Plant Functional Group Diversity as a Mechanism for Invasion Resistance

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Abstract

A commonly cited mechanism for invasion resistance is more complete resource use by diverse plant assemblages with maximum niche complementarity. We investigated the invasion resistance of several plant functional groups against the nonindigenous forb Spotted knapweed (*Centaurea maculosa*). The study consisted of a factorial combination of seven functional group removals (groups singularly or in combination) and two *C. maculosa* treatments (addition vs. no addition) applied in a randomized complete block design replicated four times at each of two sites. We quantified aboveground plant material nutrient concentration and uptake (concentration × biomass) by indigenous functional groups: grasses, shallow-rooted forbs, deep-rooted forbs, spikemoss, and the nonindigenous invader *C. maculosa*. In 2001, *C. maculosa* density depended upon which functional groups were removed. The highest *C. maculosa* densities occurred where all vegetation or all forbs were removed. *Centaurea maculosa* densities were the lowest in plots where nothing, shallow-rooted forbs, deep-rooted forbs, grasses, or spikemoss were removed. Functional group biomass was also collected and analyzed for nitrogen, phosphorus, potassium, and sulphur. Based on covariate analyses, postremoval indigenous plot biomass did not relate to invasion by *C. maculosa*. Analysis of variance indicated that *C. maculosa* tissue nutrient percentage and net nutrient uptake were most similar to indigenous forb functional groups. Our study suggests that establishing and maintaining a diversity of plant functional groups within the plant community enhances resistance to invasion. Indigenous plants of functionally similar groups as an invader may be particularly important in invasion resistance.

Key words: *Centaurea maculosa*, functional group diversity, grasslands, invasion resistance, nutrient concentration, nutrient uptake, plant functional groups, Spotted knapweed.

Introduction

Ecologists have recognized the importance of diverse plant communities in maintaining vigorous ecosystems (MacArthur & Wilson 1967; Goodman 1975; Pimm 1991). Increased diversity has been positively correlated with increased community productivity and stabilization (Naeem et al. 1994; Tilman et al. 1997; Anderson & Inouye 2001; Tilman et al. 2001) because of more complete use of resources (Tilman 1997; Brown 1998; Levine & D'Antonio 1999; Carpinelli 2001). Increased diversity is also thought to decrease community invasibility, although this point is disputed. Studies have found that increased indigenous species diversity decreases the chance of alien plant invasion (McGrady-Steed et al. 1997; Tilman 1997), whereas others maintain that species-poor communities resist invasion better than species-diverse communities (Robinson et al. 1995; Stohlgren et al. 1999). Disagreement of the effects of species diversity on invasion may be scale dependent (Stohlgren et al. 1999; Prieur-Richard & Lavorel 2000; Davis & Pelsor 2001). Additionally, species may be redundant in function so that species richness alone may be irrelevant to invasion resistance (Lawton & Brown 1993; Diaz & Cabido 2001). The relationship between species diversity, production, and community invasibility needs further investigation so that restoration and land management activities can design and maintain plant communities more resistant to invasion.

Increasing evidence suggests that plant functional group diversity is more important to ecological integrity than plant species diversity (Walker 1992; Power et al. 1996; Sala et al. 1996; Hooper & Vitousek 1997; Tilman et al. 1997; Mack & D'Antonio 1998). We define a functional group as species that share morphological, and perhaps physiological, traits (Lauenroth et al. 1978). Functional groups can provide a link between life history strategies at the plant level and processes at the ecosystem level (Chapin 1993). The greater the functional group diversity, the less the chance for species redundancy in ecosystem functions. This has important implications in managing invasion-resistant grassland communities. For example, researchers have suggested that functionally diverse plant assemblages resist invasion better than less diverse

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assemblages (Elton 1958; Burke & Grime 1996; Levine & D'Antonio 1999). Some experimental evidence also suggests that functionally similar species interact more intensely and resist each other more than nonsimilar species (Dukes 2001), but in some cases, this evidence was weak (Symstad 2000). A better understanding of the functional group diversity and composition that decreases nonindigenous invaders' likelihood of establishment, survival, and dominance in a community is needed to improve management and restoration efforts.

