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Competitive interactions between native and invasive exotic plant species are altered under elevated carbon dioxide

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Abstract We hypothesized that the greater competitive ability of invasive exotic plants relative to native plants would increase under elevated CO_2 because they typically have traits that confer the ability for fast growth when resources are not limiting and thus are likely to be more responsive to elevated CO_2. A series of competition experiments under ambient and elevated CO_2 glasshouse conditions were conducted to determine an index of relative competition intensity for 14 native-invasive exotic species-pairs. Traits including specific leaf area, leaf mass ratio, leaf area ratio, relative growth rate, net assimilation rate and root weight ratio were measured. Competitive rankings within species-pairs were not affected by CO_2 concentration: invasive exotic species were more competitive in 9 of the 14 species-pairs and native species were more competitive in the remaining 5 species-pairs, regardless of CO_2 concentration. However, there was a significant interaction between plant type and CO_2 treatment due to reduced competitive response of native species under elevated compared with ambient CO_2 conditions. Native species had significantly lower specific leaf area and leaf area ratio under elevated compared with ambient CO_2. We also compared traits of more-competitive with less-competitive species, regardless of plant type, under both CO_2 treatments. More-competitive species had smaller leaf weight ratio and leaf area ratio, and larger relative growth rate and net assimilation rate under both ambient and elevated CO_2 conditions. These results suggest that growth and allocation traits can be useful predictors of the outcome of competitive interactions under both ambient and elevated CO_2 conditions. Under predicted future atmospheric CO_2 conditions, competitive rankings among species may not change substantially, but the relative success of invasive exotic species may be increased. Thus, under future atmospheric CO_2 conditions, the ecological and economic impact of some invasive exotic plants may be even greater than under current conditions.

Keywords Alien plants · Competition · Climate change · Specific leaf area · Leaf area ratio

Introduction

Over the past two decades, the potential for invasive exotic plants to alter ecosystem structure and function has been increasingly recognized (Levine et al. 2003; Dassonville et al. 2008). The invasion of ecosystems by exotic plants has been identified as a major threat to biodiversity (Mack et al. 2000; van der Wal et al. 2008; Roura-Pascual et al. 2009) and is considered a significant management and economic concern (Pimentel et al. 2005; Beck et al. 2009).

When exotic plants become dominant in the vegetation communities they invade, this dominance is generally attributed to their superior competitive ability (Maron and Connors 1996; Hamilton et al. 1999; Callaway and Aschehoug 2000; Ewing 2002; Groves et al. 2003; Miller and Duncan 2004; White and Holt 2005; Coleman and Levine 2007; Pfeifer-Meister et al. 2008). However, there are relatively fewer studies that have measured competitive

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ability of native and exotic species directly. These studies have generally found that invasive exotic plants are competitively superior to their native counterparts in both terrestrial (Barney et al. 2009; Werner et al. 2010) and marine environments (Bando 2006; Wang et al. 2006; Rhazi et al. 2009), although there are exceptions (Vila et al. 2003; Corbin and D'Antonio 2004; Li et al. 2008).

An important applied question in ecological research is whether interactions between invasive exotic and native species will be affected by predicted future climate change (Dukes and Mooney 1999; Hellmann et al. 2008). One critical component of global change that will directly affect plant species' interactions is increasing atmospheric CO_2 concentration. Over the last two decades, the amount of CO_2 available to plants has increased significantly and this increase is predicted to continue under a range of emission scenarios (IPCC 2007). Plants with fast growth have been shown to be favored by this increased availability of CO_2 (LaDeau and Clark 2001; Tangley 2001; Poorter and Navas 2003). Leaf traits that are associated with carbon capture strategies resulting in fast growth when resources are not limited are strongly correlated with invasiveness (Smith and Knapp 2001; Grotkopp et al. 2002; Burns 2006; Grotkopp and Rejmanek 2007; Leishman et al. 2007; Leishman et al. 2010). Therefore, it can be hypothesized that invasive exotic plants will have a greater positive response to elevated CO_2 conditions than their native counterparts, resulting in an increase in their competitive ability relative to slower growing species. Open top chamber (Dukes 2002; Hattenschwiler and Korner 2003), controlled environment glasshouse (Smith et al. 1987), environmental controlled growth chamber (Sasek and Strain 1991; Ziska 2003; Baruch and Jackson 2005; Ziska et al. 2005; McPeek and Wang 2007; Song et al. 2009), and FACE (Smith et al. 2000; Huxman and Smith 2001; Belote et al. 2003; Nagel et al. 2004) experiments that have manipulated CO_2 levels have provided evidence to support this hypothesis (but see Taylor and Potvin 1997; Dukes 2000; Bradford et al. 2007 for exceptions).

