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Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability

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Abstract Changes in competitive interactions under conditions of enhanced resource availability could explain the invasion success of some problematic plant species. For one invader of North American grasslands, *Centaurea diffusa* (diffuse knapweed), we test three hypotheses: (1) under ambient (high resource) conditions, *C. diffusa* is better able to tolerate competition from the resident community (competitive response), (2) under ambient conditions, *C. diffusa* strongly impacts the competitive environment (competitive effect), and (3) reductions in nitrogen and/or phosphorus availability diminish these advantages. In support of our first hypothesis, *C. diffusa* was the most tolerant to neighbor competition of the four focal species under current resource conditions. In opposition to our second hypothesis, however, neighborhoods that contained *C. diffusa* and those where *C. diffusa* had been selectively removed did not differ in their impact on the performance of target transplant individuals or on resource conditions. Reduction in resource availability influenced competitive tolerance but not competitive impact, in partial support of our last hypothesis. Reduction in soil nitrogen (via sucrose carbon addition) enhanced the degree of neighbor competition experienced by all species but did not change their relative rankings; *C. diffusa* remained the best competitor under low nitrogen conditions. Reduction of soil phosphorus (via gypsum addition) weakened the ability of *C. diffusa* to tolerate neighbor

competition proportionately more than the other focal species. Consequently, under low phosphorus conditions, *C. diffusa* lost its competitive advantage and tolerated neighbor competition similarly to the other focal species. We conclude that *C. diffusa* invasion may be double-edged: *C. diffusa* is less limited by nitrogen than the other focal species and is better able to utilize phosphorus to its competitive advantage.

Keywords *Centaurea diffusa* · Competitive response and competitive effect · Resource ratios · Reverse fertilization

Introduction

Invasion of exotic plant species is a global phenomenon that poses a critical problem for the conservation and management of many ecosystems (Vitousek et al. 1996). The ability of species to invade new communities is influenced by traits of the invader (Rejmanek and Richardson 1996; Smith and Knapp 2001; Grotkopp et al. 2002; Prinzing et al. 2002) and characteristics of the resident community (Lonsdale 1999; Davis et al. 2000; Mack et al. 2000; Levine et al. 2003). Often, invaders become problematic due to complex interactions between the traits of the invader and resident community characteristics (Mack et al. 2000; Lambrinos 2002; Shea and Chesson 2002; Ehrenfeld 2003).

We focus on one such interaction: how competitive dynamics between invader and resident species depend on environmental resource characteristics. Some invasions are successful because exotic species are able to preempt resources and strongly impact resource fluxes in that environment (D'Antonio et al. 1998; Dukes and Mooney 1999; Shea and Chesson 2002). This ability to exert strong impacts may depend on environmental conditions such as resource availability, characteristics of the dominant species, or disturbance regime (Mack et al. 2000; Shea and Chesson 2002). In other environments, the invader may impact resources similarly to the resident species (Hoopes and Hall 2002), and may be able to invade and

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rapidly increase in abundance if it is better able to tolerate competition. Thus, environmental characteristics may influence both the competitive impacts of an invader on resident communities and the competitive tolerance of an invader to resident competition.

Centaurea (knapweed) species are among the most widespread invaders of North American prairies historically dominated by C₃ and C₄ grasses (Skinner et al. 2000). The dominance of many *Centaurea* species has been attributed to their ability to shift plant–plant interactions through allelochemical (Callaway and Aschehoug 2000; Ridenour and Callaway 2001; Bais et al. 2003; Hierro and Callaway 2003), microbial (Zabinski et al. 2002; Callaway et al. 2003, 2004) and resource depletion (Callaway et al. 2001; Herron et al. 2001; Gerlach and Rice 2003) mechanisms. Given the range of such competitive mechanisms, our goal was to determine whether the dominance of one *Centaurea* species, *C. diffusa*, is related to its ability to strongly impact the resident community or to tolerate competition from the resident community (competitive effect and response, respectively, after Goldberg and Werner 1983; Goldberg 1990).

Rapid dominance by an invasive species could suggest that the invader is able to take advantage of changed resource levels in a system, to exploit resources not previously accessed by the resident species, or to better compete for resources that limit the resident community. In systems where the historically strong nitrogen (N) limitation has been reduced such as in many regions of western North America (Hooper and Johnson 1999; Matson et al. 2002), increased nitrogen availability may directly change competitive dynamics for nitrogen or it may create a situation where another resource (e.g., phosphorus, water) becomes more limiting (LeJeune and Seastedt 2001). Both processes can shift competitive dynamics in favor of invading species (Huenneke et al. 1990; Sher and Hyatt 1999; Davis et al. 2000). Thus, a second goal of this study was to test whether reductions in resource availability or changes in the relative ratio of resources alter interactions between *C. diffusa* and the resident community.

Centaurea diffusa is a biennial or short-lived perennial forb (Watson and Renny 1974). Seed production can range as high as 18,000 seeds per plant (Watson and Renny 1974; Schirman 1981). Seed viability is high, typically exceeding 90% germination, and seeds can germinate at any time during the year. Nitrogen use efficiency is low in comparison with the native grasses (LeJeune 2002) and tissue chemistry is complex with high concentrations of sesquiterpene lactones (Hierro and Callaway 2003).

Because *C. diffusa* is associated with disturbed as well as undisturbed grasslands, we hypothesized that the invasion success of *C. diffusa* is due to its superior competitive ability under the currently enhanced resource conditions. Specifically we test three hypotheses: (1) *C. diffusa* is better able to tolerate competition from the resident community under current resource conditions, (2) *C. diffusa* exerts strong impacts on the competitive environment under current resource conditions, and (3)

reductions in nitrogen and/or phosphorus availability diminish these advantages.