Identifying mechanisms of invasion resistance may improve prevention and management of plant invasions. Emerging theories of invasion resistance are mechanistically linked to nutrient availability. Functionally diverse communities may resist invasion through resource preemption (Davis & Pelsor 2001; Dukes 2001). Niche differentiation is the suggested mechanism for resource depletion (Naeem et al. 1994; Tilman et al. 1996, 1997; Hooper & Vitousek 1997; Hooper 1998), and maximizing niche complementarity has been shown to increase productivity and decrease community invasibility (Tilman et al. 1997; Brown 1998; Carpinelli 2001).

Because a generalized objective for invasive plant management is to establish and maintain invasion-resistant plant communities that meet other land use objectives (Sheley et al. 1996), understanding and identifying functional groups, or combinations of functional groups, that resist invasion through niche complementarity is critical. Research implies indigenous functional groups evolved to fill selected ecological roles because they differ in nutrient accumulation, storage, conservation strategies, and concentration (Parrish & Bazzaz 1976; McJannet et al. 1995; Carrera et al. 2000; Duke & Caldwell 2001; Reich et al. 2001). Indigenous functional groups may be utilizing soil nutrients from separate temporal and spatial niches (Parrish & Bazzaz 1976; Berendse 1979; McKane et al. 1990; Golluscio & Sala 1993), allowing them to coexist. Some studies suggest that indigenous and nonindigenous plants may have similar ecological roles (Johnson 1985; Thompson et al. 1995; Reich et al. 2001), whereas others disagree (Vitousek 1990; LeJeune & Seastedt 2001). The degree of similarity could have profound implications on productivity, invasion risk, and our ability to design or maintain invasion-resistant plant communities.

The overall objectives of this research were to investigate the role of functional groups and functional group diversity in producing biomass and resisting invasion by a nonindigenous species and to quantify net nutrient accumulation of several functional groups. We define plant community resistance to invasion as plant assemblages where, under the same number of introductions and propagule supply, less invasive species persist. Our specific objectives were (1) to test the invasibility of communities that vary in functional group diversity by the nonindigenous invader, Spotted knapweed (*Centaurea maculosa* Lam.); (2) to compare various indigenous functional group's biomass and this contribution toward resisting

invasion; and (3) to quantify the concentration (percent) and net nutrient uptake (concentration × biomass) of nitrogen (N), phosphorus (P), potassium (K), and sulfur (S) in aboveground plant tissue (hereafter referred to as plant tissue or plant material) of the indigenous functional groups: shallow-rooted forbs, deep-rooted forbs, grasses, spikemoss, and a nonindigenous invader, *C. maculosa*.

We hypothesized that removing one or more functional groups would yield less total plot biomass, and *C. maculosa* densities and biomass would increase over that of the unaltered control because more resources would be available for the invader. We also hypothesized that removing forb functional groups would increase *C. maculosa* biomass and density more than removing grasses because indigenous and nonindigenous forbs share morphological traits and, perhaps, physiological traits, and ecological roles. We hypothesized that different indigenous functional groups have different nutrient concentrations and nutrient uptake. Finally, we hypothesized that indigenous and nonindigenous forbs have similar ecological demands and percent concentration and uptake of N, P, K, and S in aboveground plant tissue because they share morphological and, perhaps, physiological traits.

Methods

Study Sites

This study was conducted on two sites within the Idaho fescue/Bluebunch wheatgrass (*Festuca idahoensis/Agropyron spicatum* (*Pseudoroegneria spicata* (Pursh) A. Löve)) habitat type (Mueggler & Stewart 1980). This habitat type lies at the cool-wet end of grassland habitat types. Besides the perennial grasses *F. idahoensis* Elmer and *P. spicata*, predominant forbs include *Artemisia ludoviciana* Nutt., *Balsamorhiza sagittata* Nutt., and *Lupinus* spp. (Mueggler & Stewart 1980). Our sites were near enough (0.25 km) to one another to be considered similar, although they had some community composition differences. Total preremoval treatment biomass, richness, and density for each functional group and the overall plot are presented in Table 1. Tiller and stem density per square meter was greater on site 2 than on site 1, whereas overall biomass did not differ between sites. Site 1 had greater richness of shallow-rooted forbs, grasses, and spikemoss than did site 2. At site 1, grasses, shallow-rooted forbs, and the total species per plot had a greater diversity index than at site 2, indicating that they were more evenly distributed ($p < 0.0001$). Site 2 had a greater biomass and percent cover ($\overline{X}_{s1} = 46$, $\overline{X}_{s2} = 66$, $p < 0.0001$) of spikemoss than site 1 (Pokorny et al. 2004).

