

# Biotic constraints on the invasion of diffuse knapweed (*Centaurea diffusa*) in North American grasslands

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**Abstract** Knapweeds (*Centaurea* spp.) are among the most invasive of non-indigenous plant species that have colonized western North America over the last century. We conducted a 4-year experiment in a reconstructed grassland to test hypotheses related to the ability of grasslands to resist the invasion of diffuse knapweed (*C. diffusa*). We experimentally invaded *C. diffusa* and three native species into areas where we manipulated soil nitrogen (N) and phosphorus (P) availability and removed extant grasses to reduce competition. We evaluated the growth response of these species to these resources and competitive manipulations. Of the native species that were experimentally added, only one species, *Ratibida pinnata* (prairie coneflower), established in any numbers. Establishment values in intact vegetation were low for both species, but establishment by *C. diffusa* (0.02%) clearly outperformed that of *R. pinnata* (0.001%). Under reduced grass competition, establishment was enhanced, but the values for *C. diffusa* (0.68%) were not statistically different from those of *R. pinnata* (0.57%). Neither species performed better under

higher soil nutrients in the presence of competing grasses. In plots with both species, biomass of the two planted species was positively correlated, but the biomass of both species was negatively correlated with non-added weedy species. Subsequent harvests of *C. diffusa* indicated that establishment was enhanced in treatments with higher soil nutrients but that the biomass of these plants could only be enhanced when plant competition was also reduced. These results indicate that *C. diffusa* can establish in intact grasslands at rates higher than natives, but opportunism rather than competitive ability best describes the invasiveness of *C. diffusa*. Thus, the mechanisms contributing to the establishment of this knapweed species are different from factors identified as contributing to the dominance of this invader.

**Keywords** Competition · Fertilization · Nutrient limitation · Seedling establishment · *Ratibida*

## Introduction

For an exotic plant to reach problematic densities in native communities, it needs to be successful at several stages: colonization, when propagules disperse into a system; establishment, when the propagules develop into a reproducing population; spread, when that population moves across the landscape; and impact, when the invader reaches high densities and alters the ecosystem (Sakai et al. 2001; Kolar and Lodge 2001; Levine et al. 2004; Ortega and Pearson 2005). In a comprehensive review, Levine et al. (2004) found that the negative effects of competitors, soil fungal communities, and herbivores were critical processes that regulated plant

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invader abundance and spread but that these same processes did not affect the invaders' ability to initially colonize and establish. Thus, the mechanisms that allow a species to establish in a system may be very different than mechanisms that allow a species to spread and dominate once established.

Here, we test the idea that successful invasion may often result from the combination of several mechanisms that lead to success at different stages in the invasion process. There have been few tests of this idea because most work in invasion ecology has focused on post-establishment mechanisms, such as competition, herbivory, and allelopathic effects, that should predominantly regulate invader success at the dominance and spread stages. We know much less about the ecological mechanisms that enable success in the initial colonization and establishment stages of invasion (Sakai et al. 2001).

The literature on the subject of invasive species is replete of contrasts between arguments that the successful invaders are strong competitors and/or resistant to herbivores (i.e., able to combat strong biotic resistance) and those that their weedy opportunistic nature allow invaders to succeed (i.e., able to take advantage of low biotic resistance) (Dethier and Hacker 2005; Gelbard and Harrison 2005; MacDougall and Turkington 2005). For instance, propagule pressure and disturbance are often associated with increased invasion success (Davis et al. 2000; Williamson and Harrison 2002; Beckstead and Augspurger 2004; Gelbard and Harrison 2005; Hansen and Clevenger 2005). On the other hand, strong effects through allelopathy or impacts on ecosystem processes may be critical for many exotic species to achieve dominance (Mack et al. 2001; Ehrenfeld 2003; Hierro and Callaway 2003). One resolution of these contrasting arguments is that different mechanisms are important at different stages of invasion: species that are able to be opportunistic during the invading stages and competitive during the spread and impact stages are most likely to become problematic invaders.

Species in the genus *Centaurea*, which are among the most problematic plant species found in western North America, are prime candidates to test these ideas. The mechanisms by which *Centaurea* spp. dominates huge expanses of grasslands and rangelands have been well studied (e.g., Roche and Roche 1999; Callaway and Ridenour 2004; Myers and Bazely 2003; Callaway et al. 2005). These species are able to dominate native communities due to some combination of the allelopathic properties of root exudates (Bais et al. 2002; Vivanco et al. 2004), neutral or positive feedbacks from the microbial community (Marler et al. 1999; Callaway

et al. 2001; 2004a, b, 2005), and competitive ability under modified or high resource conditions (LeJeune and Seastedt 2001; Suding et al. 2004). Despite this evidence, many studies find that competition and soil effects do not wholly explain the success of these invaders (Blicker et al. 2002, 2003; Lowe et al. 2002; Sperber et al. 2003), suggesting that other mechanisms may be important in the invasion process.

The mechanisms by which the *Centaurea* genus are able to invade and proliferate to reach high densities may be very different than the mechanisms associated with the ability of the *Centaurea* genus to dominate western rangelands in North America. However, these early stages in the invasion process have been less studied, particularly in experimental work. Evidence suggests that elevated resource availability (LeJeune and Seastedt 2001), disturbance (Gelbard and Harrison 2003; Pokorney et al. 2005; LeJeune et al. 2006), and propagule pressure (Gerlach and Rice 2003; Seastedt et al. 2005) may be important factors leading to the establishment of *Centaurea* populations.