Materials and methods

Study site

We conducted this study in historically grazed mixed-grass prairie located 10 km east of the Colorado Front Range near Superior, Colorado (39°55'35"N, 105°11'8"W). The surface soils are predominantly clay loam over cobbly loamy alluvium. Average annual precipitation is 48.5 cm with 30% falling in the summer. During the course of this experiment, the site received 82% of average precipitation (Fig. 1) with most of the reduction due to low precipitation levels in October 2001 and April 2002.

The site was heavily invaded by *C. diffusa* (18–30% of total cover), while other non-native species (e.g., *Thiopyrum intermedium*, *Agropyron cristatum*, *Alyssum minus*, *Bromus japonicus*) comprised another 30% of species cover. The rest of the community (approximately 40–50%) was composed of native grasses and forbs, including *Pascopyrum smithii*, *Aristida longiseta*, *Bouteloua gracilis*, *Buchloe dactyloides*, *Koeleria macrantha*, *Erigeron flagellaris*, *Sphaeralcea coccinea*, and *Gutierrezia sarothrae*. In the 1990s biocontrol insects were released or colonized the study site, and by 2001 they reached high enough densities to affect adjacent populations of *C. diffusa* (Seastedt et al. 2003). To control for the possible confounding effects of herbivory in this experiment, we sprayed a systemic wide-ranging insecticide, imidacloprid (Merit, Bayer, 0.13 ml/l), on all plots June 2001 and May 2002. We observed only modest evidence of herbivory in the experimental plots (less than 5%).

Experimental manipulations

We manipulated aboveground plant biomass (three levels: all species present, *C. diffusa* removed, all species removed) and resource availability (four levels: no amendments, carbon (sucrose) addition to reduce nitrogen availability, gypsum addition to reduce phosphorus

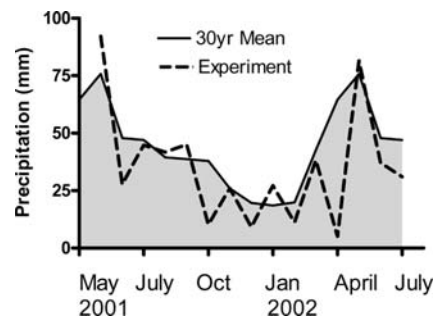


Fig. 1 Monthly precipitation in Boulder, Colorado (3 km from the study site) during the experiment (May 2001–July 2002) compared to the 30-year average. Total precipitation over the course of the experiment was 82% of average

availability, and both carbon and gypsum addition) in all possible combinations in seven replicate blocks. For each treatment combination, one individual target seedling for each of four species (*C. diffusa*, *B. dactyloides*, *G. sarothrae*, *A. cristatum*) was planted. Blocks were located in an area that was uniform in production, land use, and community composition, and treatments within each block were randomly assigned to plots arranged in a grid pattern. Plots measured 1×1.5 m, except for the complete removals that measured 0.75×1 m, with 1 m buffer between each plot. Subsections (0.25 m²) of each plot were designated for soil sampling and for the transplanted target individuals.

To manipulate plant biomass and neighborhood composition, we either selectively removed *C. diffusa* or completely removed all plants from plots. During the week of 10 May 2000, biomass of *C. diffusa* was removed by painting all individual plants with glyphosate (Roundup Super Concentrate, Monsanto), a systematic herbicide at the recommended concentration of 7 ml/l. One week later, the dead aboveground biomass was removed by clipping, dried to a constant weight, and weighed; the dead roots were left intact to avoid soil disturbance. We removed an average of 21.6±1.5 g/m² *C. diffusa* biomass (approximately 25% of the total aboveground biomass). In the complete neighbor removal treatments, herbicide was sprayed on all the vegetation and removed as above. To minimize the effects of dead roots left in the removal treatments and to allow production levels recover in the neighborhoods where *C. diffusa* was removed, target seedlings were not transplanted into the experimental plots until the following growing season. Removal treatments were maintained by periodic weeding. Soil disturbance due to the subsequent weeding was minimal because colonization was slow and most of the individuals removed were small seedlings.

To manipulate resource availability, we added sucrose carbon to reduce nitrogen availability, gypsum to reduce phosphorus availability, and carbon and gypsum in combination to reduce both resources but to keep the relative ratio of resources similar to control conditions. The manipulations were started May 2000, immediately following initial neighbor removals and a year prior to transplanting the target seedlings. Carbon was added at a rate of 200 g sucrose/m² twice during the 2000 growing season, three times during the 2001 growing season and once early in the 2002 growing season. In 2001 and 2002, a small amount of phosphorus (0.2 g/m²) was added with the carbon to counteract the increased uptake of phosphorus by the microbial community. Phosphorus was not added to the combined carbon and gypsum treatment as not to neutralize the effect of the gypsum treatment. To reduce phosphorus availability, gypsum (CaSO₄) was added at a rate of 10 g Ca/m² twice during the 2000 and 2001 growing season and once during the 2002 growing season. Neither resource manipulation affected soil pH (LeJeune 2002).

Soil resources and aboveground production

We measured resin-extractable phosphorous and inorganic nitrogen in September 2001 and potential net N mineralization in July 2002. Soil samples were taken from the top 10 cm using a 2 or 5 cm diameter soil corer and kept on ice until extraction. Inorganic nitrogen was extracted within 24 h of collection with KCl (50 ml 2N KCl to 10 g dry soil) and analyzed on an Alpkem autoanalyzer (Alpkem, Ore.). To assess potential net nitrogen mineralization rates, an initial set of soil samples was extracted as above and a second set was incubated for 28 days in moisture-adjusted flasks in the lab prior to extraction. Labile phosphorus of 0.5 g air-dried samples was quantified by sequential extraction of the resin-extractable and bicarbonate-extractable inorganic and organic fraction. Due to sampling constraints, we did not measure phosphorus in complete removal plots. All measures were corrected for soil moisture.

