

Elevated carbon dioxide is predicted to promote coexistence among competing species in a trait-based model

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Introduction

Increases in atmospheric CO₂ concentration (C_a) have been shown to differentially affect plant species, with some species being more strongly responsive than others (Bazzaz 1990; Lloyd and Farquhar 1996; Poorter 1998). This difference among species in responsiveness to ele-

Abstract

Differential species responses to atmospheric CO₂ concentration (C_a) could lead to quantitative changes in competition among species and community composition, with flow-on effects for ecosystem function. However, there has been little theoretical analysis of how elevated C_a (eC_a) will affect plant competition, or how composition of plant communities might change. Such theoretical analysis is needed for developing testable hypotheses to frame experimental research. Here, we investigated theoretically how plant competition might change under eC_a by implementing two alternative competition theories, resource use theory and resource capture theory, in a plant carbon and nitrogen cycling model. The model makes several novel predictions for the impact of eC_a on plant community composition. Using resource use theory, the model predicts that eC_a is unlikely to change species dominance in competition, but is likely to increase coexistence among species. Using resource capture theory, the model predicts that eC_a may increase community evenness. Collectively, both theories suggest that eC_a will favor coexistence and hence that species diversity should increase with eC_a. Our theoretical analysis leads to a novel hypothesis for the impact of eC_a on plant community composition. This hypothesis has potential to help guide the design and interpretation of eC_a experiments.

vated C_a (eC_a) could change the outcome of competitive interactions among plants (Bazzaz and McConnaughay 1992; Körner and Bazzaz 1996; Reynolds 1996; Brooker 2006), with cascading effects on the composition and diversity of plant communities (Zavaleta et al. 2003; Suding et al. 2005). However, there is currently relatively little theory predicting what kind of change in community

composition should be expected, or what types of species should be favored under eC_a .

Experimental work with young, individually grown plants shows that fast-growing species typically benefit most from eC_a (Poorter and Navas 2003). One reason is that inherently fast-growing species exhibit a greater absolute relative growth rate response to eC_a than their slow-growing counterparts (Poorter 1993, 1998; Atkin et al. 1999). The difference can also be attributed in part to the greater allocation of biomass to leaf tissue and higher photosynthetic rates in fast-growing species under eC_a (Oberbauer et al. 1985). In consequence, it is commonly assumed that community composition might shift toward fast-growing (Körner and Bazzaz 1996) or weedy species (Bazzaz 1990) under eC_a .

However, a recent study (Ali et al. 2013) showed on theoretical grounds that eC_a should only benefit fast-growing species during the initial exponential growth phase; as plants reach canopy closure, slower-growing plants should benefit the most (Ali et al. 2013). This theoretical prediction was supported by data from the Biodiversity \times CO₂ \times N (BioCON, St Paul, MN, USA; Fig. 1) FACE experiment, in which relative biomass responses to eC_a were highest for the slowest-growing species in plots where plants were grown in monocultures for 8 years. These results suggest that we need to rethink our predictions for how community composition may change under eC_a in field conditions. Given that experimental results appear to be somewhat mixed, with no consistent pattern emerging (Morgan et al. 2004), there is a clear need for theory-based hypotheses against which to evaluate experimental data.

The goal of this study was to explore theoretically how community composition may change under eC_a . As eC_a principally affects plant carbon uptake, with feedbacks via nitrogen availability (Comins and McMurtrie 1993), we examined competition between plants in terms of carbon and nutrient cycling. Similar frameworks to model competition have been widely used (Miki and Kondoh 2002; Rastetter and Agren 2002; Herbert et al. 2004; Daufresne and Hedin 2005; Ju and DeAngelis 2009). We simulated the effects of eC_a on long-term outcomes of interspecific competition using the plant carbon–nitrogen model of Ali et al. (2013). This model represents a species as a vector of plant traits that determine carbon and nutrient uptake, such as photosynthetic nitrogen use efficiency and specific leaf area. By examining competition among species with different trait values, we aimed to identify which trait values would be most successful in competition under eC_a , and whether communities would change in composition toward species with these trait values. Our ultimate goal was to generate testable hypotheses to guide experimental work.

As there is no consensus that a single mechanism of competition exists (Grime 1979; Chapin 1980; Tilman 1982; Thompson 1987; Huston and DeAngelis 1994; Hubbell 2001; Craine 2005; Craine et al. 2005), we implemented two alternative theories for competition in our model, so that our conclusions would not be contingent on the choice of the theory. Firstly, we implemented “resource use” theory (Tilman 1982), which predicts that the species that can reduce the monoculture soil nutrient availability to the lowest level (called R^*) should, when grown in mixed-species plots, eventually completely displace all other species if they are nutrient-limited. The theory also predicts that the species that can reduce the incident light at the surface to lowest level (I^*) should eventually displace all other species limited by light. There is some experimental evidence in support of this resource use theory (Tilman and Wedin 1991; Wedin and Tilman 1993; Huisman et al. 1999; Pasarge et al. 2006; Dybzinski and Tilman 2007).

The second theory implemented is “resource capture” theory (Grime 1979), which hypothesizes that the outcome of competition is determined by the capacity of plants to capture and retain resources. A high rate of resource capture from the environment means “a high capacity for photosynthesis and nutrient uptake per unit tissue mass” (Chapin 1980). Herbert et al. (1999) proposed a theoretical framework based on this theory, whereby the model partitions resources captured between species according to their relative biomasses and rates of resource capture per unit biomass.

In this study, we implemented both competition theories (resource use and resource capture) in a plant C–N model and investigated shifts in plant community composition and species richness under eC_a . Two types of sensitivity analysis were made for both competition theories: one where species differed from each other in one trait value, and another where species differed in all trait values. Our goals were to determine, on theoretical grounds, whether eC_a is likely to change the outcome of



Figure 1. Mixtures of plant species in the BioCON FACE experiment at the University of Minnesota’s Cedar Creek Ecosystem Science Reserve, MN, USA. Image courtesy of Kristine Y. Crous.

plant competition; what types of species should emerge as successful competitors under eC_a ; and whether species richness is likely to be affected.

Materials and Methods

Plant production model

The simple plant production model used in this study (Fig. 2) was fully described in Ali et al. (2013). The model simulates plant nitrogen (N) and carbon (C) dynamics using a set of difference equations. The processes simulated include photosynthesis, respiration, carbon and nitrogen allocation, turnover, and nitrogen uptake. At the leaf scale, the response of photosynthesis to variations in light, temperature, and CO_2 concentration is represented using the standard biochemical model of C_3 photosynthesis (Farquhar and von Caemmerer 1982) and depends on the maximum Rubisco activity (V_{cmax}), which is a function of leaf nitrogen content. The leaf intercellular CO_2 concentration, C_i , is calculated from the optimal stomatal conductance model of Medlyn et al. (2011). Instantaneous leaf photosynthesis is calculated for sunlit and shaded leaf separately (Medlyn et al. 2000) using leaf area index (LAI, $m^2 m^{-2}$) and incident radiation. Daily canopy photosynthesis was calculated as the integral of the instantaneous photosynthesis. Whole-plant respiration is assumed to be proportional to whole-plant photosynthesis. Biomass increment of leaves and roots is a function of C allocation and turnover rates. N uptake is represented as a saturating function of root biomass (B_r , $g C m^{-2}$). For this study, the net soil N mineraliza-

tion is held constant and equal to $3 g N m^{-2} year^{-1}$. The model is deterministic, in common with other models examining grassland community dynamics (Parton et al. 1994; Cannell and Thornely 1998).

The model has twelve parameters that represent plant traits, which are listed in Table 1. In the model, a species is characterized as a vector of values for these plant trait parameters. Thus, growth rate of a range of different species can be simulated by varying the input parameters to the model.

Incorporating resource use theory

The idea behind resource use theory is that the species that depletes a limiting resource the most in monoculture (than any other) will be the winner of competition in a mixture. We consider two resources (light and nutrients) and focus on plants growing in conditions where these two resources are limiting.