We conducted a field experiment to test what factors regulate the initial colonization and establishment of diffuse knapweed, *C. diffusa*. We experimentally invaded propagules of *C. diffusa* into a restored grassland where we manipulated resource availability and grass competition for four growing seasons. We then compared the response of *C. diffusa* to the response of seeded native species as well as other weed species that had invaded the site on their own. This experiment allowed us to test the hypothesis that the initial colonization and establishment of *C. diffusa* often depends on factors associated with opportunism rather than competition; these include high propagule pressure, ability to exploit high resource availability, and opportunistic responses to a reduction in grass competition.

## Materials and methods

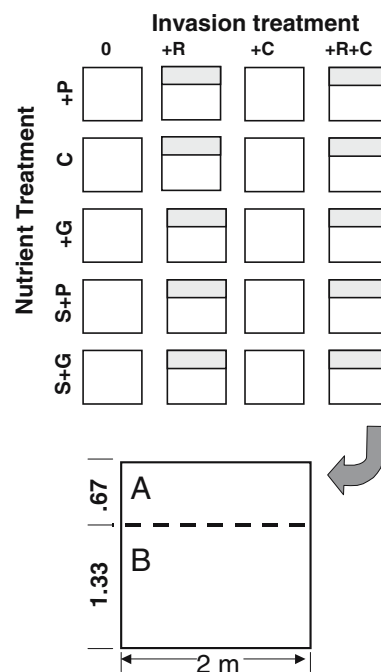
This research was conducted on the University of Colorado's 'South Campus', a former gravel pit located just south of Boulder, Colorado, and restored to a grassland in 1998. The restoration procedure involved filling gravel pits with materials previously excavated from this site and adjacent areas, leveling the field, and finally applying 12–18 cm of topsoil that had formerly occupied the area. The site was then drill seeded with a mix of six native species that were a mix of warm-season grasses, particularly *Sporobolus airoides* (alkali sacaton), and the cool-season grass, *Pascopyrum smithii* (western wheatgrass). By 2004, the relative vegetation cover at the site was over 90% grasses and was

dominated by warm season species, which constituted about 60–80% of the total vegetation cover (Karie Cherwin, University of Colorado, unpublished results). In addition to *S. airoides*, which averaged about 50% of the relative species cover, blue grama, (*Bouteloua gracilis*) side-oats grama (*B. curtipendula*), and buffalo grass (*Buchloe dactyloides*) were abundant warm-season grasses and collectively contributed to what appeared to be a semi-arid, mixed grass community. In addition to these species, about 20 species of grasses and forbs that were either contaminants of the seed mix or had invaded from adjacent roadsides, old-fields, and lawns adjacent to this field were also found on the site. These included non-native species considered to be invasive problems in other regions of the country (e.g., the annual grasses *Bromus tectorum* and *B. japonicus*), abundant weedy annual forbs such as storksbill (*Erodium cicutarium*) and pepper grass (*Alyssum parviflorum*), and additional non-native species not considered to be invasive in this area. The original vegetation of this site was most likely a relict tallgrass prairie that is still found in nearby areas of the Colorado Front Range (Bennett 1997).

### Experimental design

In 2001 we set out one hundred and forty  $2 \times 2\text{-m}$  ( $4\text{ m}^2$ ) plots in seven blocks of 20 plots each. Buffer areas (3–4 m) separated the blocks, and the total study area occupied a rectangle of approximately  $70 \times 90\text{ m}$ . Each of the 20 plots in a block consisted of one replicate of a specific nutrient amendment (five different levels) and an experimental invasion treatment (four different levels) that was located randomly within each block (Fig. 1).

The goal of our soil nutrient manipulations was to generate two levels of nitrogen (N) availability and three levels of phosphorus (P) availability. The current nominal level of plant-available N in our region is believed to be above historical background amounts due to atmospheric N deposition (Baron et al. 2006) and, as such, may be affecting plant community composition (Stevens et al. 2004). Thus, we chose ambient and a reduced level of plant-available N as appropriate treatments to assess N limitation. Based upon results suggesting that *C. diffusa* was responsive to levels of soil P (LeJeune and Seastedt 2001), we attempted to create three levels of P (reduced, nominal, and enhanced or fertilized). Soil amendments involved combinations of adding sucrose (table sugar), calcium sulfate ( $\text{CaSO}_4$ , gypsum), and superphosphate ( $\text{P}_2\text{O}_5$ ) for the 2002–2004 interval. Gypsum was added alone in an attempt to



**Fig. 1** Experimental design. Seven blocks of 20 plots were created; each plot was assigned an invasion treatment and a nutrient amendment treatment. Nutrient amendments included sugar + gypsum ( $S + G$ ), sugar + phosphorus ( $S + P$ ), gypsum ( $G$ ), no amendments (control;  $C$ ), or phosphorus addition ( $+P$ ). Invasion treatments included none ( $0$ ), *Ratibida pinnata* seeds ( $+R$ ), *Centaurea diffusa* seeds ( $+C$ ), or *R. pinnata* plus *C. diffusa* seeds ( $+R+C$ ). Invasion plots  $+R$  and  $+R+C$  were divided into grass-removal areas ( $A$ ) and intact vegetation areas ( $B$ ). Plots were randomized in the field experiment

bind soluble P in the soil with excess Ca, thereby producing largely insoluble calcium phosphate and reducing plant available P, a procedure that has been successful previously (LeJeune et al. 2006).