In July 2002, vegetation was harvested from a 1×0.25 m subplot where no soil sampling had occurred and no target individuals had been planted. All aboveground biomass was collected, oven dried at 60°C for 48 h, and weighed to estimate aboveground production.

Target growth and survival

A year after the resource amendments were initiated, on 8 May 2001, seedlings of four focal species were planted in the experimental plots: *C. diffusa*, an exotic C₃ forb; *G. sarothrae*, a native forb/sub-shrub; *A. cristatum*, an exotic (naturalized) C₃ grass; and *B. dactyloides*, a native C₄ grass. Seeds from *C. diffusa* were collected during fall 2000 and seeds for the other species were purchased locally from Applewood Seed Company (Golden, Colo., USA). Seeds were sown in the greenhouse (University of Colorado, Boulder), grown for 8 weeks, and then acclimated to outdoor conditions for 3 weeks. Height and leaf number were recorded for each transplant as well as for a set of individuals that were dried and weighed to estimate the initial weight of the transplanted individuals. One individual per species was planted as the focal target in each treatment combination. The transplants were watered for 2 weeks following transplantation. Mortality during those 2 weeks was ascribed to transplanting stress and individuals were replaced. After the initial 2-week period, no watering or replacement occurred.

On 8–9 July 2002, 14 months after transplanting, the surviving target individuals were harvested (roots and shoots), dried to a constant weight, and weighed. Due to the hard-packed clay soil conditions, we were only able to harvest roots within a 20 cm wide and 15 cm deep soil volume. Although most individuals were relatively small, the root mass for deeply rooted individuals was probably underestimated.

We analyzed two aspects of species response: performance in the presence of neighbors, which we term realized performance, and the effect of neighbors on

performance, which we term competitive response (Goldberg and Werner 1983; Goldberg 1996). We measured realized performance as the proportional survival or relative growth of the transplanted target seedlings in the presence of neighbors. The effect of neighbors (competitive response) was quantified using a response ratio metric (ln RR): $\ln(\text{target performance}_{w/\text{neighbors}}/\text{target performance}_{w/o\text{ neighbors}})$. Response ratio values were calculated for each target species, resource manipulation, and type of neighborhood (no removal or with *C. diffusa* selectively removed) within a block. Thus, for a block, we used the performance in no-neighbor conditions for a given resource as the basis of response ratio calculations in that resource treatment for both neighborhood types. To account for differences in neighbor biomass on competition intensity, we also present response values standardized by aboveground production. We term this metric “per-gram competitive response” and calculated it as ln RR divided by aboveground biomass in a subplot (adjusted to g/m^2) adjacent to where the target grew.

Statistical analyses

Statistical analyses were done using SYSTAT 10.2 for Windows (Systat Software, 2002). Some soil measures (inorganic nitrogen, resin-extractable phosphorus), aboveground production, and growth measures were natural log transformed; no other departures from the assumptions of normality and homogeneity were evident. Because sample sizes were often unequal, Type III sums of squares were used in all analyses. Block terms were also included in all analyses. Three sets of analyses were performed. First, to describe treatment effects on soil and production characteristics, we used a fully-crossed ANOVA model with neighborhood type (complete removal, without *C. diffusa*, no removal), carbon sucrose addition (added, not added), and gypsum addition (added, not added) as fixed factors. Inorganic nitrogen, net nitrogen mineralization, phosphorus, and aboveground production were analyzed with this model structure, with two exceptions. Because we did not sample resin extractable phosphorus in complete removal plots, this treatment was not included in the model examining phosphorus availability. We also did not include the complete removal treatment in the model examining aboveground production because once the vegetation was treated with herbicide, subsequent productivity was minimal over the course of the experiment.

Then, to describe how the *relative* amount of inorganic nitrogen and resin-extractable phosphorus changed due to resource manipulations in intact neighborhoods, we normalized the N and P values (log normal distribution) and calculated the ratio of soil N to P. The effect of resource manipulations on N:P ratios was analyzed using a three-way ANOVA model with carbon addition, gypsum addition, and neighborhood type (*C. diffusa* removed or present) as fixed factors. This analysis allowed us to confirm that the relative effects of the resource reduction treatments were what we intended.

Lastly, we analyzed realized target performance and competitive response in models similar to those used to analyze the effect on soil and production characteristics, with the addition of a species identity term (i.e., *C. diffusa*, *A. cristatum*, etc.). The complete removal (no neighbor) term was not included in these analyses because competitive response measures (ln RR) already consisted of comparisons with no-neighbor conditions and realized growth measures only describe performance in the presence of neighbors. We focused on effects on growth and survival of target individuals as two distinct measures of individual performance; we also analyzed per-gram competitive response measures in term of growth. The sample size for proportion survival was too small to include all terms, so effects of *C. diffusa* removal were dropped (exploratory analyses indicated that these effects were small and similar to those on growth). In addition, the mortality of one of the target species, *G. sarothrae*, was too high to include it in the analyses of growth; only survival responses are reported for this species. One case (of over 100) was excluded as an outlier in all analyses because values exceeded three standard deviations from cell means.