The outcome of competition between two species (A and B) is determined by comparing their R^* and I^* values (Tilman 1997). The outcome is given as follows:

$$\begin{aligned}
 R^*_A < R^*_B \text{ and } I^*_A < I^*_B & \text{ Species A wins} \\
 R^*_A > R^*_B \text{ and } I^*_A > I^*_B & \text{ Species B wins} \\
 (R^*_A > R^*_B \text{ and } I^*_A < I^*_B) \text{ or } (R^*_A < R^*_B \text{ and } I^*_A > I^*_B) & \text{ Both species coexist}
 \end{aligned}
 \tag{1}$$

That is, if either species has the lowest values for both R^* and I^* , that species wins; otherwise, both species can coexist.

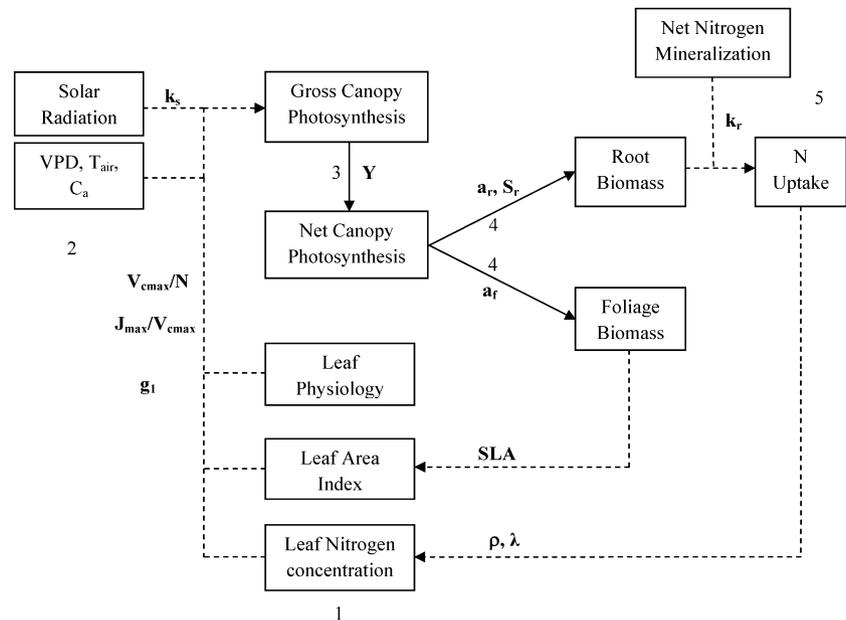


Figure 2. Flowchart of the model used in this study, showing how species traits (abbreviations in bold; defined in Table 1) are linked. Dashed lines are the flows of information (parameters, conversion, etc.), and solid lines are flows of carbon. Numbers indicate processes as follows: (1) scaling of 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.

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 (Ali et al. 2013)). 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 $\pm 50\%$.

Trait	Definition	Baseline trait value [Range]	Units
V_{cmax}/N	Maximum leaf carboxylation rate per unit leaf nitrogen	52 [26,78]	$\mu\text{mol g}^{-1} \text{N s}^{-1}$
$J_{\text{max}}/V_{\text{cmax}}$	Ratio of maximum electron transport to maximum carboxylation rate	1.86 [held constant]	Unitless
g_1	Stomatal conductance operating point	3.7 [1.85,5.55]	$\text{kPa}^{0.5}$
Y	Carbon use efficiency	0.5 [0.25,0.75]	Unitless
k_s	Light extinction coefficient	0.6 [held constant]	$\text{m}^2 \text{ ground m}^{-2} \text{ leaf}$
SLA	Specific leaf area	14 [7,21]	$\text{m}^2 \text{ leaf kg}^{-1} \text{ DM}$
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]	per year
k_r	Nitrogen uptake parameter related to root biomass	0.0239 [0.01195,0.03585]	$\text{m}^2 \text{ ground g}^{-1} \text{ C}$
ρ	Ratio of root N: C to leaf N: C	0.6 [0.3,0.9]	Unitless
λ	Fraction of N retranslocated to the functioning foliage before senescence	0.5 [0.25,0.75]	Unitless

The model has a well-defined equilibrium point (NPP*) that can be obtained by considering the carbon and nitrogen balances (see Appendix) (Ali et al. 2013). We calculated R^* and I^* values of each monoculture species at equilibrium as follows.

We calculated R^* as the difference between annual net soil N mineralization rate, N_{min} ($\text{g N m}^{-2} \text{ year}^{-1}$), and the annual plant N uptake, N_{up} ($\text{g N m}^{-2} \text{ year}^{-1}$). N_{min} was held constant. Nitrogen uptake N_{up} was modeled as a saturating function of root biomass, B_r (g C m^{-2}), and specific uptake rate, k_r ($\text{m}^2 \text{ g}^{-1} \text{ C}$), which is analogous to the light extinction coefficient:

$$N_{\text{up}} = N_{\text{min}} (1 - \exp(-k_r B_r)) \quad (2)$$

The R^* value of each species in monoculture was calculated at equilibrium. At equilibrium, the root biomass is related to equilibrium NPP by:

$$B_r = \frac{1 - a_f}{S_r} \text{NPP}^* \quad (3)$$

where NPP^* ($\text{g C m}^{-2} \text{ year}^{-1}$) is the equilibrium value of net primary production of the species, S_r (year^{-1}) is the root turnover rate, and a_f (dimensionless) is the fraction of carbon allocated to foliage. Thus, R^* is given by:

$$R^* = N_{\text{min}} \exp(-k_r \frac{1 - a_f}{S_r} \text{NPP}^*) \quad (4)$$

Similarly to R^* , I^* was calculated as the difference between the annual incident photosynthetically active radiation (IPAR) ($\text{MJ m}^{-2} \text{ year}^{-1}$), which is constant, and the total amount of absorbed photosynthetically active radiation (APAR) ($\text{MJ m}^{-2} \text{ year}^{-1}$), which is a saturating function of the leaf area index (LAI, $\text{m}^2 \text{ m}^{-2}$). At equilibrium, the leaf area index is given by:

$$\text{LAI} = \frac{0.4 * \text{SLA} a_f}{[C]_f} \text{NPP}^* \quad (5)$$

where SLA is the leaf area of the species ($\text{m}^2 \text{ leaf area kg}^{-1} \text{ DM foliage biomass}$), 0.4 is a factor that scales specific leaf area to canopy-level specific leaf area, and $[C]_f$ is the foliage carbon concentration, taken to be $0.44 \text{ g C g}^{-1} \text{ DM}$. Thus, I^* is given by:

$$I^* = \text{IPAR} \exp(-k_s \frac{0.4 * \text{SLA} a_f}{[C]_f} \text{NPP}^*) \quad (6)$$

where k_s is the light extinction coefficient ($\text{m}^2 \text{ m}^{-2}$). The values of R^* and I^* can then be compared among pairs of species to determine the outcome of competition between those species.

Incorporating resource capture theory

In the resource capture theory, the amount of a resource captured by one species in competition depends on its biomass relative to that of competitors, as well its rate of resource capture per unit biomass. To implement this theory, the plant production model of Ali et al. (2013) was generalized to simulate the growth of two species growing in competition. Light and nutrients are the two limiting resources. The capture of these two resources between the competing species is calculated as a function of their relative biomass. We use equations presented by Herbert et al. (2004) to calculate the capture of these resources between the species, making the simplifying assumption that all species have equal canopy dominance, that is, no species is able to overtop another ($f_i = 1$ for all i , in Herbert et al. (2004)'s notation).