Sites were located approximately 70 km west (lat 45°34′N, long 111°34′W) of Bozeman, Montana, on an east-northeast aspect of a 20° slope at 1,624-m elevation. Site 1 soils were a loamy-skeletal, mixed, frigid, active Typic Haplocryolls (Haplo Cryic Mollisol), and site 2 soils were a coarse-loamy, mixed, frigid, active Typic

Table 1. Means and *p* values generated from independent *t* tests for species density, biomass, and richness at two sites west of Bozeman, Montana, U.S.A.

Functional Group	Site	N	Density (stems/m²)	Biomass (g/m²)	Richness (species/m²)
Grass	1	24	187.6	27.3	5.5
	2	24	434.6	29.7	4.0
df			46	40	46
p value			<0.0001	0.303	<0.0001
Deep-rooted forbs	1	32	1.9	47.5	10.8
	2	32	1.9	40.3	12.3
df			62	32	62
p value			0.813	0.266	0.001
Shallow-rooted forbs	1	32	2.6	23.5	26.9
	2	32	3.3	17.2	23.2
df			62	32	62
p value			<0.0001	0.017	<0.0001
Spikemoss	1	8/56[a]	n/a[b]	168	2.6
	2	8/56[a]	n/a	366	2.1
df			n/a	14	110
p value			n/a	0.002	0.009
Overall plot	1	16	22.9	89.1	43.6
	2	16	45.3	74.8	39.4
df			30	30	30
p value			<0.0001	0.053	0.017

[a] Sample size per site for spikemoss was 8 for biomass and 56 for richness.
[b] "n/a" indicates that the measure was not taken for the life-form.

Haplocryolls (Haplo Cryic Mollisol). In 2001, soil samples from two soil-depth increments (0–15 cm and 15–40 cm) were collected from each site to measure total N, nitrate (NO_3-N), ammonium (NH_4-N), S, P, and K using the methods of Olsen et al. (1954), Hamm et al. (1973), Jones (1977), and Westerman (1996). In the 0- to 15-cm depth increment, NO_3-N and S were greater on site 1 than on site 2 (NO_3-N: $\overline{X}_{s1} = 3$ mg/kg, $\overline{X}_{s2} = 2$ mg/kg, $p = 0.01$; S: $\overline{X}_{s1} = 9$ mg/kg, $\overline{X}_{s2} = 7$ mg/kg, $p = 0.05$), whereas P was lower on site 1 ($\overline{X}_{s1} = 4$ mg/kg, $\overline{X}_{s2} = 6$ mg/kg, $p = 0.01$). At the 15- to 40-cm depth increment, NO_3-N was higher on site 1 ($\overline{X}_{s1} = 3$ mg/kg, $\overline{X}_{s2} = 2$ mg/kg, $p = 0.03$) (Pokorny et al. 2004). Annual average precipitation is 41 cm and temperature is 6.5°C.

These sites have been grazed for 50–60 years. Grazing during the past 10 years has been sporadic. In 2000, each site was fenced with a 2-m, eight-strand fence to prevent grazing by livestock and wildlife.

Experimental Design

Species of grass, forbs, and spikemoss were combined into functional groups based on morphology. Forbs were divided into two functional groups based on average rooting depth. Prior to applying treatments, all forbs were excavated and their root structure and rooting depth determined. The distinction between a shallow and a deep

depth was based on a natural break within the roots sampled, which occurred at 15 cm. The nonindigenous species, *Centaurea maculosa*, is a late-season, deep-rooted forb from Eurasia (Jacobs & Sheley 1998) and was considered separate from other indigenous functional groups.

The study was designed as a randomized complete block with four replications at each site. A factorial arrangement of treatments (7 removal treatments × 2 *C. maculosa* treatments) was applied to 2 × 2–m experimental plots. The seven removal treatments included removal of (1) nothing (control); (2) spikemoss; (3) shallow-rooted forbs; (4) deep-rooted forbs; (5) all grasses; (6) all forbs; and (7) all plant material. The two nonindigenous invader treatments were (1) *C. maculosa* absent and (2) *C. maculosa* seeds added.