Annual application amounts of soil amendments were scaled to growing season precipitation. The study area averages about 51 cm of precipitation per year based on the 1971–2000 average, and the 2001–2004 interval saw 90, 69, 109 and 134% of average annual precipitation, respectively (NOAA 2006). Gypsum was added at rates of  $10\text{ g/m}^2$  Ca twice in 2002 and four times each in 2003 and 2004. Table sugar (sucrose) at a rate of  $200\text{ g C/m}^2$  was used to reduce inorganic soil N (Blumenthal et al. 2003). A modest amount of inorganic P fertilizer ( $0.25\text{ g P m}^{-2}$ ) was added to the sugar in an attempt to maintain levels of available P. Sugar and gypsum were added together to attempt to reduce both N and P. Sugar + P or sugar + gypsum were added three times in 2002 and four times each in 2003 and 2004. Phosphorus addition as super phosphate ( $\text{P}_2\text{O}_5$  at a rate of  $1\text{ g P m}^{-2}$ ) was used to supplement plant available P and was added twice in 2002 and three times

each in 2003 and 2004. Twenty-eight of the plots (four per block) received no soil amendments.

Experimental invasions involved adding non-native *C. diffusa* seed, adding native seed, adding both native and non-native seed, or no additional seed. We first conducted lab germination tests to determine the expected germination rates of seeds. A regression analysis between the weight and number of seeds was used to determine the appropriate seed additions. In September 2001, *C. diffusa* seeds ( $2 \text{ g m}^{-2}$ ; approximately 1400 viable seeds per square meter) were added to the designated plots; in the fall of 2002, we added an additional  $250 \text{ seeds m}^{-2}$  to each of the plots. Native seed additions consisted of a mixture of four species ( $2 \text{ g m}^{-2}$ ;  $0.5 \text{ g}$  of each species per square meter): prairie coneflower (*Ratibida pinnata*,  $1280 \text{ seeds g}^{-1}$ ), blue flax (*Linum lewisii*,  $450 \text{ seeds g}^{-1}$ ), gayfeather, (*Liatris punctata*,  $190 \text{ seeds g}^{-1}$ ) and blanket flower (*Gaillardia grandiflora*,  $245 \text{ seeds g}^{-1}$ ). Only *R. pinnata* established successfully enough to be included in our results here. For *R. pinnata*, we added  $640 \text{ seeds m}^{-2}$  to each plot in 2001 and an additional  $120 \text{ seeds m}^{-2}$  to each plot in 2002.

We experimentally reduced grass abundance in a portion of the plots receiving seeds (Fig. 1) by applying herbicides to a  $2 \times 0.67\text{-m}$  strip with a grass-specific herbicide (Ortho Grass-B-Gone) in each of the plots. This effectively removed most grasses in  $1.33 \text{ m}^2$  of the plot while leaving the remaining  $2.67 \text{ m}^2$  intact. Following treatment in the spring of 2002, these areas were allowed to revegetate from existing seed banks or from grasses that had survived the herbicide application, thereby creating a split plot consisting of grass removal and intact vegetation areas. We tested the extent to which *C. diffusa* could influence abundances or amounts of planted native species by treating portions of the plots receiving native seeds, or those with native seeds plus knapweed seeds. We did not apply herbicides to any plots not receiving seeds or to plots receiving only *C. diffusa* seeds. Thus, we could test *C. diffusa* effects on *R. pinnata* establishment, but the reverse question could not be addressed. Following a census and harvest of *C. diffusa* and *R. pinnata* in May of 2004, these plots were subsequently used to assess the overall numerical and biomass response of *C. diffusa* to nutrient amendments and partial grass removal. Only information from whole plots was collected. The analysis consisted of comparing *C. diffusa* seeded into 35 plots with partial grass removal with the 35 plots of *C. diffusa* seeded into intact vegetation. We believe this design best represents a test of factors influencing the invasibility of *C. diffusa* into degraded versus intact grasslands in the area.

## Measurements and analyses

We periodically sampled inorganic N and P concentrations in surface soils during the summers of 2003 and 2004 to document the effects of soil amendments as well as to test for potential effects on soils by the various vegetation manipulations. The level of inorganic N in the soils was measured using  $2 \text{ M}$  KCl extractions of soil cores,  $4 \text{ cm}$  in diameter by  $10 \text{ cm}$  deep, as described by Robertson et al. (1999). Nitrate and ammonium were measured colorimetrically on a Lachat autoanalyzer following the recommendations of the manufacturer (Lachat, Milwaukee, Wis.). The sum of nitrate and ammonium was taken as an index of plant-available N in the soil. Plant-available P was assessed using the first two steps of the Hedley fractionation for soil P (Hedley et al. 1982), which provides an estimate of resin-extractable P and sodium bicarbonate-extractable P. The procedures followed were those used by Tiessen and Moir (1993), and the concentrations were measured colorimetrically on an Alpkem autoanalyzer (Alpkem, Wilsonville, Ore.). The sum of these two P fractions was used as an index of plant-available P in the soil. Both inorganic N and inorganic P measurements are “snapshots” of soil N and P availability and are influenced by atmospheric inputs, organic matter mineralization, soil characteristics, and plant uptake. To provide an average index of N and P in the soils of our plots, the average of four measurements – two measurements taken in June and July of 2003 and 2004, respectively – are presented here. Total carbon (C) and N concentrations in the top  $10 \text{ cm}$  of the restored grassland site were measured on all plots in 2004 by means of Micro-Dumas combustion on a Carlo-Erba CHN analyzer (Carlo Erba Strumentazione, Milan, Italy).