The total amount of PAR absorbed by both plant species is

$$\text{APAR}_{\text{tot}} = \text{IPAR}(1 - \exp(-k_{s1}\text{LAI}_1 - k_{s2}\text{LAI}_2)) \quad (7)$$

where IPAR is the incoming irradiance ($\text{MJ m}^{-2} \text{ year}^{-1}$), k_{s1} and k_{s2} ($\text{m}^{-2} \text{ m}^2$) are the light extinction coefficients, and LAI_1 and LAI_2 are the leaf area indices of species 1 and 2, respectively. Following Herbert et al. (2004) and Ju and DeAngelis (2009), the fraction of this total radiation absorbed by species i in the presence of species j is given by:

$$\frac{\text{APAR}_i}{\text{APAR}_{\text{tot}}} = \frac{w_{C_i}}{w_{C_i} + w_{C_j}} \quad (8)$$

where the weighting factors w_{C_i} are given by:

$$w_{C_i} = (1 - \exp(-k_{si}\text{LAI}_i))(1 + \exp(-k_{sj}\text{LAI}_j)) \quad (9)$$

The first factor in equation 8 represents the fraction of incident light that would be absorbed by species i in the absence of competition, while the second factor in equation 8 represents the competitive effect of species i on species j in absorbing light.

Combining equations (6–8), we obtain the amount of PAR absorbed by species i in competition with species j :

$$\text{APAR}_i = 0.5 \text{IPAR}(1 - \exp(-k_{si}\text{LAI}_i - k_{sj}\text{LAI}_j) + \exp(-k_{sj}\text{LAI}_j) - \exp(-k_{si}\text{LAI}_i)) \quad (10)$$

The effect of equation 9 is that the fraction of total APAR partitioned to the species with the lowest light capture potential ($k_i \text{LAI}_i$) is slightly greater than the ratio of the two species' light capture potentials ($k_i \text{LAI}_i/k_j \text{LAI}_j$). Where the light capture potentials are the same, the two species will absorb the same amount of light.

Net carbon production of species, NPP_i , is then determined from the PAR absorbed by species i by multiplying it by a light use efficiency term that depends on leaf nitrogen concentration (Ali et al. 2013).

Competition for nutrients by root biomass is modeled in a very similar way. Total root nitrogen uptake for both species combined is given by:

$$\text{N}_{\text{up}} = \text{N}_{\text{min}}(1 - \exp(-k_{r1}B_{r1} - k_{r2}B_{r2})) \quad (11)$$

where N_{min} is the net nitrogen mineralization ($\text{g N m}^{-2} \text{ year}^{-1}$), k_{r1} and k_{r2} ($\text{m}^2 \text{ g}^{-1} \text{ C}$) are the root N uptake coefficients, and B_{r1} and B_{r2} (g C m^{-2}) are the root biomass values for species 1 and 2, respectively. Note that in this model, N_{min} is assumed constant, that is, we ignore possible feedback effects via changing nitrogen mineralization rates. Following similar logic to the derivation for light capture, we obtain the root nitrogen uptake for species i as:

$$\text{N}_{\text{up},i} = 0.5 \text{N}_{\text{min}}(1 - \exp(-k_{ri}B_{ri} - k_{rj}B_{rj}) + \exp(-k_{rj}B_{rj}) - \exp(-k_{ri}B_{ri})) \quad (12)$$

As with light capture, the outcome of this equation is that the fraction of total nitrogen uptake obtained by the species with the lowest nitrogen capture potential ($k_i B_{ri}$) is slightly more than the ratio of the two species' nitrogen capture potentials ($k_i B_{ri}/k_j B_{rj}$).

The resource capture model with two species has a well-defined equilibrium point (NPP_i^* , NPP_j^*) (see Appendix). Numerical simulation of the model with a daily time step was used to find this equilibrium point. The outcome of competition between two species is quantified by comparing the total biomass of the species. We defined the dominance ratio as the winning species' share of total biomass. This ratio ranges from 0.5 to 1. Both species are considered to coexist unless the biomass of one species vanishes to zero, in which case the dominance ratio = 1.

Simulations

The simulation model was implemented as a discrete time-step model in FORTRAN. Meteorological data were recycled each year. The model was run for 23 years, by which time the system was observed to have equilibrated. Simulated equilibrium points were verified against exact equilibrium values, calculated using the equations given in the Appendix, for a number of test cases.

Two types of simulations were run for both competition theories. Firstly, we examined the effects of individual trait values by considering competition between species which differed from each other in only one trait value. A set of species was generated by varying one trait at a time by $\pm 50\%$ of the base value and pairwise competition among this set of species was examined, using both resource use and resource capture theories. Secondly, we examined competition among species with trait values that were chosen from a random uniform distribution covering $\pm 50\%$ of the base value for each trait. For simplicity, we assumed that traits vary independently of one another; the effect of correlations among traits is considered in the Discussion. For resource use theory, we generated a set of 10,000 species and examined the outcome of competition among all possible pairs (10^8 species pairs) of these species. Resource capture theory is more time-intensive, so for this theory, we generated a second random set of 10,000 species and paired them with the first set of 10,000 species, thus generating 10,000 random species pairs, and examined competition between each pair. All model runs were carried out at ambient C_a (aC_a , 360 ppm) and eC_a (550 ppm). Model simulations were carried out for aC_a at 360 ppm because it was near the level just prior to the start of the BioCON FACE experiment (Reich et al. 2001a,b; Crous et al. 2010).

Results

Competition among “species” differing in one trait value only

The results of the simulations where traits were varied singly are shown in Table 2. For resource use theory, species were ranked by assigning one point for each time the species won in paired competition, and 0.5 points for each time the outcome was coexistence. For resource capture theory, species were ranked by calculating their average fraction of total biomass in all possible pairwise competitions. While there are some differences in relative rankings of traits between resource use and resource capture theory, the two theories agree on the direction in which traits should change in order to increase success in competition. In both theories, the traits yielding the most success in competition were high fraction of carbon allocated to foliage (a_f) and high carbon use efficiency (Y) (Table 2). The principal difference in trait rankings between theories was that slow root turnover (S_r) promotes success in competition in resource capture theory, but has no effect on competition in resource use theory.

Table 2. Ranking of species traits by their effect on competitive ability under ambient and elevated C_a . The rankings are shown for resource use and resource capture theories. Rankings were obtained by considering pairwise competition among a set of species differing by only one trait value. For resource use theory, each species was assigned 1 for each win, 0.5 for coexist, and 0 for each loss. For resource capture theory, the proportion of biomass obtained by the species in competition was averaged across the 17 pairwise competitions. High and low trait values are represented by “+,” “-,” respectively.

Resource use			Resource capture		
Trait	Ability aC_a	Ability eC_a	Trait	Ability aC_a	Ability eC_a
$+a_f$	17.0	16.0	$+a_f$	0.82	0.80
$+Y$	15.5	16.0	$+Y$	0.81	0.78
$+SLA$	15.5	16.0	$-S_r$	0.74	0.71
$+V_{cmax}/N$	13.5	13.5	$+V_{cmax}/N$	0.73	0.71
$-\rho$	13.5	13.5	$-\rho$	0.73	0.70
$+\lambda$	12.0	12.0	$+SLA$	0.71	0.70
$+g_1$	9.5	9.0	$+\lambda$	0.66	0.64
$-S_r$	9.0	9.0	$+k_r$	0.63	0.60
$+S_r$	9.0	9.0	$+g_1$	0.60	0.59
$+k_r$	9.0	9.0	$-g_1$	0.50	0.51
$-k_r$	8.5	9.0	$-\lambda$	0.49	0.50
$-g_1$	5.5	5.5	$+\rho$	0.43	0.44
$-\lambda$	5.5	5.5	$+S_r$	0.40	0.43
$+\rho$	4.0	4.0	$-k_r$	0.27	0.35
$-V_{cmax}/N$	3.0	3.0	$-SLA$	0.20	0.23
$-SLA$	1.5	1.5	$-V_{cmax}/N$	0.19	0.22
$-Y$	1.5	1.5	$-a_f$	0.07	0.07
$-a_f$	0.0	0.0	$-Y$	0.02	0.03

Using resource use theory, the effect of eC_a on competition outcomes among pairs of species differing by single trait values was small, with the outcome of competition changing in only three species pairs (Table 2). In one of the three cases, a win–lose outcome became a coexistence outcome. As a result, the competitive ranking of species under eC_a barely changed.