Functional groups were removed in May 2000 by carefully brushing a 6% glyphosate [*N*-(phosphonomethyl) glycine] solution on foliage of target species, minimizing disturbance to surrounding soil and nontarget plants. Maintenance of treatments was minimal. However, treatments were checked biweekly throughout the 2000 and 2001 growing seasons for nontarget plants, and these nontargets were removed with glyphosate. We chose plant removals over additions because experimental removals can detect interaction strengths (Wootton 1994) and intertaxa competition (Goelz 2001), and because of the time required to establish mature plant communities. Through plant removals and addition of *C. maculosa* seeds, we reduce the possibility that the invader has altered the plant and soil community. Because the invader was present at less than 1% cover prior to the experiment, the invasion reflects the features of the community and not the propagule supply. Alternatively, a disadvantage of removals is the inability to remove belowground biomass and control for nutrient turnover from decomposing roots.

From 19 September 2000 to 31 October 2000, *C. maculosa* treatments were applied biweekly by broadcast seeding 2,000 seeds randomly on one-half of the plots. *Centaurea maculosa* seeds were collected in August 2000 from Plains, Montana (lat 47°28′N, long 114°53′W). Seed germination and viability (AOSA 2000) were 55 and 94%, respectively. Seeding rate totaled 8,000 seeds per plot (2,000 seeds/m²; Sheley et al. 1997; Jacobs & Sheley 1998). After *C. maculosa* established, seed production was prevented by clipping individual flower heads.

Sampling and Data Collection

Centaurea maculosa density was counted in the spring, summer, and fall of 2001 in the entire 2 × 2–m plot. Spring sampling occurred when the majority of the spring ephemeral forbs were blooming (late May), summer sampling coincided with peak standing crop (mid-July), and fall sampling occurred after 95% of the vegetation was senescent (late August). Functional group biomass, except for spikemoss, was collected at the same three sampling periods. Because spikemoss does not recover quickly after

defoliation, its biomass was not collected in a unit area during sampling periods. Instead, 10 g of spikemoss was collected from plots during the three sampling periods, and spikemoss biomass per square meter was averaged during the spikemoss removal treatment. Plots were divided into three subplots, which were randomly assigned to either of the spring, summer, or fall sample periods during 2001. Functional group biomass was collected within three 0.2 × 0.5–m frames randomly located within the subplots. Average spring, summer, and fall postremoval treatment total plot biomass (hereafter referred to as postremoval plot biomass) was calculated by adding weights of individual functional groups per plot. *Centaurea maculosa* biomass was collected only in the fall of 2001 because harvesting during the spring and summer would have affected seedling establishment. Aboveground current year growth was harvested by functional group, dried (40°C, 160 hr), weighed, ground, and analyzed for N, P, K, and S. Plant tissue analysis for S was conducted in spring and fall only. Chemical analyses for N and S were performed using a Leco CNS-2000 dry combustion analyzer (LECO Corporation, St. Joseph, MI, USA). Plant P and K analyses were performed by dry ashing subsamples and using inductively coupled plasma membrane spectroscopy (Jones 1977; Jones & Case 1990). Net nutrient uptake was determined by multiplying biomass of a functional group by its nutrient concentrations.

Data Analysis

Data were analyzed separately for each site. First, analysis of variance (ANOVA) was used to determine effects of removal treatment, season, and a removal treatment by season on *C. maculosa* density after accounting for no blocking effects. Square root transformations were used to meet the homogeneity of variance assumption. The error term included removal treatment by season by block plus block by removal treatment and had 60 degrees of freedom (*df*). Multiple comparisons were achieved using Tukey post hoc tests in SAS (version 8, SAS Institute Inc. 1999; Zar 1999). *Centaurea maculosa* biomass was analyzed using ANOVA. A square root biomass transformation for site 1 and a reciprocal transformation for site 2 were used to meet ANOVA assumptions. Removal treatment and block were main effects. The error term had 18 *df*.