We used green biomass to assess the established and planted vegetation response to soil amendments. Biomass estimates were obtained in 2004 from clip harvests of  $0.25\text{-m}^2$  quadrats in both grass removal and undisturbed portions of plots seeded with both *C. diffusa* and *R. pinnata*. Living and dead vegetation was separated, dried at  $60^\circ\text{C}$ , and weighed. The dead material likely included some production from 2004, but here we refer to the green material as aboveground net primary production. The biomass of green material was weighed and classified on a per species basis, but only total biomass and the contribution provided by non-seeded (weedy) species are reported here.

The densities of *C. diffusa* and *R. pinnata* were monitored throughout the 2001–2005 interval. Both species were producing flowering plants by 2004. In late May 2004 we completely harvested all of the aboveground biomass of *C. diffusa* and *R. pinnata*. The values

obtained from the grass removal and intact vegetation portions of the plots were recorded separately.

Following this late spring harvest and perhaps due to the unusually wet weather of 2004, the *C. diffusa* in some of the plots exhibited resprouting and, consequently, additional seed germinated after this harvest. We therefore repeated the complete harvesting of all *C. diffusa* in late July of 2004 and in late May of 2005. Very few *R. pinnata* were found in subsequent collections, and further comparisons using this species were not conducted. The *C. diffusa* results from grass removal and from the intact vegetation portions of the plots for these subsequent collections were not recorded separately. While the possibility of resprouting confounds the values reported here (artificially inflating the numbers), the ability to sprout is viewed as an index of plant vigor and does not confound treatment comparisons. The plants were dried at 60°C for 48 h and weighed.

For the analysis of questions that utilized the entire 140-plot experiment or a portion of the experiment not involving split-plot analyses, we used a randomized blocked ANOVA model (SAS 1999). While we initially intended to use the N and P manipulations in a complete factorial analysis, data on the soils of the various treatments suggested that individual soil treatments be analyzed as separate levels in a one-way ANOVA (see Results). When significant differences at  $P = 0.05$  were detected, a post hoc Student-Newman-Keuls (SNK) test was performed to identify differences among treatments. Numerical values for inorganic N and P content of soils, vegetation biomass, and *C. diffusa* and *R. pinnata* numbers and biomass were log-transformed before analysis to homogenize variances. To address the effects of grass reduction on the establishment of *C. diffusa* and *R. pinnata* and to test the effect of *C. diffusa* on the establishment of *R. pinnata*, a split-plot ANOVA was conducted using the SAS mixed model procedure (SAS 1999).

## Results

### Effects of treatments on soil characteristics

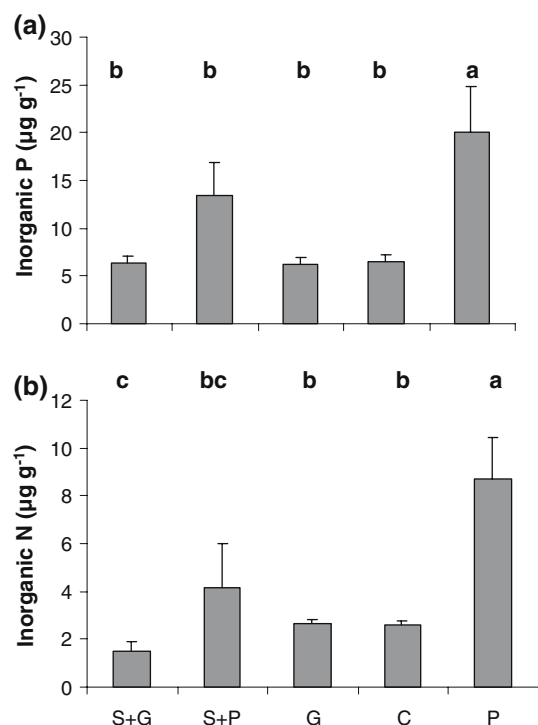
Nutrient amendments had measurable effects on plant available P ( $F_{4,95} = 6.41$ ,  $P < 0.0001$ ; Fig. 2a) and plant available N ( $F_{4,89} = 14.75$ ,  $P < 0.0001$ ; Fig. 2b). Based upon the analysis of log-transformed values, the amounts of P in soils of the P addition (+P) plots were significantly greater than values obtained in all other treatments (SNK test,  $P < 0.05$ ). Unexpectedly, inorganic N also significantly increased in the +P plots

(SNK test,  $P < 0.05$ ). The analysis of log-transformed numbers indicated that the inorganic N concentrations in the gypsum and control plots had intermediate values and were significantly different than all others. The results from the sugar + P treatment were influenced by a few very high values, but the results from the log-transformed data indicated that this treatment was similar to that of the gypsum, control and sugar + gypsum plots. The inorganic soil N of the sugar + gypsum treatment had the lowest value of all treatments and was significantly lower than all treatments except that of the sugar + P (SNK test,  $P < 0.05$ ). The increased N in the +P plot does not appear to be due to contamination of the P fertilizer but represents inorganic N created by increased N fixation in P-fertilized plots (Sasha Reed, University of Colorado, personal communication to TRS). Because the +P plots were enriched with both P and N, we chose to analyze soil amendments as five separate treatments rather than as a N and P factorial experiment. The addition of seeds and the grass reduction treatment had no effect on the inorganic soil nutrient measurements obtained in this study (data not shown).

The organic C and N content in the top 10 cm of soil of the plots was unaffected by nutrient amendments or by vegetation treatments. This result reveals the conservative nature of organic C and N measurements as well as the fact that the inorganic N increases attributed to N fixation were not measurable in the organic N pool. When measured in summer 2004, average total C and total N content in the top 10 cm of the soil was 1.25% ( $\pm 0.03$ ) and 0.10% ( $\pm 0.002$ ,  $n = 82$  for both), respectively. The average C:N ratio of soils in the top 10 cm of the study site was 12.4.

