ranking of responsiveness is likely to change over time. The leaf-area feedback works in the opposite direction once plants become larger, becoming increasingly self-shaded. Under these conditions, species with low LAI have the potential to respond most strongly to elevated C_a, because they can significantly increase light capture by increasing LAI (Fig. 6). This conclusion implies that species that are most responsive to C_a in the exponential growth phase will not necessarily be the most responsive in the closed-canopy stage. This view is corroborated by trends seen even during a single growing season for five woody species (Tjoelker, Oleksyn & Reich 1998) and is supported by the observation that the C_a response of individual plants does not help to predict the performance of a species in a monoculture (Poorter & Navas 2003).

Importantly, our model suggests that species that are most responsive to elevated C_a in short-term glasshouse experiments with no competition for light or nutrients will not be the most responsive species to elevated C_a in long-term field conditions. Our model suggests instead that slow-growing plant species might be more responsive to elevated C_a in the long term, when resources become limiting. This result is not dependent on our model assumptions; any model using Beer's Law to represent light interception would make the same prediction, as it is a logical consequence of the leaf-area feedback to growth.

ADDITIONAL TRAITS AFFECTING RESPONSIVENESS TO C_A

Plant species with a high J_{max}/V_{cmax} ratio were found to be more responsive to elevated C_a than plant species with lower J_{max}/V_{cmax}. This outcome was also reported by Ainsworth & Rogers (2007). However, the ratio of J_{max} to V_{cmax} does not appear to vary much among species (Wullschleger 1993; Medlyn *et al.* 2002; Crous 2008; Crous *et al.* 2010), indicating that it is unlikely to be an important factor in determining which species will be most responsive to elevated C_a. One suggestion for the tight coupling of V_{cmax} and J_{max} among plant species grown under different light and nutrient conditions is that plant species are able to optimize the allocation of resources, particularly nitrogen, in order to preserve a balance between enzymatic (i.e. Rubisco) and light-harvesting (i.e. chlorophyll) capabilities (Thomson, Huang & Kriedemann 1992; Wullschleger 1993).

Our model also suggests that plant species with a low stomatal conductance operating point (g_1) should be more responsive to elevated C_a under canopy closure than plant species with high g_1. When the stomata are closed, plant species have low C_i, becoming more responsive to elevated C_a. This argument has been made previously by a number of authors, including Lloyd & Farquhar (1996) and McMurtrie *et al.* (2008), but has not been experimentally tested. For simplicity, water limitation was not considered in this model. It has been observed in some factorial $C_a \times$ water limitation experiments that the C_a response under low water availability is amplified (Kimball & Mauney 1993; Field *et al.* 1997; Arp *et al.* 1998; Morgan *et al.* 2004). Future work could explore how species traits affect the interaction between C_a and water availability and whether the amelioration of drought by elevated C_a is likely to be stronger in some species types than others.

With respect to photosynthetic nitrogen use efficiency, we found that C_a responsiveness decreased with increasing V_{cmax}/N. This result disagrees with Berry & Roderick (2002), who hypothesised that elevated C_a would increase the availability of carbon relative to nitrogen and that this increase would favour nutrient-use efficient species. Although this hypothesis is intuitively appealing, it does not have a quantitative basis. The logical consequence from our model assumptions is that, in nitrogen-limited conditions, nutrient-use efficient species perform relatively well at ambient C_a, and therefore, it is relatively *in*efficient species that can gain most from rising C_a.

CAVEATS

Our goal in carrying out this study was to start from a simple set of assumptions about how species traits affect plant growth, and examine the logical consequences of these assumptions for species differences in C_a responsiveness. We aimed to develop testable theoretical predictions that would stimulate more targeted experimental studies investigating species differences in responsiveness to C_a in the field.

As with all models, our results are dependent on our assumptions. Perhaps the most vulnerable assumption made is that plant species traits are assumed to be fixed. Many plant species show plasticity to environmental conditions (Bazzaz 1979), thereby enabling them to take advantage of increased resource availability. If species traits change dramatically at elevated C_a, our modelling results will not apply. However, we argue that differences in trait values among plant species are greater than changes within plant species traits in response to elevated C_a, so the rankings predicted by our modelling still apply. For example, in meta-analyses carried out by Poorter & Navas (2003) and Ainsworth & Long (2005), SLA of plant species was changed by *c.* 10% in response to elevated C_a. In comparison, inherent differences in traits among plant species were >30% (Hunt *et al.* 1993; Poorter 1993; Roumet *et al.* 1996; Atkin *et al.* 1999) and can be far more (Wright *et al.* 2004). Furthermore, changes in SLA in response to elevated C_a were similar among species; thus, this evidence suggests that the rankings for species traits would not change with elevated C_a.

A further assumption made was that down-regulation of photosynthesis under elevated C_a is driven by decreased leaf-level nitrogen content. Nitrogen-driven down-regulation was found to be an important process in the BioCON experiment (Ellsworth *et al.* 2004; Crous *et al.* 2010; Lee, Barrott & Reich 2011). Alternative causes of down-regulation of photosynthesis, such as sink limitation via accumulation of starch in the leaves, were not considered (Stitt 1991; Kirschbaum 2011). Potentially, there is more starch accumulation for slow-growing plant species (Poorter 1998), which could reduce the responsiveness of slow-growing species to C_a. However, sink-driven down-regulation is rarely observed in the field, is not always confined to slow-growing species or functional groups (Roumet *et al.* 1996; Ellsworth *et al.* 2004; Crous *et al.* 2010) and therefore is unlikely to be a limitation to the model.

We focussed on herbaceous species in order to allow testing against the BioCON data set. Some of the details of model outcomes may change if woody perennials were considered: for example, the ranking of the species traits may vary. However, because we have examined the logical basis underlying each of the model predictions (see

Results), we can be confident that the overall direction of sensitivity to traits will be similar irrespective of vegetation type.

Our model demonstrates that slow-growing species may be most responsive to C_a in the field. However, the consequences for community composition are complex and will be explored using modelling techniques in future work (Ali 2012; A.A. Ali, B.E. Medlyn, P.D. Smith, K.Y. Crous & P.B. Reich, unpublished).

Conclusions

Using a plant carbon–nitrogen model, we investigated the sensitivity of plant responses to elevated C_a under resource-limited conditions in the field. The model predicted that a number of species traits affected the C_a response strongly, leading to several testable theoretical hypotheses that have the potential to guide experimental research into interspecific differences in C_a response.

Our main finding was that species traits that yield high growth rates, although they may lead to high C_a responses in the initial exponential growth phase of plants or in non-resource limiting conditions, eventually lead to relatively low C_a responses when resources become limiting. Species with low productivity and low LAI at ambient C_a are likely to benefit most from rising C_a when light and nutrient availability are limiting. The time-scale of interest thus determines which species are most responsive. This finding is important because it implies that species that respond strongly to elevated C_a in short-term glasshouse experiments are unlikely to also be the most responsive in the field and therefore that we cannot directly extrapolate from glasshouse experiments to the field.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Equilibrium analysis of the model for baseline trait values.

Table S1. List of traits and values for C_3 grass and forb species in the BioCON experiment.

Table S2. Details of sensitivity analysis output for the case when respiration is assumed proportional to photosynthesis (case (a) in Table 2).

Appendix S1. Equilibrium analysis.