Results

Soil resources and production

Carbon (sucrose) reduced absolute inorganic nitrogen pools ($F_{1,41}=38.7$, $P<0.005$); in unmanipulated neighborhoods, inorganic nitrogen was reduced by an average of 69%. Gypsum had no effect on inorganic N availability, regardless of neighborhood type. The effect of carbon addition on N was not dependent on gypsum addition (non-significant interaction $F_{1,41}=1.7$, $P=0.21$).

In plots where neighbors were completely removed, inorganic nitrogen availability significantly increased ($F_{1,41}=32.4$, $P<0.005$), indicating that neighbors reduced N availability (Fig. 2a). The addition of carbon significantly diminished the effect of neighbors on nitrogen availability ($F_{1,42}=20.5$, $P<0.005$): neighbors decreased nitrogen availability more strongly (85%) under ambient resource conditions compared to when carbon was added (Fig. 2a). There were no differences in inorganic N availability between neighborhoods where *C. diffusa* had or had not been removed, regardless of resource amendment.

Carbon addition slowed potential net rates of N mineralization plots. The effect of carbon was not as strong in complete removals (carbon \times removal interaction, $F_{3,34}=4.6$, $P<0.01$) (Fig. 2b). Mineralization rates in neighborhoods where *C. diffusa* had been removed did not differ from where it was still present, regardless of resource amendment. Gypsum also did not influence net N mineralization rates.

Resin-extractable phosphorus was reduced by gypsum addition by an average of 34% ($F_{1,41}=10.5$, $P<0.001$) and did not influence inorganic N availability. The effect of

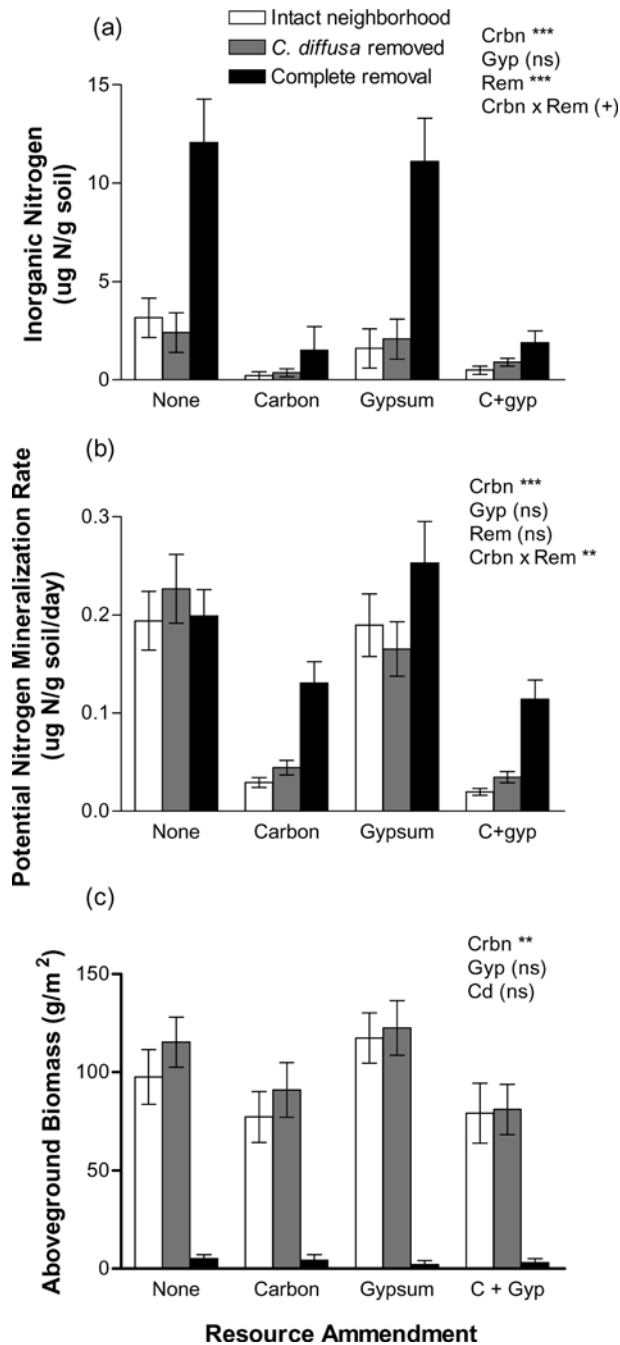


Fig. 2a–c Effects of resource amendments and neighborhood removals on **a** inorganic N availability, **b** potential net nitrogen mineralization rates, and **c** aboveground biomass production. (*Crbn* Carbon, *Gyp* Gypsum, *Rem* Neighborhood removals). In **c** effects of removal were tested with no removal and *C. diffusa* removal (*cd*) only. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, + $P < 0.10$)

gypsum addition on phosphorus availability was not influenced by carbon addition (non-significant interaction $F_{1,41}=0.77$, $P > 0.05$). Phosphorus availability did not differ between neighborhoods where *C. diffusa* was present and where it had been selectively removed.

Aboveground biomass production was significantly reduced by carbon addition ($F_{1,43}=11.6$, $P=0.001$). The addition of gypsum did not affect aboveground production

(Fig. 2c). Three growing seasons after the selective removal of *C. diffusa* (and initial reduction in aboveground biomass by an average of 25% due to the removal), the biomass fully recovered. Aboveground production did not differ between neighborhoods where *C. diffusa* had or had not been removed (Fig. 2c).