We employed an experimental design that measured the relative competitive ability of native and exotic species grown in pairs, rather than inferring competitive ability based on abundance and growth data. Such a measure of competitive ability has the advantage that it encompasses a suite of potential mechanisms, e.g., increased photosynthetic rates (Poorter and Navas 2003; Long et al. 2004; Song et al. 2009), and decreased leaf construction costs (Nagel et al. 2004; Baruch and Jackson 2005) and expresses them as an outcome of the interaction between two species. However, this method has the disadvantage of being based on interactions of only two plant species. We attempted to overcome this by measuring competitive outcomes for 14 native-invasive exotic species-pairs that encompassed a range of growth forms and families. We are unaware of any previous study that has utilized a competitive index for measuring competitive interactions between plants with CO_2 concentration as a factor. As the competition index is based on biomass, it is reasonable to assume that the more competitive species will become relatively more abundant than the less-competitive species. However, it should be noted that our measure of competitive ability does not include some mechanisms, such as increased reproductive output (Smith et al. 2000; Nagel et al. 2004; McPeek and Wang 2007) or enhancement in germination rates (Baruch and Jackson 2005; McPeek and Wang 2007), that may also be affected by elevated CO_2.

The general question addressed in this study is: are competitive interactions between native and invasive exotic plant species altered under projected future CO_2 conditions? We grew co-occurring common native and invasive exotic species of the Cumberland Plain Woodland of western Sydney in non-limiting water and nutrient conditions in a series of paired competition experiments. The hypothesis we tested was that the superior competitive ability of invasive exotic plant species relative to co-occurring native plant species of the same functional type will be enhanced under elevated CO_2 levels. We then asked: what growth and allocation traits contribute to changes in competitive ability under elevated CO_2?

Materials and methods

Experimental design

Fourteen native and invasive exotic plant species-pairs were grown in a series of competition experiments under ambient (380–420 ppm) and elevated (675–715 ppm) CO_2 concentrations. The ambient treatment represents the atmospheric CO_2 concentration during the turn of the twenty-first century (IPCC 2007). The elevated treatment represents the predicted atmospheric CO_2 concentration by 2100 (IPCC 2007). Target plants were grown either singly in pots, or surrounded by three neighbors of the other species from the species-pair. For each species-pair, the competitive response of the target native and invasive exotic species was determined. There are a number of methods that have been developed to measure competitive ability, including the relative competition index (Grace 1995), relative neighbor effect (Markham and Chanway 1996) and logarithm of response ratio (Goldberg et al. 1999), that have varying advantages and disadvantages (Goldberg et al. 1999; Oksanen et al. 2006). We chose to measure the corrected index of relative competition intensity (CRCI) following the method of Oksanen et al. (2006).

There were eight replicates of each of the four competition treatments for each species-pair (each species within the pair grown singly and in competition). This design resulted in a total of 896 pots (i.e. 2 CO_2 treatments × 4 competition treatments × 8 replicates × 14 species-pairs). Each CO_2 treatment was split between two glasshouses to ensure that the CO_2 treatments were not confounded with the glasshouse. The temperature of the glasshouses was set for a maximum of 28°C and a minimum of 21°C. Within each glasshouse, treatments were randomly assigned to pots. On a fortnightly basis for the duration of the experiment, the pots within each glasshouse were randomly assigned to new positions to reduce bias caused by variation across the different areas within each glasshouse.