Predicted values of NPP for two competing species differing in one trait value only using the resource capture theory are shown in Table 3, under aC_a and eC_a . The outcome of competition in each case is shown by the dominance ratio, which is the dominant species’ fraction of total productivity. In each case, the least productive species at aC_a is the most responsive to eC_a . However, in no case does the least productive species at aC_a become the most productive species at eC_a . Similarly, Table 2

Table 3. Outcome of competition between two plant species differing in one trait, according to resource capture theory. One species had a high trait value while the other had a low trait value. The predicted values of net primary productivity (NPP) for each species at equilibrium under aC_a and eC_a are shown. The numbers in the brackets indicate the winning species dominance ratio. The enhancement ratios (E/A) are also shown for each species. Values for the winning species are indicated in bold.

Traits	NPP ($gC \cdot m^{-2} \cdot year^{-1}$)		E/A ratio
	aC_a	eC_a	
V_{cmax}/N			
High	348 (0.98)	403 (0.93)	1.16
Low	7	22	3.34
g_1			
High	148 (0.63)	176 (0.58)	1.19
Low	87	127	1.47
Y			
High	457 (1.00)	592 (1.00)	1.30
Low	0.05	0.21	4.53
SLA			
High	294 (0.99)	367 (0.98)	1.24
Low	3	8	2.84
a_f			
High	418 (1.00)	530 (1.00)	1.27
Low	0.07	0.29	4.51
S_r			
High	61	114	1.86
Low	187 (0.75)	199 (0.60)	1.07
λ			
High	183 (0.71)	216 (0.66)	1.18
Low	74	110	1.49
k_r			
High	236 (0.91)	253 (0.78)	1.07
Low	24	71	2.91
ρ			
High	45	79	1.74
Low	256 (0.85)	287 (0.78)	1.11

demonstrates that the competitive rankings of species differing in only one trait value were unchanged between aC_a and eC_a . However, the average dominance ratio of the top nine species decreased under eC_a and that of the bottom nine species increased. Thus, according to resource capture theory, eC_a does not alter which species dominates, but in each case competition becomes more even.

Competition among randomly generated species

We followed the simulations of competition between species differing in one trait only, with competition simulations among randomly generated species. Table 4 shows the mean trait values for the winning and losing species in pairs of randomly selected species under aC_a for both theories. For resource use theory, we compared the trait values of species that were outright winners of competition with those of the species that were losers in competition, whereas for resource capture theory, winners were classified as the species with a biomass share greater than 50%. The importance of each trait in determining the outcome of competition was evaluated by calculating the difference between the mean trait value of winners and the mean trait value of losers, divided by the mean trait value overall. Under resource use theory, the traits favoring success in competition were, in decreasing order of importance: high carbon use efficiency (Y), high fraction of carbon allocated to foliage (a_f), high maximum leaf carboxylation rate per unit leaf nitrogen (V_{cmax}/N), high specific leaf area (SLA), high root nitrogen uptake parameter (k_r), low root turnover rate (S_r), low root to leaf nitrogen ratio (ρ), high fraction of nitrogen retranslocated to foliage (λ), and high stomatal conductance operating point (g_1) (Table 4). Resource capture theory highlighted

a similar set of traits as important in determining the outcome of competition; however, low S_r and low ρ were more important than high SLA and high k_r .

To further compare the predictions for the outcome of competition by the two theories, we applied resource use theory to the 10,000 species pairs considered for resource capture and identified each species as winning, losing, or coexisting. Figure 3 shows the biomass share predicted by resource capture theory for species identified as winning, losing, or coexisting by resource use theory. Overall, the theories generally agree about the outcome of competition: “winners” in resource use theory almost always have a biomass share greater than 0.5 in resource capture theory, while “losers” almost always have a biomass share less than 0.5 (Fig. 3). “Coexisters” in resource use theory may have a biomass share anywhere from 0 to 1 in resource capture theory, but the values are centered on 0.5.

Effect of eC_a on random species competition: Resource use theory

Using resource use theory, we calculated the frequency distributions of pairwise competition outcomes among 10,000 randomly generated species (Fig. 4). Competition outcomes were calculated for aC_a and eC_a . For each species, the number of wins, losses, and coexistence cases was recorded. Under aC_a , the frequency distributions of the number of wins and the number of losses are skewed to the right. Few species win often; most species win less than 3500 times of 9999. Similarly, only a few species lose often; most species lose less than 3500 times of 9999. However, the frequency distribution of coexistence is roughly normally distributed, with most species coexisting about 3500 times of 9999, and no species coexisting more than 8000 times.

Table 4. Comparison of mean trait values of winning and losing species when randomly generated species are compared for resource use and resource capture theories under aC_a . Importance of each trait in determining the outcome of competition is calculated as the difference between the average winning and losing trait values, divided by the average trait value overall. Traits are ordered (in the descending order) by importance.

Resource use theory				Resource capture theory			
Trait	Mean trait value, winning species	Mean trait value, losing species	Importance	Trait	Mean trait value, winning species	Mean trait value, losing species	Importance
Y	0.55	0.45	0.21	Y	0.55	0.46	0.17
a_f	0.44	0.36	0.20	a_f	0.43	0.37	0.14
V_{cmax}/N	55.17	48.35	0.13	V_{cmax}/N	54.71	49.22	0.11
SLA	14.78	13.19	0.11	S_r	0.72	0.78	-0.08
k_r	0.025	0.023	0.10	SLA	14.6	13.56	0.07
S_r	0.71	0.79	-0.09	ρ	0.58	0.62	-0.06
ρ	0.58	0.63	-0.08	k_r	0.025	0.023	0.05
λ	0.52	0.49	0.05	λ	0.51	0.49	0.04
g_1	3.75	3.66	0.03	g_1	3.74	3.67	0.02

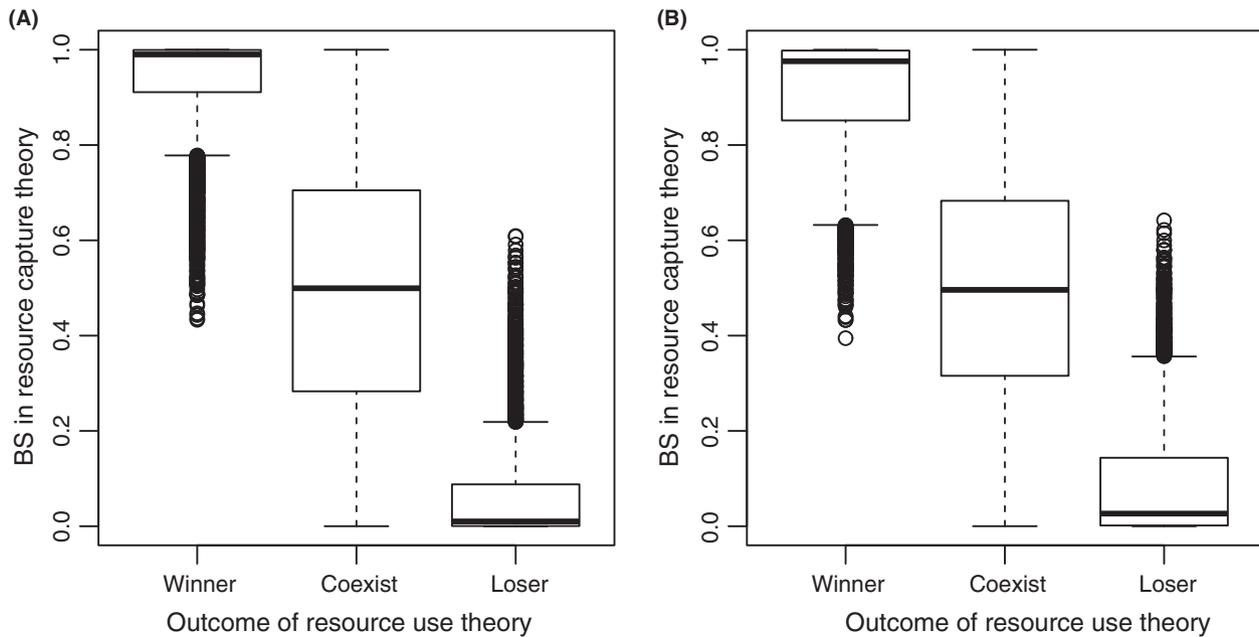


Figure 3. Comparison of the two competition theories. Both theories were applied to the same 10000 species pairs. The biomass share (BS) of each species predicted by resource capture theory is plotted against the outcome of resource use theory of the same species under aC_a (A) and eC_a (B).