We were concerned that removal treatments may have affected the remaining total indigenous plot biomass and, in turn, invasion success. Therefore, we initially used the postremoval indigenous plot biomass (average plot biomass 1 year after removal treatments were applied and remaining functional groups had time to recover) as a covariate in the above ANOVAs. Postremoval indigenous plot biomass was included in each model as a main effect, or interaction term (removal treatment by biomass, season by biomass, or removal treatment by season by biomass). In no case was postremoval indigenous plot biomass or its interaction significant. Therefore, it was not included in the final ANOVA models.

We also used ANOVA to investigate the recovery rate of the plot's aboveground biomass after removal treatments and this potential impact on invasion success. Postremoval plot biomass of each removal treatment was analyzed using ANOVA. In this analysis, we did not account for remaining spikemoss biomass on plots because of its slow recovery after defoliation. Also, plots where all the plant material was removed had zero indigenous plant biomass and were not included in the analysis because they did not have a normal distribution. Removal treatment, season, and block were all main effects, and removal treatment by season was the interaction term. Tukey's multiple comparisons were calculated in SAS.

ANOVA was used to compare plant nutrient concentrations of N, P, K, and S among all five functional groups: grasses, shallow-rooted forbs, deep-rooted forbs, spikemoss, and *C. maculosa*. Separate ANOVAs were conducted for each nutrient. Functional group and season were main effects, and functional group by season was the interaction term. Indigenous functional group nutrient data were included in the model if the plot had no *C. maculosa* addition. *Centaurea maculosa* plant tissue data were included in the model if grown in a monoculture. The same ANOVA model was used for plant nutrient uptake analysis except the spikemoss group was not included because it was not sampled on a unit area basis. Data were transformed as necessary. Tukey post hoc tests were used to elucidate significant differences.

Results

Centaurea maculosa Density and Biomass

The influence of removal treatments on *Centaurea maculosa* density depended upon the season at both sites ($\overline{X}_{s1} = 20$, $p_{s1} < 0.0001$; $\overline{X}_{s2} = 10$, $p_{s2} = 0.02$). Seasonal variation in *C. maculosa* density followed a bell-shaped curve for most treatments (data not shown). *Centaurea maculosa* density increased from spring to summer on all treatments, except the control on site 1 and where all plant material was removed at both sites. *Centaurea maculosa* seedlings decreased from summer to fall except on plots where all vegetation was removed on site 1 and where all forbs were removed on site 2.