Species selection, seed collection and germination

The plant species used in this study are common co-occurring species of the Cumberland Plain Woodland, western Sydney, Australia. Cumberland Plain Woodland typically consists of open eucalypt woodland with a diverse grassy and herbaceous ground cover (Little 2003). All the exotic species are considered to be successful invaders rather than simply exotics that have become naturalized in Cumberland Plain Woodland. Species pairs were selected based on three criteria: the species within each pair were (1) from the same functional group (grass, vine, herb or shrub/tree); (2) utilized the same photosynthetic pathway (C_3 or C_4); and (3) had the same life history (i.e. annual or perennial). Seeds for each of the 28 plant species were collected from a range of individual plants from sites in the Hawkesbury region of western Sydney or were obtained from a commercial supplier (Nindethana Seed Service, Albany, WA, Australia). All species and their traits are shown in Table 1. Once collected, the seeds for each of the 28 plant species were germinated on moist filter paper within petri dishes. To spread the risk of germination failure, each plant species was germinated in a number of different petri dishes.

Planting and growth

The seedlings were transplanted at the stage of cotyledon emergence into the treatments described above, with all pots for each species-pair being planted within 24 h of each other. This removed the effects of differences between species in time of germination. For each individual target or neighbor plant, multiple seedlings were transplanted as insurance against seedling mortality. After 3 days, the remaining excess seedlings were removed from the pots.

The seedlings were grown in pots with a diameter of 175 mm and a depth of 195 mm. The pots contained 2.4 L of a soil mixture consisting of Cumberland Plain Woodland soil, organic garden mix and coarse river sand in a ratio of 2:1:1. The Cumberland Plain Woodland soil was obtained from Mt Annan Botanical Gardens while the organic garden mix and river sand were obtained from a commercial supplier (Australian Native Landscapes, Terrey Hills, NSW, Australia). To prevent any soil being lost from the holes in the bottom of the pots during the experiment, the pots were lined with newspaper.

The plants were grown for a period of 12 weeks under the specified glasshouse conditions. The plants were mist watered for 2 min three times daily to ensure that they were not water-limited. To counteract the nutrient loss resulting from this daily watering, 6.5 ± 0.2 g of slow release native plant fertilizer (23N:2P:17K; J.R. Somplo, Lathrop, CA, United States) was added to each pot. After 4 weeks of growth, lattices were placed around the perimeter of the pots that contained vine species which allowed them to climb. This ensured that the vine species were localized to their own pots so that they did not influence the growth of plants in neighbouring pots.

Harvesting and measuring competition

After the 12-week growth period the target plants were harvested into the following components: (1) three fully expanded outer canopy leaves, (2) the remaining leaf biomass, (3) the belowground biomass, and (4) the stem biomass. All plant parts were washed free of soil before being oven-dried at 80°C for 48 h and weighed using a Mettler Toledo B-S electronic balance. The weights of the different components were then added together to give the total biomass of the target plant. Using this data the relative neighbor effect (RNE) was calculated by randomly pairing target plants grown in competition with those grown without competitors within each species-pair.

$$\mathrm{RNE} = (X - Y)/\max(X, Y)$$

where X is the total biomass of plants grown without competitors and Y is the total biomass of plants grown in competition.

Subsequently, using the RNE value, the corrected index of relative competition intensity (CRCI) was calculated (Oksanen et al. 2006).

$$\mathrm{CRCI} = \arcsin(\mathrm{RNE})$$

Therefore a CRCI value = 0 indicates there is no effect of competition on the target plant, >0 indicates that competition has a negative effect, and <0 indicates that competition has a positive effect on the target plant. Thus low CRCI values indicate a greater competitive response.