As a result of the effect of the resource manipulations on N and P, the relative amount of inorganic nitrogen and resin-extractable phosphorus (the N:P soil ratio) also shifted due to resource manipulations. Neighborhoods where *C. diffusa* had or had not been removed did not differ in N:P soil ratios. In both types of neighborhoods, gypsum addition significantly increased the N:P ratio ($F_{1,41}=7.5$, $P < 0.001$), and carbon addition significantly decreased the N:P ratio ($F_{1,41}=11.5$, $P < 0.001$). When both carbon and gypsum were added, the N:P soil ratio was similar to the ratio with no resource manipulations (Fig. 3).

Target survival and growth

While over 90% of *B. dactyloides* transplants survived under ambient nutrient conditions, less than half of the transplants of the other three species, *A. cristatum*, *C. diffusa*, and *G. sarothae*, survived in these unmanipulated resource conditions (Table 1). Carbon (sucrose) addition, which decreased inorganic nitrogen availability as well as decreased aboveground productivity, enhanced the survival of all species ($F_{1,15}=16.4$, $P < 0.01$), probably due to reduced water stress caused by the reduction of leaf area. Selective removal of *C. diffusa* from neighborhoods did not differentially affect any aspect of target survival (Table 1).

Of the plants that survived, *C. diffusa* grew almost five times faster than *B. dactyloides* under unmanipulated resource conditions (Table 1). While it grew fastest under

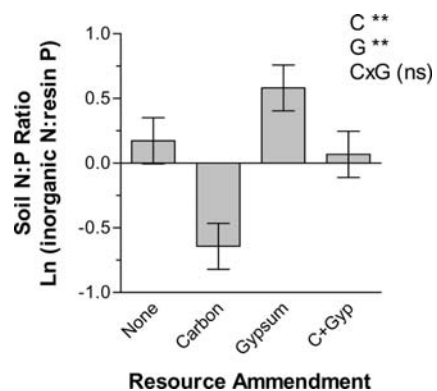


Fig. 3 The effect of carbon (C) and gypsum (G) amendments on resin extractable phosphorus and inorganic nitrogen two growing seasons after the initiation of treatments. Carbon addition decreased nitrogen availability, decreasing the relative N:P ratio in the soil, and gypsum decreased phosphorus availability, increasing the relative N:P ratio. The combined addition of carbon and gypsum decreased both resources, but did not change the relative N:P ratio. Resin-extractable phosphorus and inorganic nitrogen measures were normalized prior to the ratio calculation. ** $P < 0.01$, NS non-significant ($P > 0.05$)

Table 1 Aboveground relative growth and survival of the four focal species in ambient, reduced nitrogen (N), reduced phosphorus (P) and reduced N+P conditions, in neighborhoods with and without *C. diffusa* selectively removed. Mean \pm 1 SE is given for relative growth rate (aboveground growth/initial shoot mass). Proportional

Resource conditions	Species	Neighborhoods w/ <i>C. diffusa</i> present		Neighborhoods w/ <i>C. diffusa</i> removed	
		RGR (g/g/year)	Survival (proportional)	RGR (g/g/year)	Survival (proportional)
Ambient	<i>B. dactyloides</i>	2.1 \pm 0.7	1.00	3.3 \pm 1.0	0.86
	<i>A. cristatum</i>	0.6 \pm 0.3	0.42	1.2 \pm 1.1	0.29
	<i>C. diffusa</i>	9.4 \pm 0.1	0.29	7.5 \pm 0.4	0.42
	<i>G. sarothae</i>	1.4 \pm 0.3	0.43	1.2 \pm 0.8	0.43
Reduced N	<i>B. dactyloides</i>	1.6 \pm 0.5	1.00	2.0 \pm 0.5	1.00
	<i>A. cristatum</i>	0.7 \pm 0.2	0.71	0.9 \pm 0.4	0.57
	<i>C. diffusa</i>	2.36 \pm 0.6	0.71	2.8 \pm 0.4	0.71
	<i>G. sarothae</i>	2.3 \pm 0.8	0.57	0.8 \pm 0.2	0.57
Reduced P	<i>B. dactyloides</i>	2.2 \pm 0.4	0.57	2.2 \pm 0.5	0.86
	<i>A. cristatum</i>	1.6 \pm 0.5	0.57	2.8 \pm 3.0	0.29
	<i>C. diffusa</i>	1.2 \pm 0.3	1.00	1.7 \pm 0.5	0.86
	<i>G. sarothae</i>	–	0.14	–	0.14
Reduced N+P	<i>B. dactyloides</i>	2.7 \pm 1.3	1.00	3.0 \pm 0.9	1.00
	<i>A. cristatum</i>	0.6 \pm 0.2	0.57	0.5 \pm 0.2	0.57
	<i>C. diffusa</i>	5.8 \pm 3.2	0.86	3.3 \pm 1.5	0.71
	<i>G. sarothae</i>	2.0 \pm 0.7	0.57	0.9 \pm 0.4	0.43

survival is based on seven individuals per species. Measures are not standardized by differences in neighbor biomass (the reduced N treatments reduced neighbor biomass and could cause indirect effects)

unmanipulated conditions, the growth of *C. diffusa* was more responsive to reductions in resource availability than the other species. All resource amendments slowed the relative growth rate of *C. diffusa*, the most severe being with gypsum addition where *C. diffusa* growth rate was slower, or equal to, the other species (Table 1). Although the species differed in their root:shoot ratios (*B. dactyloides* allocated more to roots than *C. diffusa*; $F_{3,96}=13.3$, $P<0.001$), these allocation patterns only slightly changed due to reductions in nitrogen availability ($F_{3,96}=3.2$, $P=0.06$) and did not change due to reductions in phosphorus availability. Removal of *C. diffusa* from neighborhoods did not differentially affect any aspect of target growth (Table 1).