On both sites in the fall, plots with all plant material removed had the highest *C. maculosa* densities (Fig. 1). *Centaurea maculosa* had greater density where all forbs were removed than all other treatments, except where all plant material was removed at both sites. On site 1, the lowest *C. maculosa* densities occurred on plots where nothing, deep-rooted forbs, shallow-rooted forbs, spikemoss, or grasses were removed. On site 2, treatments where nothing, spikemoss, or shallow-rooted forbs were removed had similar *C. maculosa* densities, and plots where deep-rooted forbs or grasses were removed had similar *C. maculosa* densities.
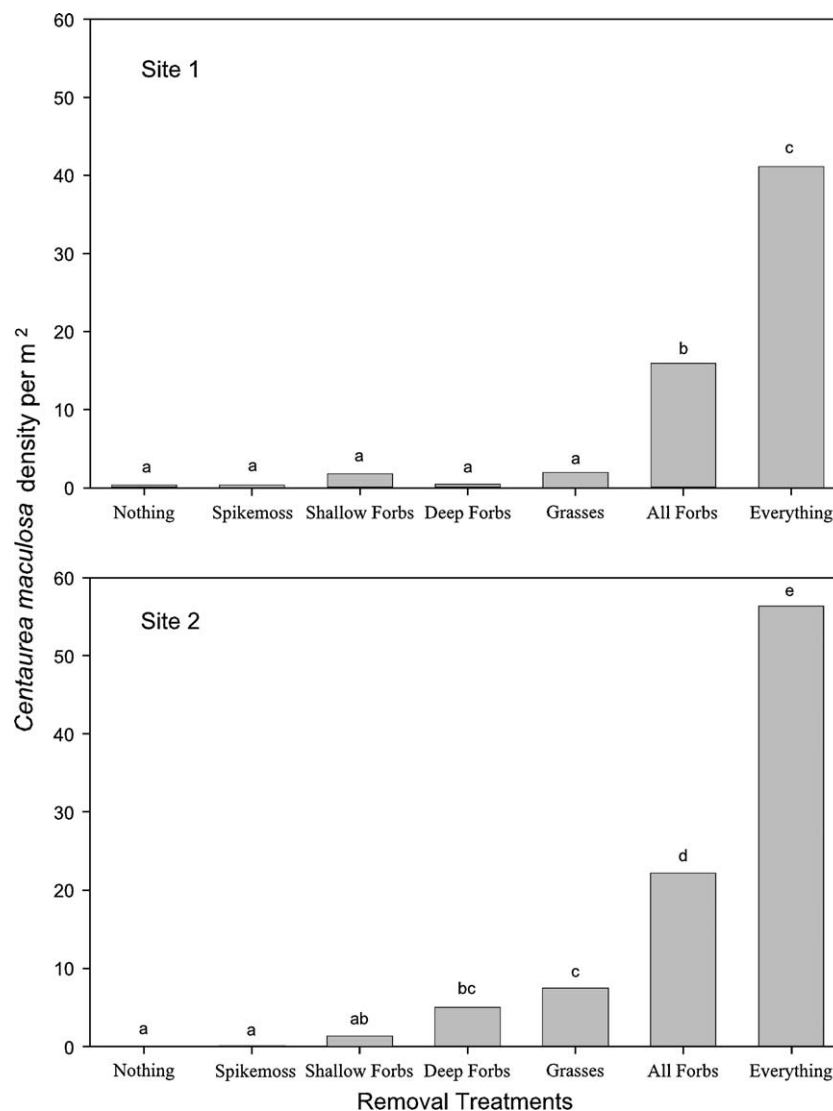
Figure 1. *Centaurea maculosa* densities in plots where functional groups had been removed at two sites, west of Bozeman, Montana, U.S.A. Removal treatments were initiated in spring 2000, and means are from fall 2001. Letters represent density differences among treatments at the alpha less than 0.05 level.

Centaurea maculosa biomass depended on removal treatment at both sites ($\overline{X}_{s1} = 2$, $\overline{X}_{s2} = 0.5$, $p < 0.0001$). Removing all plant material produced the highest *C. maculosa* biomass at both sites (Fig. 2). At site 1, *C. maculosa* biomass was similar among plots where shallow-rooted forbs, grasses, or all forbs were removed. On site 2, removing deep-rooted forbs produced similar *C. maculosa* biomass as removing all forbs. At each sites, all other treatments had a similar *C. maculosa* biomass.

Postremoval plot biomass was affected by removal treatment at both sites ($F_{[s1, 5,18]} = 4.35$, $p_{s1} = 0.009$, $F_{[s2, 5,18]} = 5.28$, $p_{s2} = 0.004$). Postremoval plot biomass did not consistently explain the differences in invasion success because the majority of treatments' postremoval biomass did not differ statistically. On site 1, none of the removal treatments' postremoval plot biomass differed statistically

from the control (Fig. 3). There was no significant difference in postremoval plot biomass between treatments where all forbs were removed and nothing was removed (control), but there was significantly lower postremoval plot biomass where all forbs were removed than on plots where spikemoss or grasses were removed. At site 2, removal treatments' postremoval plot biomass was not statistically different from the control except where all forbs or deep-rooted forbs were removed. Postremoval plot biomass where all forbs, shallow-rooted forbs, or deep-rooted forbs were removed was not significantly different. At both sites, a lower postremoval plot biomass did not consistently coincide with invasion success (Figs. 1 & 2).

