A trait-based ecosystem model suggests that long-term responsiveness to rising atmospheric CO₂ concentration is greater in slow-growing than fast-growing plants

Ashehad A. Ali†-¹, Belinda E. Medlyn*¹, Kristine Y. Crous²,³ and Peter B. Reich³,⁴

¹Department of Biological Sciences, Faculty of Science, Macquarie University, North Ryde, New South Wales 2109 Australia; ²Research School of Biology, The Australian National University, GPO Box 475, Canberra, Australian Capital Territory, Australia; ³Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith, New South Wales 2751 Australia; and ⁴Department of Forest Resources, University of Minnesota, St. Paul, Minnesota, USA

Summary

1. Atmospheric carbon dioxide concentration (Cₐ) 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 Cₐ responsiveness of C₃ plants when growing as established monocultures in the field. The model was tested against responses of 7 C₃ herbaceous species growing in a free-air Cₐ enrichment (FACE) experiment (BioCON) in Minnesota, USA.

3. Model simulations showed that several species traits affected the Cₐ response strongly, giving rise to a number of testable hypotheses about interspecific differences in responsiveness to Cₐ. The largest responses to rising Cₐ 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 Cₐ. 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 Cₐ. This difference in species ranking under different resource availabilities is largely explained by the indirect effects of Cₐ 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 Cₐ 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 Cₐ in the long term.

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

Introduction

The effect of rising atmospheric carbon dioxide concentration (Cₐ) 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 $C_a$, 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 limited 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%.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Definition</th>
<th>Baseline trait value [range]</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$V_{\text{max}}/N$</td>
<td>Maximum leaf carboxylation rate per unit leaf nitrogen</td>
<td>52 [26,78]</td>
<td>μmol g⁻¹ N s⁻¹</td>
</tr>
<tr>
<td>$J_{\text{max}}/V_{\text{max}}$</td>
<td>Ratio of maximum electron transport to maximum carboxylation rate</td>
<td>1.86 [0.93,2.80]</td>
<td>Unitless</td>
</tr>
<tr>
<td>$g_1$</td>
<td>Stomatal conductance operating point</td>
<td>4.8 [2.4,7.2]</td>
<td>kPa⁻⁰.⁵</td>
</tr>
<tr>
<td>$Y$</td>
<td>Carbon-use efficiency</td>
<td>0.5 [0.25,0.75]</td>
<td>Unitless</td>
</tr>
<tr>
<td>$R_f$</td>
<td>Foliage respiration per unit N</td>
<td>43 [21,56.45]</td>
<td>g C g⁻¹ N year⁻¹</td>
</tr>
<tr>
<td>$R_r$</td>
<td>Root respiration per unit N</td>
<td>50 [25.75]</td>
<td>g C g⁻¹ N year⁻¹</td>
</tr>
<tr>
<td>$k_s$</td>
<td>Light extinction coefficient</td>
<td>0.6 [0.3–0.9]</td>
<td>m² ground m⁻² leaf</td>
</tr>
<tr>
<td>SLA</td>
<td>Specific leaf area</td>
<td>14 [7,21]</td>
<td>m² leaf g⁻¹ DM</td>
</tr>
<tr>
<td>$\alpha_l$</td>
<td>Fraction of C allocated to leaves</td>
<td>0.4 [0.2–0.6]</td>
<td>Unitless</td>
</tr>
<tr>
<td>$\alpha_r$</td>
<td>Fraction of C allocated to roots (=1 – $\alpha_l$)</td>
<td>0.6 [0.8–0.4]</td>
<td>Unitless</td>
</tr>
<tr>
<td>$S_r$</td>
<td>Turnover rate of roots</td>
<td>0.75 [0.375–1.125]</td>
<td>year⁻¹</td>
</tr>
<tr>
<td>$k_r$</td>
<td>Nitrogen uptake parameter related to root biomass</td>
<td>0.0239 [0.01195,0.03585]</td>
<td>m² ground g⁻¹ C</td>
</tr>
<tr>
<td>$\rho$</td>
<td>Ratio of root N : C to leaf N : C</td>
<td>0.6 [0.3–0.9]</td>
<td>Unitless</td>
</tr>
</tbody>
</table>

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 the 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 $C_\nu$.

PHOTOSYNTHESIS

At the leaf scale, photosynthesis is represented using the standard biochemical model of leaf photosynthesis (Farquhar & von Caemmerer 1982). The species traits for photosynthesis required for this model are $V_{\text{max}}/N$ (μmol CO₂ g⁻¹ N s⁻¹), the maximum carboxylation rate per unit leaf nitrogen, which indicates the potential photosynthetic nitrogen use efficiency; and $J_{\text{max}}/V_{\text{max}}$ (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:

$$C_i = \frac{g_1}{g_1 + \sqrt{D}},$$

where $g_1$ is the stomatal operating point (kPa⁻⁰.⁵), $D$ is the vapour pressure deficit (kPa) and $C_i$ 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 heterogeneous; (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, $g \text{ C m}^{-2} \text{day}^{-1}$) of the plant as the product of photosynthetic light-use efficiency (LUE, $g \text{ C MJ}^{-1}$) 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 $V_{\text{max}}/N$, $J_{\text{max}}/V_{\text{max}}$, and $g_t$. 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 ($R_{\text{tot}}$) is assumed to be a constant fraction of gross canopy photosynthesis. Under this assumption, annual plant respiration is given by

$$R_{\text{tot}} = (1 - Y) \cdot \text{GPP,}$$

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 $C_0$ 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

$$R_{\text{tot}} = R_t N_t + R_r N_r,$$

eqn 3

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

$$\text{NPP} = \text{GPP} - R_{\text{tot}},$$

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

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

eqn 5

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

eqn 6

where $B_f(t)$ and $B_r(t)$ are foliage and root biomass at time $t$ ($g \text{ C m}^{-2}$), 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 $a_r$; note that $a_f + a_r = 1$.