### Vegetation response to soil amendments

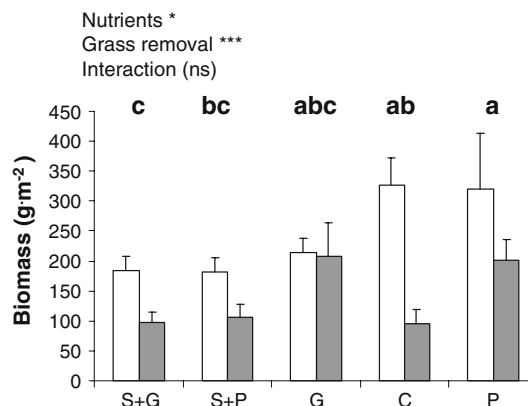
In 2004, total aboveground green biomass (a proxy for aboveground net primary production, ANPP), exclusive of seeded plants, was estimated at 260 g m<sup>-2</sup> for intact vegetation areas and 138 g m<sup>-2</sup> for areas that had been treated with grass herbicide in 2002 (Fig. 3). Grasses constituted 93% of this biomass in untreated plots, and the perennial grasses, while harmed by the herbicide treatment in 2002, were not completely killed and recovered to produce 79% of the unplanted vegetation biomass by 2004 in the treated plots. The nutrient amendments affected this pattern ( $F_{4,22} = 4.51$ ,  $P = 0.01$ ), with the plots receiving sugar (both sugar + gypsum and sugar + P, respectively) showing the lowest biomass of the planted grasses and non-seeded weedy species (SNK test,  $P < 0.05$ ).



**Fig. 2** **a** Average inorganic P concentrations in the top 10 cm of soil of the study plots, 2003–2004, as a function of nutrient amendments. **b** Average soil inorganic N concentrations in the top 10 cm of soil from same samples shown in (a). Symbols for the treatments: sugar + gypsum (S + G), sugar + phosphorus (S + P), gypsum (G), control (C), phosphorus (P). Values are means  $\pm$  one standard error (SE) ( $n = 14$  per treatment). Significantly different values for the treatments are indicated by *different letters* (SNK test,  $P < 0.05$ )

#### Effects of grass removal and soil amendments on the establishment of *C. diffusa* and *R. pinnata*

Based on the May 2004 harvest from all 70 plots containing one or both planted species, the establishment of *C. diffusa* in intact vegetation areas averaged  $0.019 \pm 0.004\%$  (SE), which is substantially higher than  $0.001 \pm 0.0006\%$  establishment observed for *R. pinnata* ( $F_{1,138} = 15.67$ ,  $P < 0.0001$ ; Fig. 4a). While only three *R. pinnata* plants were found in undisturbed plots, and several of the treatment cells (all of those treated with sugar) for *R. pinnata* contained no plants, we believe this analysis is robust despite the lack of variance in cell means (Good 2006). The *R. pinnata* seeds weighed about half that of *C. diffusa*, so even if establishment were to be scored per unit mass, the differences between these two species would remain large. While the establishment of *C. diffusa* appeared to be related to soil nutrient status, treatment means were not significantly different ( $F_{4,59} = 2.10$ ,  $P = 0.09$ ), and no relationship between

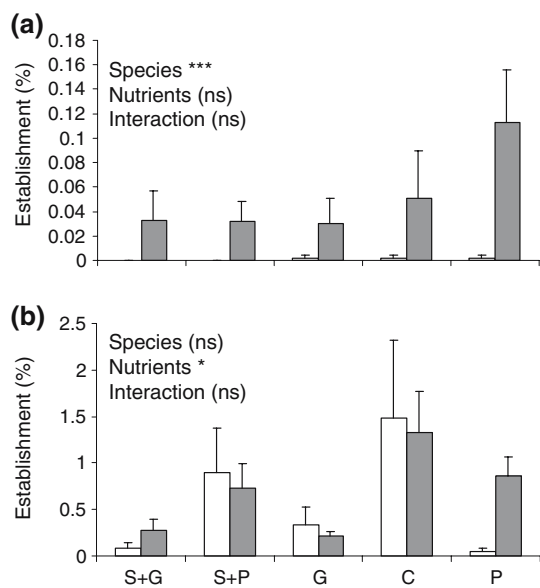


**Fig. 3** Estimates of 2004 vegetation biomass (ANPP), exclusive of planted species, taken from vegetation intact areas (*open bars*) and areas where grasses had been killed or greatly reduced in 2002 (*shaded bars*). The ANOVA indicated a significant nutrient effect ( $*P < 0.05$ ), a grass removal effect ( $***P < 0.01$ ), but no interaction between nutrients and the removal treatment. Effects of vegetation removal on individual nutrient amendments was not tested. Nutrient amendment symbols are those used in Fig. 1. Values are means  $\pm$  SE ( $n = 7$  per treatment). Significant differences among nutrient amendments are indicated by *different letters* (SNK test,  $P < 0.05$ )

*R. pinnata* establishment and soil nutrients was observed ( $F_{4,59} = 0.48$ ,  $P = 0.75$ ).

In the 35 plots where *C. diffusa* and *R. pinnata* were planted together, a paired *t*-test of the difference in establishment of the two species in the intact vegetation areas across all nutrient treatments produced the expected result that *C. diffusa* was more successful than *R. pinnata* (i.e., the difference in percentage seed establishment was significantly different from zero,  $t = 3.06$ ,  $P > 0.004$ ). Results from the grass removal area indicated that there were no differences between species establishment ( $t = 0.45$ ,  $P = 0.65$ ).