Data analysis of CRCI values

To determine if competitive interactions between the native and invasive exotic species were affected by elevated CO_2, a

Table 1 Species-pairs used in this study, with information on the family, plant type, seed mass, growth form, physiology and life history of each species

Species	Family	Plant type	Seed mass (mg)	Growth form	C3 or C4	Annual or perennial
Acacia implexa	Fabaceae	Native	21.3	Tree	C3	Perennial
Ligustrum sinense	Oleaceae	Exotic	17.7			
Acacia parramattensis	Fabaceae	Native	15.9	Tree	C3	Perennial
Olea europaea subsp cuspidata	Oleaceae	Exotic	15.8			
Atriplex semibaccata	Chenopodiaceae	Native	1.0	Herb	C3	Perennial
Sida rhombifolia	Malvaceae	Exotic	1.5			
Einadia hastata	Chenopodiaceae	Native	0.7	Herb	C3	Perennial
Phytolacca octandra	Phytolaccaceae	Exotic	5.1			
Plectranthus parviflorus	Lamiaceae	Native	0.1	Herb	C3	Annual
Bidens pilosa	Asteraceae	Exotic	1.6			
Sigesbeckia orientalis	Asteraceae	Native	1.3	Herb	C3	Annual
Conyza bonariensis	Asteraceae	Exotic	0.05			
Convolvulus erubescens	Convolvulaceae	Native	7.7	Vine	C3	Perennial
Acetosa sagittata	Polygonaceae	Exotic	2.3			
Glycine microphylla	Fabaceae	Native	4.0	Vine	C3	Perennial
Araujia sericifolia	Asclepiadaceae	Exotic	7.6			
Bothriochloa macra	Poaceae	Native	1.2	Grass	C4	Perennial
Chloris gayana	Poaceae	Exotic	0.4			
Chloris truncata	Poaceae	Native	0.3	Grass	C4	Perennial
Digitaria sanguinalis	Poaceae	Exotic	0.1			
Dichanthium sericeum	Poaceae	Native	1.1	Grass	C4	Perennial
Paspalum dilatatum	Poaceae	Exotic	0.8			
Eragostis brownii	Poaceae	Native	0.6	Grass	C4	Perennial
Sorghum halepense	Poaceae	Exotic	1.4			
Sporobolus creber	Poaceae	Native	0.1	Grass	C4	Perennial
Sporobolus indicus	Poaceae	Exotic	0.2			
Themeda australis	Poaceae	Native	2.6	Grass	C4	Perennial
Eragostis curvula	Poaceae	Exotic	0.2			

mixed model nested ANOVA was performed. The factors in the model were CO_2 concentration (i.e. elevated or ambient), plant type (i.e. invasive exotic or native) and species pair nested within plant type. Plant type and CO_2 concentration were treated as fixed factors and species-pair as a random factor. The response variable was the calculated CRCI. We did an initial analysis to determine if there was a significant difference between the two glasshouses within each CO_2 treatment, using the same mixed model nested ANOVA as above but with the additional factor 'glasshouse' added. Glasshouse was found to be not significant ($P = 0.769$) and so was removed from subsequent models. We then used paired *t* tests to test for significant differences between all possible combinations of plant type and CO_2.

Measuring growth and allocation traits

To determine the contribution of growth and allocation traits to the biomass outcomes analyzed as the CRCI values, a range of traits that reflect allocation at the leaf-level or whole-plant level were measured or calculated for each species on an individual plant basis, using the target plants grown in competition. We measured relative growth rate (RGR) and its components specific leaf area (SLA), leaf mass ratio (LMR) and net assimilation rate (NAR), as well as leaf area ratio (LAR) and root weight ratio (RWR). The measurement and calculation of each trait is described in Table 2.