Senescence traits are $S_f$ and $S_r$. $S_r$ 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 ($\text{N}_{\text{uptake}}$) 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, $N_{\text{min}}$ ($g \text{ N m}^{-2} \text{year}^{-1}$), which is an input to the model. $\text{N}_{\text{uptake}}$ is calculated on an annual time step as

$$\text{N}_{\text{uptake}}(t) = N_{\text{min}} \left(1 - \exp\left(-k_s B_r(t)\right)\right),$$

eqn 8

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

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

new N to leaves = $a_f \cdot \text{NPP}[N_f]_{\text{new}}$

eqn 9

new N to roots = $a_r \cdot \text{NPP}[N_r]_{\text{new}}$

where $[N_f]_{\text{new}}$ and $[N_r]_{\text{new}}$ 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):

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

eqn 10

The ratio of root to foliage N/C ratio, $\rho$, is the trait that characterizes the plant species. Given values of $\text{N}_{\text{uptake}}$ and $\rho$, values of $[N_f]_{\text{new}}$ and $[N_r]_{\text{new}}$ 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 ($N_{\text{min}}$) 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 biomass values 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.](image-url)
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 \( \rho \) (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

<table>
<thead>
<tr>
<th>(a) Respiration proportional to GPP (eqn 2)</th>
<th>(b) Respiration proportional to plant nitrogen content (eqn 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Baseline response = 1:22</strong></td>
<td><strong>Baseline response = 1:22</strong></td>
</tr>
<tr>
<td>Species Trait</td>
<td>Trait −50%</td>
</tr>
<tr>
<td>( V_{\text{cmax}}/N )</td>
<td>1.28</td>
</tr>
<tr>
<td>( J_{\text{max}}/V_{\text{cmax}} )</td>
<td>1.14</td>
</tr>
<tr>
<td>( g_1 )</td>
<td>1.29</td>
</tr>
<tr>
<td>( Y )</td>
<td>1.35</td>
</tr>
<tr>
<td>( k_s )</td>
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<td>( a_f )</td>
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</tr>
<tr>
<td>( k_r )</td>
<td>1.26</td>
</tr>
<tr>
<td>( \rho )</td>
<td>1.20</td>
</tr>
</tbody>
</table>

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 ±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 CO₂ response.

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 (\( R_f, R_r \)) 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 \( R_f \) and \( R_r \)) tend to be more responsive to elevated \( C_a \) than species with high LAI (such as species with high \( Y \) or low \( R_f \) and \( R_r \)).

As we show in the following sections, this feedback through LAI can be used to explain the effect of the traits \( V_{\text{cmax}}/N \), SLA, \( a_f \) and \( \rho \) 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 \( J_{\text{max}}/V_{\text{cmax}} \), \( g_1 \), \( S_r \) and \( k_r \) also affect the \( C_a \) response in other ways, which are described below.
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 ($R_k$, $R_b$) 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 ($r$)

From Table 2, plant species with low $V_{cmax}/N$, low SLA, low $a_f$ or high $p$ values were more responsive to elevated $C_a$ than species with high $V_{cmax}/N$, high SLA, high $a_f$ or low $p$ 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 $p$, 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 ($k_v$)

The trait $k_v$ 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 $k_v$ does not change this relationship. Plant species with lower $k_v$ 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 $k_v$ will have a steeper response of APAR to LAI than species with high $k_v$. Increasing $C_a$ will thus have a larger effect on APAR when $k_v$ 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 $k_r$
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
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 ($a_l$), 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 \( J_{\text{max}}/V_{\text{cmax}} \) ratio were found to be more responsive to elevated \( C_a \) than plant species with lower \( J_{\text{max}}/V_{\text{cmax}} \). This outcome was also reported by Ainsworth & Rogers (2007). However, the ratio of \( J_{\text{max}} \) to \( V_{\text{cmax}} \) 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 \( V_{\text{cmax}} \) and \( J_{\text{max}} \) 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 (\( g_s \)) should be more responsive to elevated \( C_a \) under canopy closure than plant species with high \( g_s \). When the stomata are closed, plant species have low \( C_s \), 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 & Mau- ney 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 \( V_{\text{cmax}}/N \). 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 inefficient 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-limiting 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

AA was supported by a Macquarie University Research Excellence Scholarship. This work was supported by the U.S. Department of Energy (DOE/DE-FG02-96ER62291 and DE-FC02-06ER64158) and the National Science Foundation (NSF Biocomplexity 0322057, NSF LTER DEB 9411972, DE-FG02-96ER62291 and DE-FC02-06ER64158) and the National Science Foundation (NSF Biocomplexity 0322057, NSF LTER DEB 9411972, and NSF LTREB 0716587), and the University of Minnesota. We thank participants in the BioCON FACE experiment for assistance with programming. AA thanks Drs Remko Duursma, Silvia Dezi and Andrés Roubick for assistance with programming.

References


Received 31 July 2012; accepted 19 March 2013

Handling Editor: David Whitehead

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 C₃ 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.