Similar shaped distributions are found for eC_a (Fig. 4). However, eC_a caused some changes to the distributions. We investigated these by calculating, for each species, the difference in the number of times that plant species was predicted to win, lose, or coexist under changed environmental conditions relative to the aC_a case. The frequency distributions of these differences are shown in Figure 4. eC_a decreases the average number of wins (Fig. 4C) and average number of losses (Fig. 4F) but increases the average number of cases of coexistence (Fig. 4I). The interpretation is that increasing C_a tends to favor coexistence among species.

To identify whether eC_a favored any species traits in particular, we calculated the species' competitive ability by assigning 1 point for each win and 0.5 points for each coexistence. We then calculated the difference in competitive ability under ambient and eC_a , and performed rank correlations to find which traits were most strongly associated with an increase in competitive ability (Table 5). An increase in competitive ability was strongly negatively associated with the fraction of carbon allocated to foliage (a_f), the stomatal operating point (g_1), and the maximum carboxylation rate per unit leaf nitrogen (V_{cmax}/N). These results indicate that the competitive ability of the species with low values of these traits is most strongly improved by growth under eC_a . Interestingly, the increase in competitive ability with eC_a was

not associated with carbon use efficiency (Y), despite the importance of this trait in determining competitive outcomes under aC_a .

Effect of eC_a on random species competition: Resource capture theory

Using resource capture theory, we calculated the outcome of competition between 10,000 randomly generated pairs of species, at aC_a and eC_a (Fig. 5). For each species pair, we identified the winning species as that with the highest equilibrium biomass at aC_a and calculated the winner's share of biomass at aC_a and eC_a , and the difference between the two. The frequency distributions of these numbers are shown in Figure 5.

Under aC_a , the frequency distribution of the winners' share of biomass is skewed to the left, indicating that in most species pairs, the winner has over 90% of the total biomass. Under eC_a , the frequency distribution is less skewed, indicating that the number of species with high biomass share is decreasing. In most cases, the winner's share of biomass under eC_a is lower than under aC_a (Fig. 6). However, it is rare for eC_a to change which species has the largest biomass share; this occurred in only 192 of 10,000 cases. The implication is that, although eC_a does not change the outcome of competition, it tends to make the competition more even.

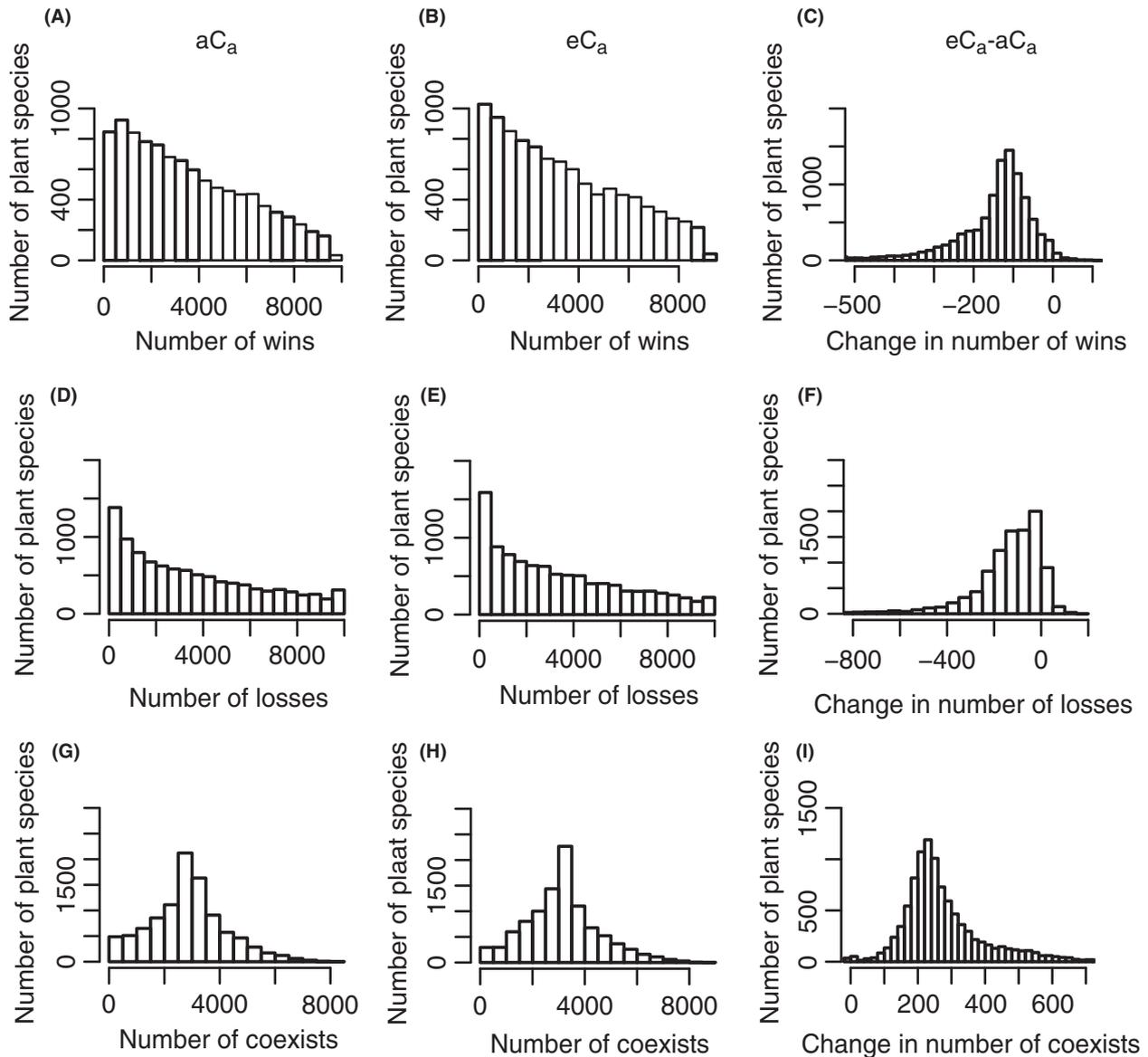


Figure 4. Outcome of pairwise competition among 10000 randomly generated species using resource use theory. For each species, the number of wins (A–C), losses (D–F), and coexistence cases (G–I) was recorded. The figures show histograms for the frequency of each of these outcomes, under (A, D, G) ambient and (B, E, H) elevated C_a . The difference in the number of times that plant species was predicted to win, lose, or coexist under eC_a relative to aC_a (C, F, I) is also shown.

Discussion

Two approaches to modeling competition give consistent results – that eC_a tends to lessen the difference in competitive differences between species and can therefore increase coexistence. Our model predicts that more species will coexist and biomass share will be more even (less likely to be one very dominant species) but does not predict that winners will change. Our model predicts reduced competition in eC_a and increased species richness. This

work provides a novel, mechanistic hypothesis for the outcomes of competition under eC_a that can be tested experimentally. Importantly, using a mathematical model to develop the hypothesis, the assumptions and logic underpinning the hypothesis are explicit, meaning that not only the overall prediction but also the underlying mechanisms can be tested against data.

The reason the model predicts increased evenness and increased diversity stems from the original prediction that eC_a will increase productivity in slow-growing plants

Table 5. Spearman's rank correlations of trait values with ambient NPP in monoculture; competitive ability at ambient C_a according to resource use theory; and with the change in competitive ability due to eC_a . Traits are ordered (in the descending order) by the strength of correlation.