Data analysis of growth and allocation traits

We used paired *t* tests to examine if there were differences in trait values for each plant type × CO_2 pair-wise combination that was found to differ significantly in CRCI values. We then wanted to examine what traits contributed to competitive ability at both ambient and elevated CO_2, irrespective of plant type. To do this, we used paired *t* tests to compare the trait values of the more-

Table 2 The growth and allocation traits measured with a description of the procedures used to measure and calculate them

Trait	Measurement and calculation
Specific leaf area ($mm^2\ mg^{-1}$)	SLA was measured as the leaf area per unit leaf mass for three randomly selected outer canopy leaves. Leaf area was measured using a LI-3100C Area Meter (LI-COR, Lincoln, NE, USA) prior to oven-drying the leaves for weighing
Leaf weight ratio ($mg_{leaf}\ mg_{plant}^{-1}$)	LWR was calculated as total plant leaf mass divided by total plant mass
Leaf area ratio ($mm_{leaf}^2\ mg_{plant}^{-1}$)	LAR was calculated as SLA × LWR
Relative growth rate (mg $mg_{plant}^{-1}\ day^{-1}$)	RGR was calculated using the equation RGR = ($\log_e P_M - \log_e S_M$)/($\log_e P_M - \log_e S_M$)T. where P_M = total plant mass; S_M = seed mass (initial plant mass); T = time of growth period (84 days). Seed mass was determined by averaging the weight of 20 mature oven-dried seeds. Seed mass was defined as the seed coat plus embryo and endosperm, excluding morphological adaptations for dispersal such as arils, wings, etc
Net assimilation rate (mg $mm_{leaf}^{-2}\ day^{-1}$)	NAR was calculated as RGR/LAR
Root weight ratio ($mg_{root}\ mg_{plant}^{-1}$)	RWR was calculated as total root biomass/total plant biomass

competitive species with the less-competitive species within each species-pair.

All statistical analyses were performed using Minitab 15 statistical software (Minitab 2007) with the significance level set at 0.05.

Results

CRCI analysis

There was no significant interaction between species-pairs (within plant type) and CO_2 treatment ($F_{26,447} = 1.05$, $P = 0.394$; Online Resource 3), indicating that the competitive rankings within each species pair were not altered by CO_2 treatment (Online Resource 2). In 9 of the 14 species-pairs the invasive exotic species was more competitive and in 5 of the 14 species-pairs the native species was more competitive, under both ambient and elevated CO_2 conditions (Online Resource 2). There was a significant difference in CRCI between species-pairs nested within plant type ($F_{26,447} = 10.89$, $P < 0.001$; Online Resource 3).

There was a significant interaction between plant type and CO_2 treatment ($F_{1,447} = 4.45$, $P = 0.045$; Online Resource 3), suggesting that the native and invasive exotic species' competitive response varied with CO_2 treatment. Paired t tests showed that on average the competitive response of the native species decreased under elevated CO_2 compared to ambient CO_2 ($\bar{y}_{\text{Ambient}\,CO_2} = 0.377$, $\bar{y}_{\text{Elevated}\,CO_2} = 0.554$; $t_{13} = 2.417$, $P = 0.031$), while no other plant type × CO_2 treatment contrasts were significant (Table 3; Fig. 1).

Table 3 Mean corrected relative competition index (CRCI) and standard error of each possible pair-wise plant type × CO_2 combination and the results of paired t tests

Comparisons (i.e. 1 vs. 2)		Combination 1	Combination 2	*df*	*t*	*P*
Native ACO_2 versus Native ECO_2	Mean	0.374	0.554	13	2.417	0.031*
	SE	0.125	0.135			
Native ACO_2 versus Exotic ACO_2	Mean	0.374	0.335	13	−0.230	0.822
	SE	0.125	0.129			
Native ACO_2 versus Exotic ECO_2	Mean	0.374	0.301	13	−0.334	0.743
	SE	0.125	0.128			
Native ECO_2 versus Exotic ACO_2	Mean	0.554	0.335	13	1.071	0.304
	SE	0.135	0.129			
Native ECO_2 versus Exotic ECO_2	Mean	0.554	0.301	13	−1.027	0.323
	SE	0.135	0.128			
Exotic ACO_2 vversus Exotic ECO_2	Mean	0.335	0.301	13	0.493	0.630
	SE	0.129	0.128			