The establishment of both species was substantially increased in the grass removal areas (paired *t*-tests of grass removal versus intact areas;  $P < 0.001$  for both species,  $n = 35$ ). Establishment averaged  $0.57 \pm 0.21\%$  ( $n = 35$ ) for *R. pinnata* and  $0.68 \pm 0.12\%$ , ( $n = 35$ ) for *C. diffusa* (Fig. 4b). Establishment was affected by nutrient amendments ( $F_{4,60} = 2.85$ ,  $P = 0.02$ ) with establishment in the control plots higher than that in the sugar + gypsum plots (SNK test,  $P < 0.05$ ). Analysis of the species separately revealed a somewhat different pattern. The *C. diffusa* in the grass removal plots continued to show a response to nutrient amendments ( $F_{4,30} = 3.82$ ,  $P = 0.02$ ), but instead of just a difference between the control and the sugar plus gypsum treatments, the densities of plants in the +P and control treatments were higher than those in the treatments containing sugar + gypsum or gypsum (SNK test,



**Fig. 4** Seed establishment (percentage of seeds that established from the 2001–2002 seed additions) of *R. pinnata* (open bars) and *C. diffusa* (shaded bars). Nutrient amendment symbols are those used in Fig. 1. **a** Results from intact vegetation areas indicate a difference between the species ( $***P < 0.001$ ), with most values for *R. pinnata* at or near zero. No significant responses to nutrients or interaction between nutrients and species were observed. **b** Results from grass removal areas indicated that responses were similar between species and that establishment was affected by nutrient amendments ( $*P < 0.05$ ). In the grass-removal plots, establishment was significantly different from the control (C) treatment and the sugar + gypsum (S + G) plots (SNK test,  $P < 0.05$ ), while all other comparisons were non-significant (ns). Values are means  $\pm$  1 SD ( $n = 14$  per treatment in **a**,  $n = 7$  per treatment in **b**)

$P < 0.05$ ). In contrast, when all data for *R. pinnata* in the 70 grass removal areas were used, this species exhibited no response to nutrient amendments ( $F_{4,65} = 0.50, P = 0.74$ ).

We tested the effect of the presence of *C. diffusa* on the establishment of *R. pinnata* by comparing the establishment of the latter species in vegetation removal or intact areas with and without *C. diffusa*. The overall establishment of *R. pinnata* was 0.36% in

plots seeded alone and 0.31% in plots seeded with *C. diffusa* ( $F_{1,137} = 0.07, P = 0.79$ , results not shown). A correlation analysis also failed to find any relationship between the densities of the two plants in the plots (Pearson’s  $R = 0.09, P = 0.25$ ).

Growth response of *C. diffusa*, *R. pinnata*, and non-seeded weeds to nutrients and grass removal

Comparisons of the total aboveground biomass of *C. diffusa*, *R. pinnata* and non-seeded weedy species harvested from the grass removal and intact portions of the 35 plots seeded with both *C. diffusa*, and *R. pinnata* indicated that the plants responded differently to resource and competition manipulations (Table 1). Weed biomass was the largest in the undisturbed vegetation plots, while *C. diffusa* dominated the biomass of the grass removal areas (Table 1). An ANOVA on the log-transformed biomass values indicated that the weeds were not responsive to either the nutrients or the removal treatment, *R. pinnata* was responsive only to the removal treatment, while *C. diffusa* responded to both treatments (Table 1). A correlation analysis of collections from individual plots found that the total biomass of *C. diffusa* and *R. pinnata* were positively correlated with one another (Pearson’s  $R = 0.33, P = 0.006, n = 70$ ), while the biomass of both of these species was negatively correlated with the biomass of non-seeded plants (Pearson’s  $R = -0.28$  and  $-0.27$  for *C. diffusa*, and *R. pinnata*, respectively;  $P < 0.05$  for both).

Effects of soil nutrient status and grass removal on the numerical and biomass response of *C. diffusa*

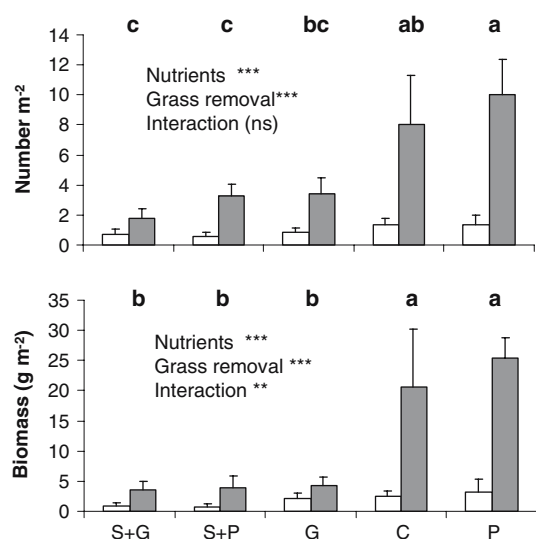
Soil nutrients affected *C. diffusa* densities ( $F_{4,54} = 5.63, P = 0.001$ ; Fig. 5a), but the grass removal impact on plant numbers ( $F_{1,54} = 48.80, P < 0.0001$ ) overshadowed the nutrient effects. Plant densities did not exhibit a significant interaction between grass removal and nutrient treatments ( $F_{4,54} = 2.06, P = 0.10$ ), and

**Table 1** Biomass<sup>a</sup> of *Centaurea diffusa*, *Ratibida pinnata*, and non-seeded weedy species in grass removal and intact vegetation plots subjected to five levels of nutrient manipulations