Trait	Rank correlation with ambient NPP in monoculture	Trait	Rank correlation with ambient competitive ability	Trait	Rank correlation with change in competitive ability due to eC_a
Y	0.60	Y	0.50	a_f	-0.50
a_f	0.51	a_f	0.47	g_1	-0.35
V_{cmax}/N	0.37	V_{cmax}/N	0.31	V_{cmax}/N	-0.27
ρ	-0.22	SLA	0.27	SLA	-0.18
λ	0.13	k_r	0.24	ρ	0.15
SLA	0.10	S_r	-0.23	λ	-0.11
g_1	0.08	ρ	-0.19	S_r	-0.10
k_r	0.02	λ	0.11	Y	-0.08
S_r	-0.01	g_1	0.06	k_r	0.06

relatively more than in fast-growing plants (Ali et al. 2013). In the resource capture theory, this results in the less dominant species being favored by eC_a , reducing the dominance ratio (Table 3). The prediction of increased coexistence using resource use theory can be understood as follows. The condition for coexistence (Eq 1) can be rewritten using equations (4) and (6) as:

$$\frac{a_fASLA_Ak_{sA}}{a_fBSLA_Bk_{sB}} < \frac{NPP_B}{NPP_A} < \frac{a_{rA}S_{rA}k_{rA}}{a_{rB}S_{rB}k_{rB}} \quad \text{if} \quad \frac{a_fASLA_Ak_{sA}}{a_fBSLA_Bk_{sB}} < \frac{a_{rA}S_{rA}k_{rA}}{a_{rB}S_{rB}k_{rB}}$$

or

$$\frac{a_fASLA_Ak_{sA}}{a_fBSLA_Bk_{sB}} > \frac{NPP_B}{NPP_A} > \frac{a_{rA}S_{rA}k_{rA}}{a_{rB}S_{rB}k_{rB}} \quad \text{if} \quad \frac{a_fASLA_Ak_{sA}}{a_fBSLA_Bk_{sB}} > \frac{a_{rA}S_{rA}k_{rA}}{a_{rB}S_{rB}k_{rB}} \quad (13)$$

where subscripts A and B indicate species A and B . That is, coexistence occurs when the ratio of NPP of the two species grown in monoculture falls within upper and lower bounds set by their relative trait values. As eC_a increases NPP of slow-growing species by more, the ratio NPP_B/NPP_A has fewer extreme values under eC_a , with the implication that it will fall more often between these bounds, making coexistence more likely.

Which trait values are favored by eC_a ?

We also examined which species traits are most strongly associated with the outcome of competition under aC_a , and which traits are associated with improved competitive status under eC_a . Although we have generalized the results to talk about slow-growing vs fast-growing species, there are some distinctions among the plant traits causing

slow growth. Three traits, low foliage allocation (a_f), low photosynthetic nitrogen use efficiency (V_{cmax}/N), and low carbon use efficiency (Y), are associated with low NPP at aC_a . However, only two of these traits, low a_f and low V_{cmax}/N , are strongly associated with increased competitive ability under eC_a . In contrast, the stomatal operating point g_1 is only weakly associated with NPP at aC_a , but was strongly associated with increased competitive ability under eC_a . This result is consistent with the conclusions of Ali et al. (2013) who found that the trait g_1 was important in determining the relative plant response to eC_a . Thus, we suggest that experiments investigating competition under eC_a should also aim to quantify species traits, as the traits themselves, rather than growth rates per se, can be important in determining the effect of eC_a on competitive ability.

When ranking the importance of the traits, it is also important to consider the range of actual trait values among the species considered. When we ran our competition model for the seven species growing in the BioCON experiment, we did not find that the trait g_1 was important in determining competition outcomes, simply because the values of g_1 were very similar among this set of species (Ali 2012).

Comparison with alternative hypotheses for plant competition outcomes under eC_a

One existing hypothesis for the effects of C_a on plant community composition is that weedy and fast-growing species may be favored, promoting invasions (Bazzaz 1990). Our model predictions differ strongly from this hypothesis; the model suggests that the dominance of fast-growing species will be reduced under eC_a compared to aC_a . The difference between these hypotheses arises from the time-scale considered: the observation that fast-growing species are more strongly responsive to eC_a derives from short-term pot experiments, whereas our model applies to longer-term field experiments (Ali et al. 2013). Our model prediction agrees with Dukes (2002) who demonstrates that the response of invasive species to eC_a in the field cannot be predicted from the response in a short-term glasshouse experiment.

A related hypothesis is the idea that eC_a can drive competitive exclusion. Elevated C_a increases ecosystem productivity (Oren et al. 2001; Ainsworth and Long 2005; Reich et al. 2006a,b) which could potentially lead to competitive exclusion and decreasing diversity (Bazzaz and Garbutt 1988; Potvin and Vasseur 1997; Körner 2003; Brooker 2006; Lau et al. 2010). Our model does not yield this result because elevated C_a is predicted to increase productivity in both strong and weak competitors. Other authors have suggested that higher productivity with eC_a

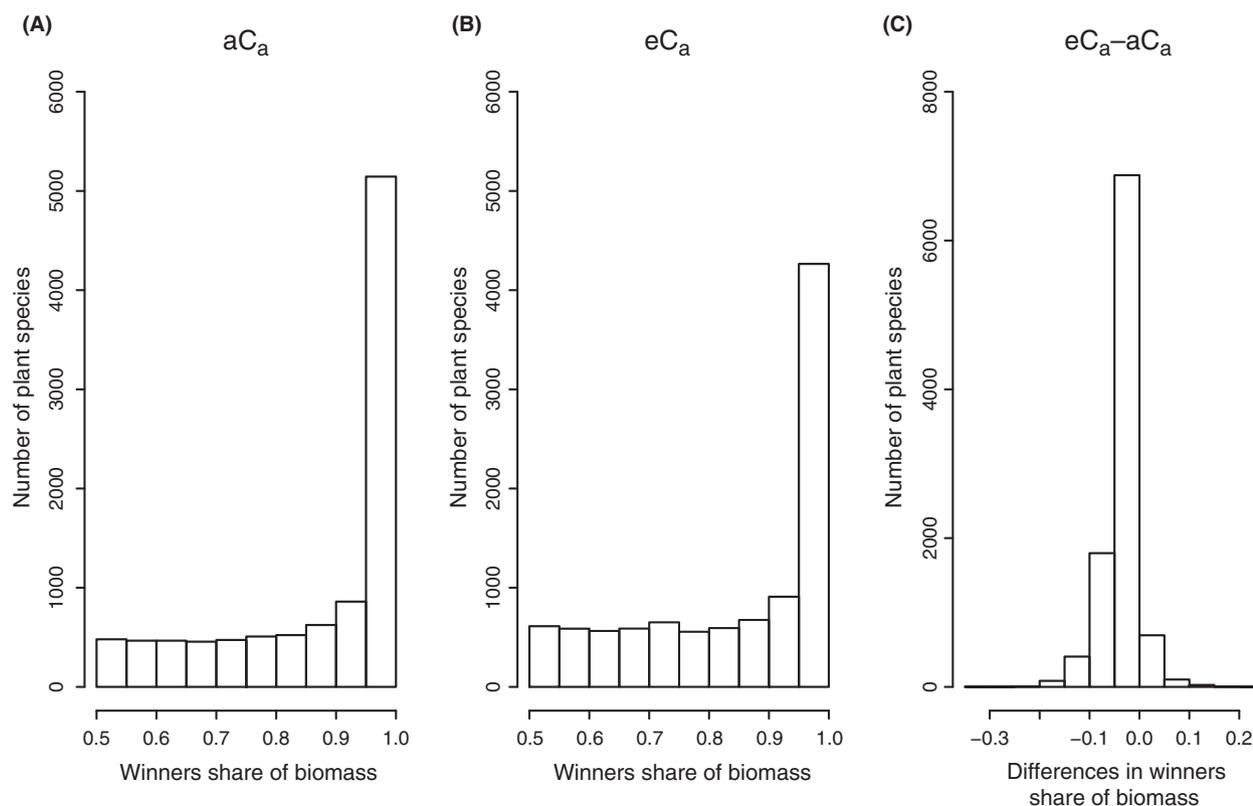


Figure 5. Outcome of competition in 10000 randomly generated pairs of species using resource capture theory. In each pair, the winner was identified and its share of biomass at equilibrium was calculated. The frequency distribution of the winners' share of biomass under (A) ambient and (B) elevated C_a is shown. The change in winners' share of biomass (C) is calculated as the share of biomass at eC_a less the share of biomass at aC_a for the winning species under aC_a .

should increase diversity, based on a large-scale empirical relationship between diversity and productivity (Woodward and Kelly 2008). Our model differs from this work because it does not assume a relationship between diversity and productivity; rather, we predict the outcome of competition based on underlying ecophysiological mechanisms.