Significant differences at $^*P < 0.05$

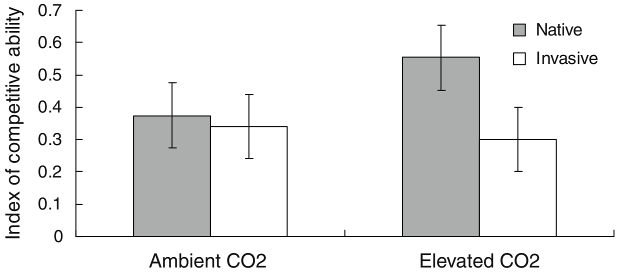

Fig. 1 Corrected relative competition index (CRCI) of 14 native and exotic species-pairs (mean ± SE) grown under ambient (380–420 ppm) and elevated CO_2 (675–715 ppm) treatments. CRCI is a measure of competitive response based on biomass, with values >0 indicating that competition has a negative effect on plant biomass. CRCI values closer to 0 indicate a stronger competitive response

Growth and allocation trait analysis

We used paired *t* tests to examine if there were trait differences between native species under ambient and elevated CO_2 treatments as these were the only plant type × CO_2 combinations that were found to differ significantly in competitive response. Both SLA and LAR of native species were significantly lower under elevated CO_2 compared with ambient CO_2 (Table 4). There were no significant differences between CO_2 treatments for LWR, NAR, RGR or RWR (Table 4).

We then examined if there were differences in trait values of more-competitive and less-competitive species within species-pairs, irrespective of plant type, at both ambient and elevated CO_2. Within species-pairs, more-competitive species had significantly smaller LWR and LAR and significantly larger RGR and NAR than less-competitive species, under both ambient and elevated CO_2 treatments (Table 5).

Discussion

In this study, we examined whether competitive interactions between native and invasive exotic plant species are affected by CO_2 conditions. We found that competitive rankings within species-pairs were not altered by CO_2 level. In 9 out of 14 species-pairs, the invasive exotic species was more competitive while in the remaining 5 species-pairs the native species was more competitive, under both ambient and elevated CO_2 treatments.

Although the competitive rankings within species-pairs were not affected by CO_2 level, the strength of the competitive interactions was affected. The corrected index of relative competition intensity (CRCI; Oksanen et al. 2006) of native species on average was significantly increased under elevated compared with ambient CO_2, indicating that the competitive response of natives under elevated CO_2 was reduced. The CRCI is based on the competitive response of the target plant grown in competition with neighbors but can also be interpreted as a measure of the competitive effect of the neighbor plants. Thus our results show that native species had on average a reduced competitive response under elevated compared with ambient CO_2 but this may also be interpreted as an increased competitive effect of invasive exotic species under elevated CO_2. These results suggest that under predicted future atmospheric CO_2 conditions, competitive rankings among species may not change substantially, but the relative success of invasive exotic species may be increased (Smith et al. 2000; Huxman and Smith 2001; Belote et al. 2003; Nagel et al. 2004).

It is often assumed that invasive exotic plants are superior competitors to native species. An interesting outcome of this study was that native and invasive exotic

Table 4 Growth and allocation trait means and standard errors for native species grown in competition under ambient and elevated CO_2 with the results of paired *t* tests

Traits		Native-ambient CO_2	Native-elevated CO_2	*df*	*t*	*P*
Specific leaf area ($mm^2\ mg^{-1}$)	Mean	31.042	27.359	13	−2.793	0.015*
	SE	3.466	2.833			
Leaf weight ratio ($mg_{leaf}\ mg_{plant}^{-1}$)	Mean	0.461	0.459	13	−0.206	0.840
	SE	0.024	0.026			
Leaf area ratio ($mm_{leaf}^2\ mg_{plant}^{-1}$)	Mean	14.228	12.672	13	−2.392	0.032*
	SE	1.764	1.687			
Relative growth rate ($mg\ mg_{plant}^{-1}\ d^{-1}$)	Mean	0.073	0.075	13	0.616	0.548
	SE	0.006	0.007			
Net assimilation rate ($mg\ mm_{leaf}^{-2}\ d^{-1}$)	Mean	0.007	0.010	13	1.530	0.150
	SE	0.001	0.002			
Root weight ratio ($mg_{root}\ mg_{plant}^{-1}$)	Mean	0.216	0.193	13	−1.422	0.179
	SE	0.026	0.018			