Species/group	Mass (g m <sup>-2</sup> )		ANOVA <i>F</i> value		
	Intact vegetation	Grass removal	Vegetation ( <i>df</i> = 1)	Nutrients ( <i>df</i> = 4)	Interaction ( <i>df</i> = 4)
<i>C. diffusa</i>	0.86 (0.28)	47.2 (11.7)	59.7***	3.57*	1.29
<i>R. pinnata</i>	0.05 (0.04)	6.7 (3.7)	10.7**	1.93	0.09
Weeds	26.75 (5.5)	18.9 (5.5)	3.1 ( $P = 0.09$ )	1.61	0.55

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

<sup>a</sup> All values are the mean  $\pm$  1 SE;  $n = 14$  per species or group



**Fig. 5** Cumulative density (**a**) and biomass (**b**) of *C. diffusa* plants harvested in late summer 2004 and 2005 in grass removal (shaded bars) and unmanipulated plots (open bars). Nutrient amendment symbols are those used in Fig. 1. Values are means  $\pm$  one SE ( $n = 7$  per treatment). Different letters in **a** indicate significantly different densities in response to nutrient amendments in both the grass-removal and control plots. Different letters shown in **b** indicate significantly different biomass means for nutrient amendments in the grass removal plots (SNK,  $P < 0.05$ ). Differences among the intact vegetation plots were not significant when analyzed separately

they were not significantly different among the gypsum, sugar + gypsum, and sugar + P plots. Plant densities in the control treatment were higher, but equal to those in the gypsum treatment, and densities in the +P plots were significantly higher than all other plots with the exception of the control plots (SNK,  $P < 0.05$ ).

The soil nutrient treatment also had a strong effect on total plant biomass ( $F_{4,50} = 7.59$ ,  $P < 0.0001$ ; Fig. 5b). Similar to the result for plant densities, the grass removal impact on total biomass ( $F_{1,50} = 40.82$ ,  $P < 0.0001$ ) exceeded that of the nutrient effects. Total biomass of *C. diffusa* exhibited an interaction between the vegetation manipulation and the nutrient amendments ( $F_{4,50} = 3.57$ ,  $P = 0.01$ ). The biomass of *C. diffusa* in intact vegetation plots, when analyzed separately, failed to exhibit a biomass response to nutrients ( $F_{4,32} = 1.38$ ,  $P = 0.27$ ), while the response in the grass removal plots remained very large ( $F_{4,32} = 10.05$ ,  $P < 0.0001$ ). Analysis of the total biomass in plots with partial grass removal indicated that the amounts in the +P plots and control plots were significantly greater than those in the other three nutrient treatments (SNK test,  $P < 0.05$ ). Average individual plant biomass in grass-removal plots was more than double that in the control plots ( $F_{1,50} = 22.82$ ,  $P < 0.0001$ ) but it was not affected by the nutrient gradient ( $F_{4,50} = 0.64$ ,  $P = 0.63$ ; results not shown).

## Discussion

Our research site provided a unique platform for assessing the ability of a fixed number of *C. diffusa* seeds to grow and colonize a site under different levels of nutrients and plant competition. If a negative relationship between plot plant diversity and invasibility is assumed (e.g., Levine 2000; Dukes 2002; Kennedy et al. 2002; Zavaleta and Hulvey 2004; Mitchell et al. 2006), this experimental area, with its low diversity, might be viewed as ‘easily invasible’. Further, the fact that this grassland was dominated by grasses – in particular, by warm-season grasses – while *C. diffusa* is a cool-season forb suggests that the biotic resistance to invasion provided by the vegetation on this site might be at most modest compared to other systems dominated with cool-season vegetation (Zavaleta and Hulvey 2004; Pokorney et al. 2005). In general, *C. diffusa* initiates growth in early spring and has initiated flowering stem production before  $C_4$  grasses become active. Conversely, *C. diffusa* attempts to add biomass and continue flowering throughout the summer, which does imply that it may be in competition with the warm-season grasses later in the season. The results from our seeding experiment into intact vegetation indicated that the site did offer substantial resistance to the introduction of both native and non-native species, regardless of the range of soil conditions generated here. However, when establishment was scored on the basis of seeds or seed mass, *C. diffusa* clearly outperformed the four native species used here when seeded into intact vegetation.

The soil organic C and N values observed at this restored site were about 50–60% of the average values reported for a mixed grass prairie located 3–4 km from the present study (LeJeune et al. 2006). While nutrient amounts should not be confused with nutrient availability, the sensitivity of the plants to the nutrient amendments indicated that the productivity of the site was limited by nutrient availability. The apparent stimulation of N fixation in +P plots changed our expectations regarding the nutrient gradient created in this experiment. Nonetheless, based upon findings of Blumenthal et al. (2003), LeJeune et al. (2006), and the measurements summarized here, we are confident that we created treatments particularly low in plant-available N, altered the relative abundance of N, P and potentially other elements in the upper soil horizon using the sugar + gypsum, sugar + P treatments, and increased N and P in the +P-treated plots.

Based on the vegetation response to the amendments (Fig. 2), N limitation was the most probable driving variable behind the pattern of vegetation

production response observed here. The productivity of the extant vegetation was not statistically different among the gypsum, control, and +P plots suggesting that, for the dominant grasses at least, any changes in P availability were not sufficient to affect productivity. The plant-available N reduction brought about by the sugar additions clearly affected the overall vegetation response. In contrast to the general vegetation response, the biomass response of *C. diffusa* did show statistically different values in the gypsum (G) versus control plots (Fig. 5b). Since we did not demonstrate a statistical reduction in average plant-available P in our gypsum plots (Fig. 2), we can only speculate about a mechanism for this effect. However, the results do suggest that *C. diffusa*'s nutrient requirements are not identical to those of the dominant grasses used here.