Other hypotheses relate to the interaction between C_a and nutrient availability. Berry and Roderick (2002) suggested that in low nutrient environments, nutrient efficient species, such as sclerophylls, might respond more to eC_a than nutrient inefficient species and hence might increase in dominance. Our model does not yield this result because it predicts that nutrient inefficient species (those with low V_{cmax}/N) should actually respond more to eC_a under nutrient limitation, than nutrient efficient species (Ali *et al.* 2013). This prediction comes from the fact that (in the model) the nutrient inefficient species have low productivity at low nutrient availability and can thus benefit more strongly from the increased carbon availability under eC_a . This prediction could also be tested experimentally.

Alternatively, it can be argued that the change in plant stoichiometry due to eC_a (Ainsworth and Long 2005; Novotny *et al.* 2007) could result in greater relative limitations by other dominant resources such as nitrogen (Reich *et al.* 2006a,b), and this effect should reduce competitive exclusion and increase species richness. Our model predictions are closest to this hypothesis, although our logic is subtly different. We assume that nitrogen is always limiting to plant growth, and the reduction in competitive exclusion arises from the fact that productivity of different plant species is more similar under eC_a than aC_a , and therefore, one species cannot outcompete another so readily.

Comparison of the model with experimental data

The purpose of our model was to provide a logical theoretical framework with which to examine the results of experiments on the effect of eC_a on plant competition. The model is based on a set of simple but defensible assumptions. If it fails to predict experimental outcomes,

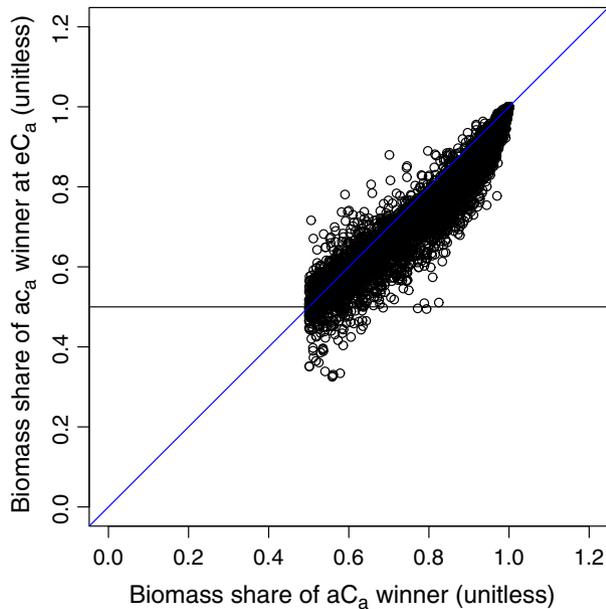


Figure 6. Biomass share (BS) of the ambient winner at eC_a as a function of its BS at aC_a . The horizontal line indicates where the biomass share of the ambient winner at eC_a is 0.5. Points falling below this line indicate species pairs where the dominant species changed between aC_a and eC_a . The blue line is the 1:1 line. Points above this line indicate species pairs where the dominance ratio of the aC_a winner was increased at eC_a .

it should be possible to identify which assumptions are at fault, and thereby increase our understanding of plant competitive relationships under eC_a .

It is important to be aware of the assumptions made when testing the model against experimental data. We assumed that the vegetation is perennial, herbaceous, C_3 and not leguminous, and that light and nitrogen availability are limiting to growth but water availability is not. As the predictions are made for the equilibrium situation, the model predictions are applicable to longer-term ecosystem-scale experiments with steady-state plant canopies, rather than short-term experiments in which canopies are still expanding. We also assumed that the canopy dominance factor (Herbert et al. 2004) was equal to one, implying that all species have similar height and rooting depth.

Although a number of experiments show results that contradict our model predictions, this may be because these model assumptions do not hold for these experiments. For example, Zavaleta et al. (2003) examined plant diversity responses in California annual grassland to eC_a and found reduced plant diversity after 3 years. However, this site experiences strong water limitation, and one reason for the reduction in plant diversity is that eC_a , by relieving water stress, can delay senescence of the domi-

nant plant canopy at the end of the growing season, narrowing the window when sufficient light would be available for the late-emerging species. Many competitive interactions are driven by water availability, and it is clear that there is an important role for water limitations in determining competitive outcomes under eC_a (e.g., Polley et al. 1997). Our model must be seen as limited because it does not consider such interactions; there is an urgent need for theoretical studies extending our work to consider water-limited environments.

A number of experimental findings on non-water-stressed C_3 -dominated herbaceous communities do provide support for our model prediction that eC_a will increase evenness and species richness, although it should be acknowledged that these experiments also include C_4 and leguminous species. In a long-term field study on biodiversity of grasslands under eC_a conditions, community evenness was increased (Leadley et al. 1999), that is, dominance was reduced, in agreement with our theory. At the BioCON FACE experiment in Minnesota, eC_a partially eliminated negative effects on diversity of elevated N supply by reducing competitive exclusion (Reich 2009), and overall tended to increase plant diversity (Isbell et al. 2013). In the New Zealand grassland FACE experiment, productivity of the dominant grasses was not increased under eC_a but productivity of the subdominant forbs was increased (Newton et al. 2006). In a mixed-grass prairie experiment, community evenness was found to increase with eC_a due to decreases in biomass of the dominant species (Zelikova et al. 2014). The support provided by these experiments for our theory is clearly insufficient as a formal test of the model, but does demonstrate that our model predictions deserve further experimental exploration.

Model limitations and further work

Our model is intentionally simple, to enable its behavior to be readily understood. As a result, however, a number of other processes that are potentially important in determining the outcome of interspecific competition are missing from our model. We mentioned the need to extend the model to consider water limitation above. Additionally, our model does not consider population-level processes, such as allocation of biomass to reproduction, recruitment, and mortality (Moorcroft et al. 2001). Neither resource use theory nor resource partitioning theory take account of these processes, so the model would need to be significantly extended to incorporate these population processes. In addition, experimental data to parameterize and test the effect of eC_a on these processes are as yet rather limited. Thus, there is considerable work to be done to add these effects into our model.

Our model does not consider the possible role of preemptive resource capture. We did not consider alternative timings for leaf area dynamics, for example. Similarly, when applying resource partitioning theory, we assumed that the canopy dominance factor, which takes into account the relative height of the two species, is zero, meaning that the species are equal in height. Similarly, the soil dominance factor was also assumed to be zero. Further work could consider how preemptive resource capture, either in time or space, may change the outcome of competition under eC_a .

In this work, we assumed that species traits could vary independently from each other. In nature, there are significant correlations among some traits, such as leaf longevity and specific leaf area (Wright *et al.* 2004). To explore such trait correlations, we used our current model and made some additional analyses that included implementation of the leaf economics spectrum (Wright *et al.* 2004). We generated additional sets of random species, where we constrained some traits by implementing linear relationships between S_f and SLA, and among the traits Y , V_{cmax}/N , and k_r (Aubier 2013). These results are not shown here because we found little impact on the outcomes of the model, indicating that our current model predictions are robust to the implementation of trait correlations (Wright *et al.* 2004).

Our model only considers competition between two species, whereas most grasslands consist of many more than two species coexisting. Resource use theory assumes that the number of resources available determines the number of potentially coexisting species. Hence, we could not extend this theory to consider more species without also considering additional resources. However, resource partitioning theory allows for many species to coexist even though they are competing for a limited number of resources (Rastetter and Ågren 2002). Thus, our resource partitioning model could be fairly readily extended to consider more than two competing species. We consider it highly likely that our main finding in this study, that eC_a promotes coexistence, would continue to hold in a model of more than two species.