Significant differences at $*P < 0.05$

Table 5 Growth and allocation trait data for the more-competitive and less-competitive species within species-pairs under ambient and elevated CO_2

Traits		Ambient CO_2 ($n = 14$)			Elevated CO_2 ($n = 14$)		
		More-competitive	Less-competitive	*t* value	More-competitive	Less-competitive	*t* value
Specific leaf area (mm^2 mg^{-1})	Mean	27.468	32.168	1.765	24.646	28.589	−1.438
	SE	1.889	3.827		1.851	3.151	
Leaf weight ratio (mg$_{\text{leaf}}$ mg$_{\text{plant}}^{-1}$)	Mean	0.395	0.503	−2.663*	0.369	0.510	−3.424*
	SE	0.030	0.021		0.030	0.021	
Leaf area ratio (mm$_{\text{leaf}}^2$ mg$_{\text{plant}}^{-1}$)	Mean	10.669	16.299	−3.205*	8.782	15.043	−3.255*
	SE	1.118	2.161		0.831	2.125	
Relative growth rate (mg mg$_{\text{plant}}^{-1}$ d^{-1})	Mean	0.092	0.070	3.393*	0.097	0.069	4.279*
	SE	0.007	0.007		0.007	0.006	
Net assimilation rate (mg mm$_{\text{leaf}}^{-2}$ d^{-1})	Mean	0.011	0.007	3.397*	0.016	0.007	2.956*
	SE	0.002	0.001		0.003	0.001	
Root weight ratio (mg$_{\text{root}}$ mg$_{\text{plant}}^{-1}$)	Mean	0.331	0.359	−0.419	0.250	0.214	1.094
	SE	0.024	0.023		0.023	0.020	

This includes growth and allocation trait means, standard errors and the results of paired *t* test analyses

Significant differences at $*P < 0.05$

plants did not differ overall in their competitive ability under either ambient or elevated CO_2 conditions. Although similar results have previously been reported for ambient CO_2 conditions (e.g., Corbin and D'Antonio 2004; Suding et al. 2004), the majority of studies have shown that invasive exotic species are better competitors than native species (e.g., Hager 2004; Miller and Duncan 2004; White and Holt 2005; Coleman and Levine 2007; Pfeifer-Meister et al. 2008). Our results suggest that there are species-specific attributes that play an important role in determining the competitive interactions between native and invasive exotic plants, and that an understanding of these traits may be more informative than knowledge of a plant's status as native or exotic for predicting the outcome of interactions between species.

Invasive exotic plants were predicted to respond more strongly than native plants to elevated CO_2 levels because they generally have growth and allocation traits that allow rapid carbon capture (Rejmanek et al. 2005; Grotkopp and Rejmanek 2007; Leishman et al. 2007, 2010). The calculated measure of competitive ability that we used (CRCI) is based on the competitive response of the target plant, but also incorporates the competitive effect of the neighbor plants. We did not find a difference in competitive response of the invasive exotics between CO_2 treatments, or between native and invasive exotics in either CO_2 treatment, in contrast to our expectations. However, we did find a difference in the competitive response of native species between CO_2 treatments which may be due to either trait differences of the target native species or to trait differences of the neighbour invasive exotics under the CO_2 treatments, or a combination of the two. However, the pairwise comparisons of trait values we used were based on the target plants only, and so we were unable to assess whether differences in traits of the invasive exotic neighbours contributed to the reduced competitive response of natives under elevated CO_2. Native species had lower SLA and LAR values under elevated compared with ambient CO_2. Reductions in both these traits would result in reduced carbon capture and hence reduced biomass, seen in this study as reduced competitive response. Previous studies that have assessed what traits contribute to greater biomass of exotic species under elevated compared to ambient CO_2 have found higher growth rate (Sasek and Strain 1988, 1991; Smith et al. 2000; Dukes 2002; Ziska 2002; Belote et al. 2003), larger leaf area (Sasek and Strain 1988, 1991; Ziska et al. 2004; Ziska et al. 2005, 2007), higher net assimilation rate (Sasek and Strain 1988) and longer stems (Hattenschwiler and Korner 2003) to be important traits.