Plant competition and soil nutrient availability represent only a portion of the myriad of factors influencing seedling survivorship and growth. Our results comparing *C. diffusa* and the native *R. pinnata* are directed at plants seeded in 2001 and 2002 that matured in 2004. The relative patterns of establishment of these plants were opposite to our expectations. The establishment of both species as a percentage of seed input was low, but that of *C. diffusa* was within the range of values reported for weedy plant species (Liebman et al. 2001). Within areas of undisturbed grasses, the native coneflower, *R. pinnata*, had much lower establishment rates compared to the non-native *C. diffusa*; however, this difference disappeared in grass removal areas. Finally, *C. diffusa*, unlike *R. pinnata* and the three other native species that failed to establish, was able to survive under the reduced nutrient regimes generated by sugar amendments. Although these individual species traits should contribute to the success of *C. diffusa*, field observations do indicate that *C. diffusa* has difficulty invading intact grasslands along the Colorado Front Range (Meiman et al. 2006).

Our study showed that the numbers of invading *C. diffusa* had a statistically insignificant effect on the establishment of *R. pinnata*. This result is perhaps not surprising given that our study focused on the establishment phase of the invasion rather than the longer-term trends and that both plant densities and biomass were relatively small. Plots with the largest densities of *C. diffusa* also tended to have the largest non-*C. diffusa* vegetation biomass (Fig. 3). Somewhat more surprising, the biomass of *C. diffusa* and *R. pinnata* obtained from intact vegetation and vegetation removal areas were positively correlated, suggesting that those factors that benefitted the growth of the native species also benefitted that of *C. diffusa*. An inverse relationship between *C. diffusa* biomass and other vegetation

biomass has been documented in studies where *C. diffusa* is dominant (LeJeune et al. 2006). Thus, the relationship we observed during the invasion phase appears to be transient. Dominance, once obtained, may be maintained through high seed production and a growth pattern capable of excluding new colonization by other species found in *C. diffusa*-dominated areas (e.g., Yurkonis and Meiners 2004). Our results, however, do not indicate that *C. diffusa* can obtain dominance immediately from the propagule densities used here, nor does the plant exhibit competitive mechanisms to negatively affect other vegetation during its establishment phase. Only when grass competition was reduced could *C. diffusa* produce more biomass than the unseeded weedy species. Even then, this result was more a function of the dramatic growth of *C. diffusa* in grass-removal areas rather than a significant reduction in non-seeded weedy biomass in those areas (Table 1).

Under the reduced competition generated in the grass-removal experiment, both the densities and size of *C. diffusa* increased substantially, and this combination of resource availability and reduction in competition resulted in greatly enhanced invasibility of these areas. Equally important, since biomass is directly related to the number of seeds produced by this species (LeJeune et al. 2006), the much larger biomass found in the high-nutrient, grass-removal sites are likely able to generate a sufficient seed supply to maintain or enhance the densities of the species. Such sites, in conjunction with seed dispersal via the tumbling of senescent adult plants, likely provide "source habitats" that allow *C. diffusa* to obtain and sustain substantial densities in more resistant intact vegetation "sink habitats". Clearly, the aerial extent of vegetation removal areas does not have to be extreme to have large impacts, as the large differences evident in Fig. 5 resulted from the removal of grass from one third of the area, and grasses subsequently recovered following that removal. In contrast to early successional weeds, however, *C. diffusa* seems to be very capable of replacing itself in such habitats as long as high seed production is maintained, a strategy presumably shared by *R. pinnata*.

Similar to this study, Pokorny et al. (2005) reported a strong inverse relationship between the densities and biomass of *C. maculosa* and competition from other plant species. Their study used seeding rates of 2000 seeds  $m^{-2}$ , similar to the 1650 seeds  $m^{-2}$  used in this study. Their results showed weed densities ranging from near zero on control plots to about 50 plants  $m^{-2}$  on plots from which all vegetation had been removed, which is again similar to our results, obtained using only a partial vegetation reduction. These two species of *Centaurea* are functionally similar and, relevant to

the management of densities of these species, mechanisms that can control of seed inputs in the presence of competing vegetation may be sufficient to regulate the abundance of these species (Seastedt et al. 2005).

Our findings offer a modification to the model proposed by Blumenthal (2005), who suggested that escape from enemies, accompanied by higher nutrient levels caused by atmospheric N deposition or other sources, could explain the success of invasive plant species. In an earlier publication we have reported that escape from enemies – or at least the absence of biological controls – appears to be important in maintaining high densities of *C. diffusa* (Seastedt et al. 2005) and that increased N availability was potentially a mechanism explaining the dominance of *C. diffusa* (LeJeune and Seastedt 2001). The availability of nutrients is clearly important (Fig. 5), but our results emphasize that it is the availability of these nutrients in conjunction with reduced grass competition that results in an explosive growth response of *C. diffusa* (LeJeune et al. 2006 and this study). Thus, this study supports the hypothesis that the success of *Centaurea* species as invaders of grasslands is primarily related to the opportunism exhibited by these species (e.g., Gerlach and Rice 2003) that allow them to maximize growth under those conditions identified by Blumenthal (2005). These traits, perhaps combined with allelopathy and the competitive dominance this trait may confer once populations are established, may work in concert to explain the widespread success of this invader and that of the *Centaurea* group in general. Alternatively, the characteristics reported here, along with an 80-year interval without enemies, may be adequate to explain the patterns of *Centaurea* invasion, establishment, and dominance in western North America.

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