Conclusion

We applied resource use theory to a plant carbon–nitrogen model in order to develop theory for how eC_a is likely to change competition among plant species. Use of the model allowed us to develop several testable hypotheses that we suggest could be examined in field experiments to enhance our understanding of competitive relations under eC_a . Firstly, we identified the species traits increasing success in competition. In all analyses, the traits of high foliage allocation, high carbon use efficiency,

and high photosynthetic nitrogen use efficiency led to strong performance in competition. These rankings among species traits could be used to examine outcomes of field-based competition experiments to test whether species performance in competition can be predicted by their trait combinations.

Secondly, our model makes the novel prediction that eC_a is likely to make competition among species more even, with fewer strongly dominant species. With resource use theory, we predicted increased coexistence, implying increased diversity. With resource capture theory, we predicted that eC_a would reduce the dominance ratio of the winning species, increasing community evenness. These predictions could form a framework for studies of eC_a effects on competition in the field.

Code availability

The present code is written in FORTRAN programming language. It uses R software for generating large set of species and MathCAD software for pairwise comparisons. It can also be obtained upon request by sending an email to ali.ashehad@gmail.com.

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Conflict of Interest

None declared.

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Appendix: Equilibrium analysis of model

Single species model

We follow the approach used by Comins and McMurtrie (1993) to derive the equilibrium values of the model. In this approach, equilibrium NPP (NPP*) is calculated by considering C and N balances of the plant.

In our simple, single species model, the N balance constraint is obtained by considering plant N balance. In equilibrium, N uptake by roots must equal N used in new growth. Hence,

$$N_{\min}(1 - \exp(-k_r B_r^*)) = \text{NPP}^*(a_f n_f^* + (1 - a_f)\rho n_f^*) \quad (\text{A1})$$

where n_f^* is foliage nitrogen concentration at equilibrium. Also at equilibrium, growth of roots must equal senescence. Thus,

$$B_r^* = \text{NPP}^*(1 - a_f)/s_r \quad (\text{A2})$$

Combining equations (A1) and (A2) yields an implicit equation for NPP* as a function of n_f^*

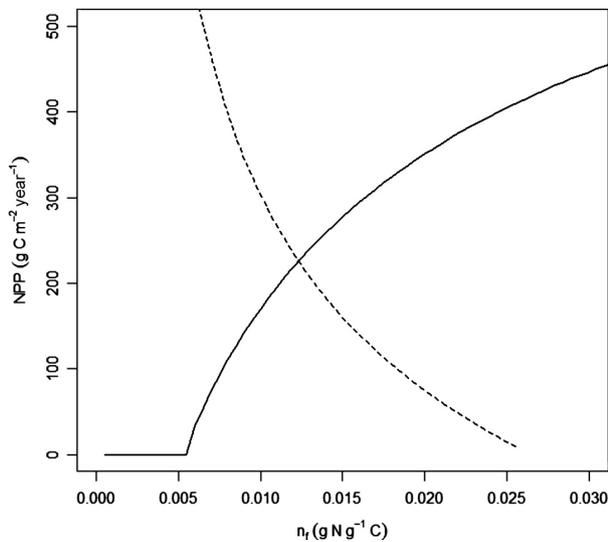


Figure A1. Equilibrium NPP for one species growing in monoculture is given by intersection of production constraint (solid line) and nutrient availability constraint (dashed line).

$$N_{\min}(1 - \exp(-k_r \text{NPP}^*(1 - a_f)/s_r)) = \text{NPP}^*(a_f n_f^* + (1 - a_f)\rho n_f^*) \quad (\text{A3})$$

The plant C balance constraint is obtained by considering the plant photosynthetic uptake. We use a simplified plant photosynthesis model here to demonstrate the equilibrium approach. We assume a light-use efficiency expression

$$\text{NPP} = I_0 \varepsilon(n_f, C_a)(1 - \exp(-k_s \text{LAI}))Y \quad (\text{A4})$$

where I_0 is annual incident radiation, the term $(1 - \exp(-k_s \text{LAI}))$ yields the fraction of radiation absorbed, and $\varepsilon(n_f, C_a)$ is the light-use efficiency, which depends on the plant traits V_{cmax}/N and g_1 .

At equilibrium, leaf area index is given by

$$\text{LAI}^* = \text{NPP}^* a_f * 0.4 * \text{SLA}/\text{Cfrac} \quad (\text{A5})$$

Combining eqs (A4) and (A5) enables us to obtain a second implicit equation for NPP* as a function of n_f^* :

$$\text{NPP}^* = I_0 \varepsilon(n_f, C_a)(1 - \exp(-k_s \text{NPP}^* a_f * 0.4 * \text{SLA}/\text{Cfrac}))Y \quad (\text{A6})$$

The equilibrium NPP is given by the intersection of the two constraints (A3) and (A6), as shown in Figure A1. Alternatively, we can rearrange equation (A3) to obtain n_f^* as

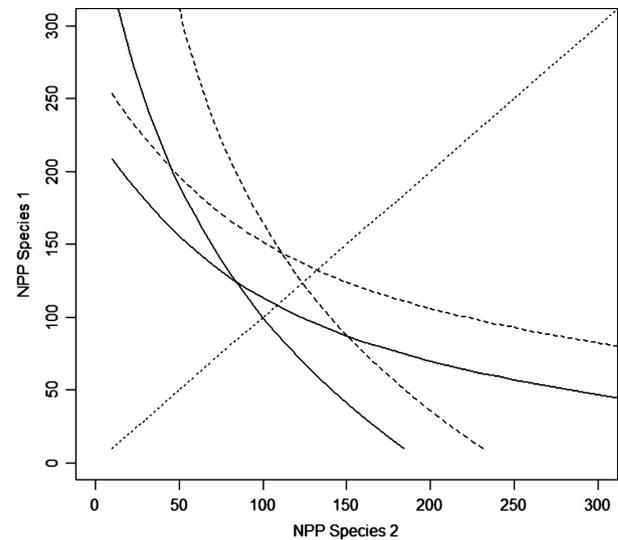


Figure A2. Graphical representation of equilibrium solution for two species growing in competition using resource partitioning model. The system equilibrium is given by the intersection of two constraint curves describing equilibrium NPP for one species as a function of the NPP of the other species. Solid lines, constraint curves at ambient C_a ; dashed lines, constraint curves at elevated C_a . In this example, the species differ in the parameter a_f .

$$n_f^* = N_{\min}(1 - \exp(-k_r \text{NPP}^*(1 - a_f)/s_r)) / (\text{NPP}^*(a_f + (1 - a_f)\rho)) \quad (\text{A7})$$

and substitute this expression into (A6), to obtain a single equation that yields NPP^* .

Two species competing

With two species, we need to find equilibrium NPP for each species, given by NPP_i^* and NPP_j^* . We can generalize the above analysis as follows.

Firstly, from equation (10) we have

$$\text{APAR}_i = 0.5 I_0 (1 - \exp(-k_{si} \text{LAI}_i - k_{sj} \text{LAI}_j) + \exp(-k_{sj} \text{LAI}_j) - \exp(-k_{si} \text{LAI}_i)) \quad (\text{A8})$$

And from equation (12) we have

$$N_{\text{up},i} = 0.5 N_{\min}(1 - \exp(-k_{ri} B_{ri} - k_{rj} B_{rj}) + \exp(-k_{rj} B_{rj}) - \exp(-k_{ri} B_{ri})) \quad (\text{A9})$$

These equations can replace their simpler single-species versions in equations (A1) and (A4). Equilibrium values of B_{ri}^* , B_{rj}^* , LAI_i^* , and LAI_j^* can be obtained from NPP_i^* and NPP_j^* by generalizing equations (A2) and (A5). Substituting and re-arranging yields two equations, one for NPP_i^* as a function of NPP_j and one for NPP_j^* as a function of NPP_i . The intersection of these two equations yields the overall equilibrium values, as shown in Figure A2.