Competitive response

In general, neighbors facilitated survival (positive lnRR values) (Fig. 4). The effect of resource reduction on competitive response, in terms of survival, differed by species (significant species \times carbon \times gypsum interaction; $F_{3,15}=8.9$, $P<0.01$): the facilitative effect of neighbors was enhanced by carbon addition for *C. diffusa*, by carbon plus gypsum addition for *A. cristatum* and *G. sarothae*, and was not affected by resource amendments for *B. dactyloides* (Fig. 4). Removal of *C. diffusa* from neighborhoods did not differentially affect competitive response in terms of survival.

While the neighbors exerted largely competitive effects on growth (negative lnRR values, Fig. 5), the presence of *C. diffusa* in neighborhoods did not influence competitive response in terms of growth ($F_{1,98}=2.7$, $P>0.05$). Under

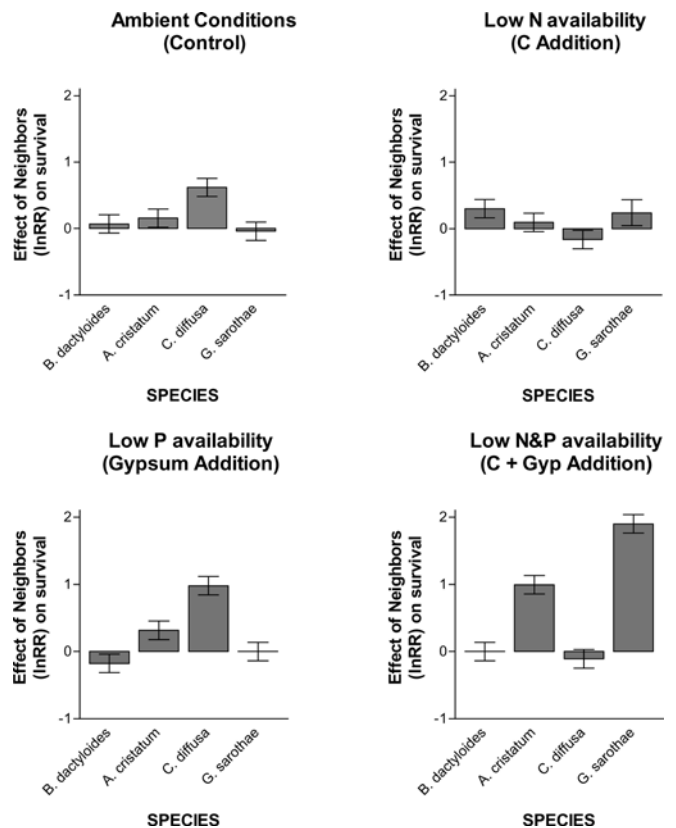


Fig. 4 Effect of neighbors on the survival of the four target species. Removal of *C. diffusa* did not have any effects on target survival, and was combined with no removal for this analysis. A positive lnRR value indicates that neighbors facilitate survival and negative values indicate that neighbors inhibit survival

ambient resource conditions, the growth of *C. diffusa* was not affected by neighbors, *A. cristatum* was more negatively affected by neighbors, and the growth of *B. dactyloides* was most negatively affected by neighbors. Carbon addition increased competitive intensity for all species in terms of growth ($F_{1,98}=4.2$, $P<0.05$), but maintained the relative competitive ranking from control conditions: growth of *B. dactyloides* and *A. cristatum* was more inhibited by neighbors than the growth of *C. diffusa* (non-significant carbon \times species interaction, $F_{2,98}=1.9$, $P>0.05$). However, when gypsum was added, competitive rankings were altered and all species experienced similar negative effects of neighbors in terms of growth (gypsum \times species interaction, $F_{2,98}=17.9$, $P<0.001$). While phosphorus reduction only slightly enhanced competitive effects on *B. dactyloides* and *A. cristatum*, it significantly enhanced competitive effects on *C. diffusa*. At low nitrogen and phosphorus availability (when both carbon and gypsum were added), competitive rankings were similar for all focal species (carbon \times gypsum interaction, $F_{1,98}=67.3$, $P<0.001$). Neighbor competition did not affect

measured root:shoot ratios and treatment effects on root growth were similar to those on aboveground growth.

Because resource amendments affected neighbor biomass, which also influences competitive effects, responses were also standardized by neighbor biomass (per-gram competitive response). With this standardization, the overall intensity of neighbor effects in the carbon addition treatments increased ($F_{1,96}=13.3$, $P<0.001$). However, relative species rankings were unchanged and the effect of reduced phosphorus availability on competitive response remained (gypsum \times species interaction, $F_{2,96}=3.08$, $P<0.05$) (Fig. 6).

Discussion

Interactions under current resource conditions

We made two hypotheses about interactions between resident species and *C. diffusa* under current resource conditions: first, that *C. diffusa* is better able to tolerate competition than the other focal species; and second, that *C. diffusa* exerts strong impacts on the competitive environment. The first of these hypotheses was supported. Effects of neighbors were less severe (in terms of growth), and at times more facilitative (in terms of survival), on *C. diffusa* compared to other species we examined.

However, our results do not support our second hypothesis that *C. diffusa* strongly impacts the competitive environment. The presence of *C. diffusa* in neighborhoods had little impact on the growth and survival of the four focal species or on any of the soil processes we measured. Although strong competitive impacts of other invasive exotic species have been measured under conditions where density is high (D'Antonio and Mahall 1991; D'Antonio et al. 1998; Dyer and Rice 1999; Hager 2004), biomass rather than species-specific effects predominately explained the competitive effects measured at lower field-densities in this study. In related work, we found few species-specific effects of *C. diffusa* growing in mono-specific patches on nutrient cycling rates, nitrogen or phosphorus levels, or microbial biomass (LeJeune 2002). Recent evidence also indicates that *C. maculosa* does not strongly affect field soil conditions (Sperber et al. 2003).