Interestingly, we found that, irrespective of plant type, traits that were associated with competitive superiority at both ambient and elevated CO_2 were LWR, LAR, RGR and NAR. LWR and LAR were significantly smaller in the more competitive plants while RGR and NAR were significantly larger. This suggests that, in the conditions of this experiment (high light, soil water and nutrient availability), plants with relatively smaller allocation to leaves and high NAR can achieve high relative growth rates and hence larger biomass, conferring a competitive advantage. A high RGR allowing rapid biomass accumulation is often associated with a superior competitive ability (Sasek and Strain 1988, 1991; Smith et al. 2000; Dukes 2002; Ziska 2002; Belote et al. 2003). These results suggest that, in general, traits associated with growth and allocation can enable predictions of outcomes of competition under particular environmental conditions.

Plant species' response to elevated CO_2 has been shown in numerous studies to be constrained by resource availability (Poorter et al. 1996; Oren et al. 2001; Reich et al. 2006). Thus, when soil resources such as nutrients or moisture are limiting, plants may be unable to take advantage of the increased CO_2 concentration. In this study, the natural soil of the Cumberland Plain Woodland made up a large component of the soil mixture that was used. This is a shale-derived soil and is consequently relatively fertile (Little 2003). We also provided slow release fertilizer to maintain soil fertility throughout the experiment and to ensure that plants received sufficient soil moisture. Previous studies have shown that invasive exotic species tend to have traits that enable rapid growth in non-limiting environments (Grotkopp and Rejmanek 2007; Leishman et al. 2010) but that water availability does not affect relative success of native and invasive exotics (Baruch and Jackson 2005; Leishman and Thomson 2005; Coleman and Levine 2007). By providing non-limiting soil resources in this experimental system, we have provided optimal conditions for the invasive exotic plants to take advantage of additional CO_2 and to increase their relative competitive ability. Thus, the conclusions from our study should be applied tentatively to environments where soil resources are limiting.

The nature of pair-wise experimental designs means that they may be influenced by the selection of species. We chose to reduce variation by controlling for photosynthetic pathway, growth form and life history within species-pairs. However, it may be these differences in plant characteristics that contribute to invasion success in exotic species (Vila and Weiner 2004). Further experimental work could examine competitive interactions under ambient and elevated CO_2 concentrations for species of contrasting growth form, physiology or allocation traits. Different results for species-pairs could also be due to seed mass contrasts within each species-pair as larger-seeded species have been shown to be more competitive (Eriksson 1997; Turnbull et al. 1999; Leishman 2001; Susko and Cavers 2008). Of the 14 species-pairs in this study, there were large (>5 times) differences in seed mass within 4 pairs (Table 1). Within these four pairs, the species with the larger seed size was more competitive. However, in these four pairs, the invasive exotic species had larger seed mass in two cases and the native species had larger seed mass in the other two cases. Thus, we do not think that consistent seed mass differences between native and invasive exotic species within species-pairs were responsible for the overall result.

Large-scale mesocosm and FACE experiments are now considered essential to understand community-level responses to elevated CO_2 (Vila et al. 2007). These experiments provide data on a range of community responses that can best be understood when all components of the system are included. However, we argue that there is still a need for glasshouse experiments to advance our understanding of the mechanisms and processes that underpin these community-level responses (Vila and Weiner 2004). This study has illustrated the role that competitive interactions may have in determining community-level outcomes under future CO_2 conditions. It has shown that the relative advantage of competitively superior invasive exotic plants compared to native neighbors may increase under elevated CO_2. This knowledge is important to help mitigate the future impact of invasive exotic plants under higher atmospheric CO_2 levels.

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