Callaway and Aschehoug (2002) argue that *C. diffusa* has a competitive advantage in its invaded range because its root exudates affect competition for resources. The presence of activated carbon, which absorbed root exudates, reduced the competitive advantage of *C. maculosa* (Ridenour and Callaway 2001). *C. diffusa* does not produce the allelochemical that Bais et al. (2003) have identified in *C. maculosa*, but it could affect competitive interactions through similar exudates (Hiero and Callaway 2003). However, we found few species-specific impacts in the field, suggesting that exudates produced by *C. diffusa* do not strongly affect soil resources or the performance of other species under these soil and environmental conditions.

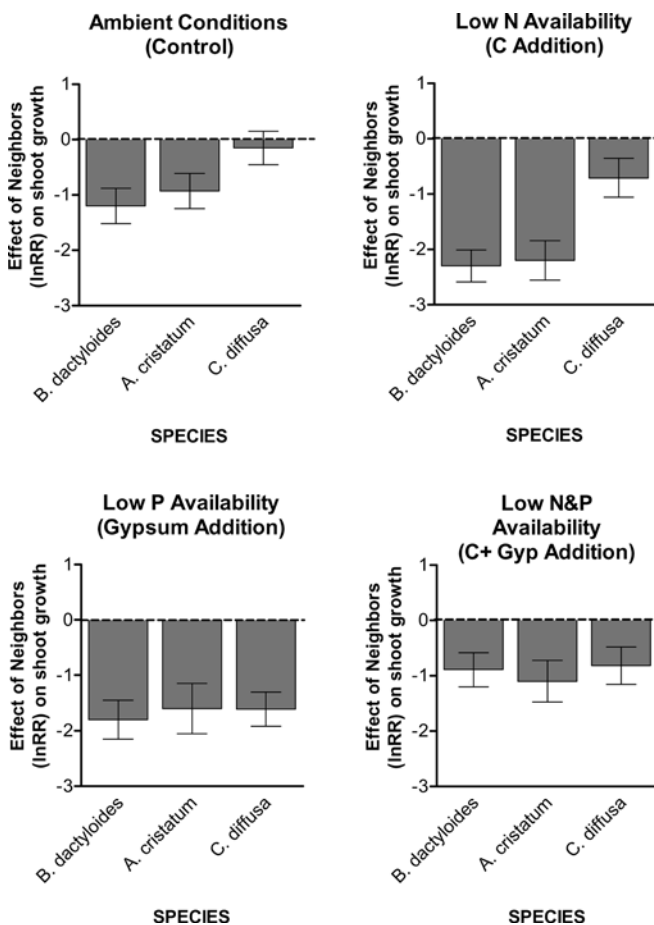
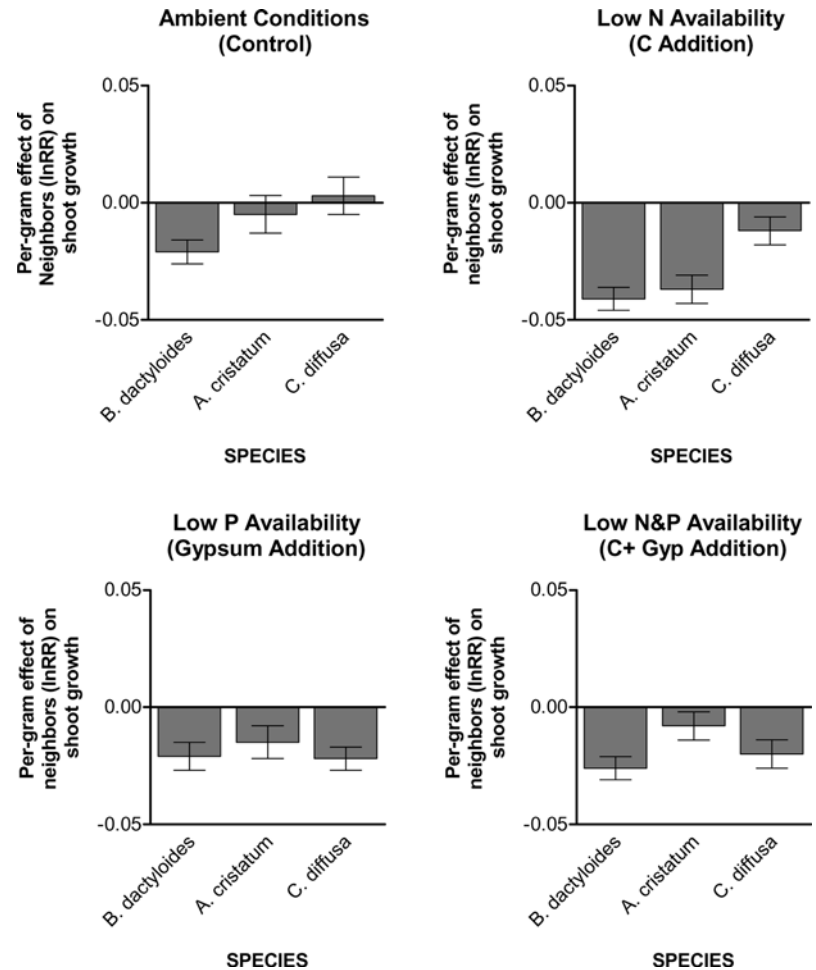


Fig. 5 Effect of neighbors (lnRR) on shoot growth of three focal species (*G. sarothae* was not analyzed due to high mortality). Removal of *C. diffusa* from neighborhoods did not have any effects on target growth and is not shown. *Negative values* indicate net competitive effects of neighbors on target, *positive values* indicate net facilitative effects

Fig. 6 Per-gram effect of neighbors (lnRR standardized by neighbor biomass) on shoot growth of three focal species. Removal of *C. diffusa* from neighborhoods did not have any per-gram effects on target growth and is not shown. *Negative values* indicate net competitive effects of neighbors on target, *positive values* indicate net facilitative effects



Interactions under reduced resource conditions

Our third hypothesis was that reductions in nitrogen and/or phosphorus availability would reduce the relative competitive advantage of *C. diffusa*. While reductions in nitrogen availability altered overall competitive intensity for all the focal species, it was phosphorus reduction that affected relative competitive ranking and eliminated the relative competitive advantage of *C. diffusa*. Reducing phosphorus availability did not change the competitive tolerance of *B. dactyloides* and *A. cristatum*. However, phosphorus reduction had a strong effect on the competitive ability of *C. diffusa*. This sensitivity to phosphorus availability suggests that *C. diffusa* has greater competitive requirements for phosphorus than the other focal species. At the same study site, *C. diffusa* is more likely to respond to phosphorus fertilization compared to the resident species, most of which respond to nitrogen fertilization (LeJeune and Seastedt 2001; LeJeune 2002). Thus, *C. diffusa* may be more limited by phosphorus and less limited by nitrogen compared to the resident community.

The sensitivity of competitive interactions to phosphorus availability may suggest that *C. diffusa* relies on mycorrhizal associations. Mycorrhizae increased the relative competitive ability of a congeneric, *C. maculosa* (Marler et al. 1999; Callaway et al. 2003), because it was

able to exploit the symbiosis more effectively than native grass species due to luxury consumption of P and efficient utilization of extra-radical hyphae (Zabinski et al. 2002). A similar dependence on mycorrhizae was found for *C. melitensis*, although the effect depended on neighbor identity (Callaway et al. 2003).

Both the absolute amount of phosphorus and the ratio of phosphorus to nitrogen appear to influence *C. diffusa* performance. *Centaurea diffusa* may be at a particular disadvantage if phosphorus levels are low in relation to nitrogen levels because the low phosphorus availability does not influence the competitive tolerances of the other species. When nitrogen levels are also low (N:P ratio similar to control conditions), low phosphorus availability may not affect the relative competitive ability of *C. diffusa* as strongly due to concurrent nitrogen limitation of its competitors.

Competition and invasion success

Experimental tests yield mixed support about the contribution of competitive ability to invasion success (e.g., Gaudet and Keddy 1998; Gordon 1998; Bakker and Wilson 2001; D'Antonio et al. 2001; Hager 2004). While *C. diffusa* tolerated competition better than the other focal

species, the competitive effect of neighborhoods containing *C. diffusa* was virtually indistinguishable from neighborhoods without *C. diffusa*. This finding is consistent with Davis (2003) and Levine et al. (2003) who argue that competitive mechanisms do not usually cause large system-level impacts. It also supports the contention that competitive response ability may be more important in determining abundance in perennial, size-structured communities (Wilson and Tilman 1995; Goldberg 1996). Both of these mechanisms are likely context-dependent. For instance, Hager (2004) found that the invasive *Lythrum salicaria* (purple loosestrife) had strong competitive effects on other species but was not a superior tolerator to neighbor competition, opposite from the pattern we found for *C. diffusa*.

We expect that the competitive impacts of *C. diffusa* should depend on land use and community composition, and may change in situations where the resident species have similar phosphorus requirements. Alternatively, strong propagule inputs from more disturbed source habitats may allow dominance without the need for strong impacts (Davis 2003) or ecosystem-level impacts may occur at other sites that differ in soil type or environmental conditions (Ehrenfeld 2003). In addition, the ability to escape the impact of herbivores may contribute to the success of the species. While we reduced the effects of herbivores in this experiment through fencing and insecticide application, evidence from other experiments at our site indicate that selective herbivory can contribute to control (LeJeune 2002; Seastedt et al. 2003). Drought conditions could also influence the competitive success of *C. diffusa*. Lower than average rainfall conditions occurred at the study site in October 2001, 5 months after transplanting the target individuals, and the following April. Low moisture levels particularly during April 2002 could have been relatively disadvantageous to *C. diffusa* because it often starts growing during this period, earlier than most species at the study site.

Implications

To facilitate re-establishment of native species in exotic-dominated systems, we must identify the factors constraining their success (D'Antonio and Meyerson 2002; Suding et al. 2004). Reductions in resource availability through the addition of soil amendments, topsoil removal, or removal of biomass have been used in systems where enhanced fertility levels have altered community structure (Marrs 1993; Blumenthal et al. 2003). For *C. diffusa*, reduction of phosphorus by adding gypsum may be a reasonable management technique in small but vulnerable areas such as along reserve edges or adjacent to disturbances. Areas with naturally low levels of soil phosphorus may also be more resistant to invasion by *C. diffusa*.

We tested the dependency of invader-resident interactions on two soil resources, nitrogen and phosphorus. Rather than strong impacts on soil processes, different

resource requirements appear to contribute to the success of *C. diffusa*. More tests in other environments and with other invaders, focusing on the dependencies of multiple resources in competitive interactions, are needed to determine whether invaders may often escape resource limitations of the resident community and use other resources to their competitive advantage.

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