To measure postremoval plot biomass after functional group removal treatments, we clipped and weighed aboveground biomass of remaining grasses and forbs because
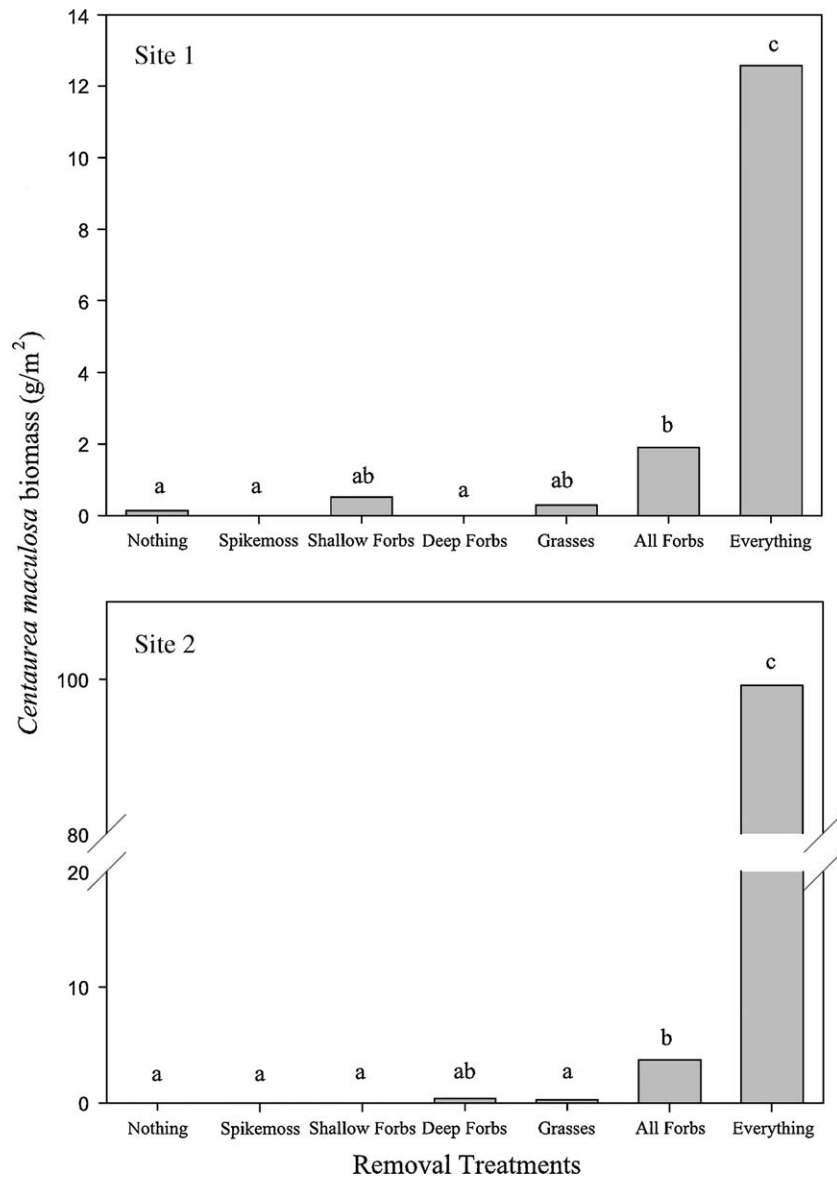
Figure 2. *Centaurea maculosa* biomass in plots where functional groups had been removed at two sites, west of Bozeman, Montana, U.S.A. Removal treatments were initiated in spring 2000, and means are from fall 2001. Letters represent biomass differences among removal treatments at the alpha less than 0.05 level.

they recover relatively quickly from defoliation. Because spikemoss does not recover quickly after defoliation, it was not included in the analysis. We can extrapolate the amount of spikemoss remaining in plots by looking at the amount of spikemoss biomass removed from those treatment plots (Table 1). If we included spikemoss remaining on plots in the analysis, it would add an average of 168 and 366 g/m², sites 1 and 2, respectively, to all treatments in Figure 3 except the treatment where spikemoss was removed.

The spikemoss removal treatments had the second greatest amount of aboveground biomass removed; the only plots with less postremoval plot biomass were where all plant material was removed. Even so, *C. maculosa*

density and biomass in spikemoss removal plots were similar to the control on both sites, suggesting no direct link between amount of biomass removed and invasion success.

Ecological Role of Indigenous Functional Groups and *Centaurea maculosa*

Aboveground Plant Tissue Concentration. Aboveground plant tissue concentration of N, P, K, and S depended on the interaction of functional group and season on both sites ($F_{[N, 6,218]} = 46.5$, $F_{[P, 6,218]} = 28.2$, $F_{[K, 6,218]} = 10.9$, $F_{[S, 3,147]} = 18.6$; all nutrients $p < 0.0001$). Most functional groups decreased in nutrient concentrations from the spring to the fall.
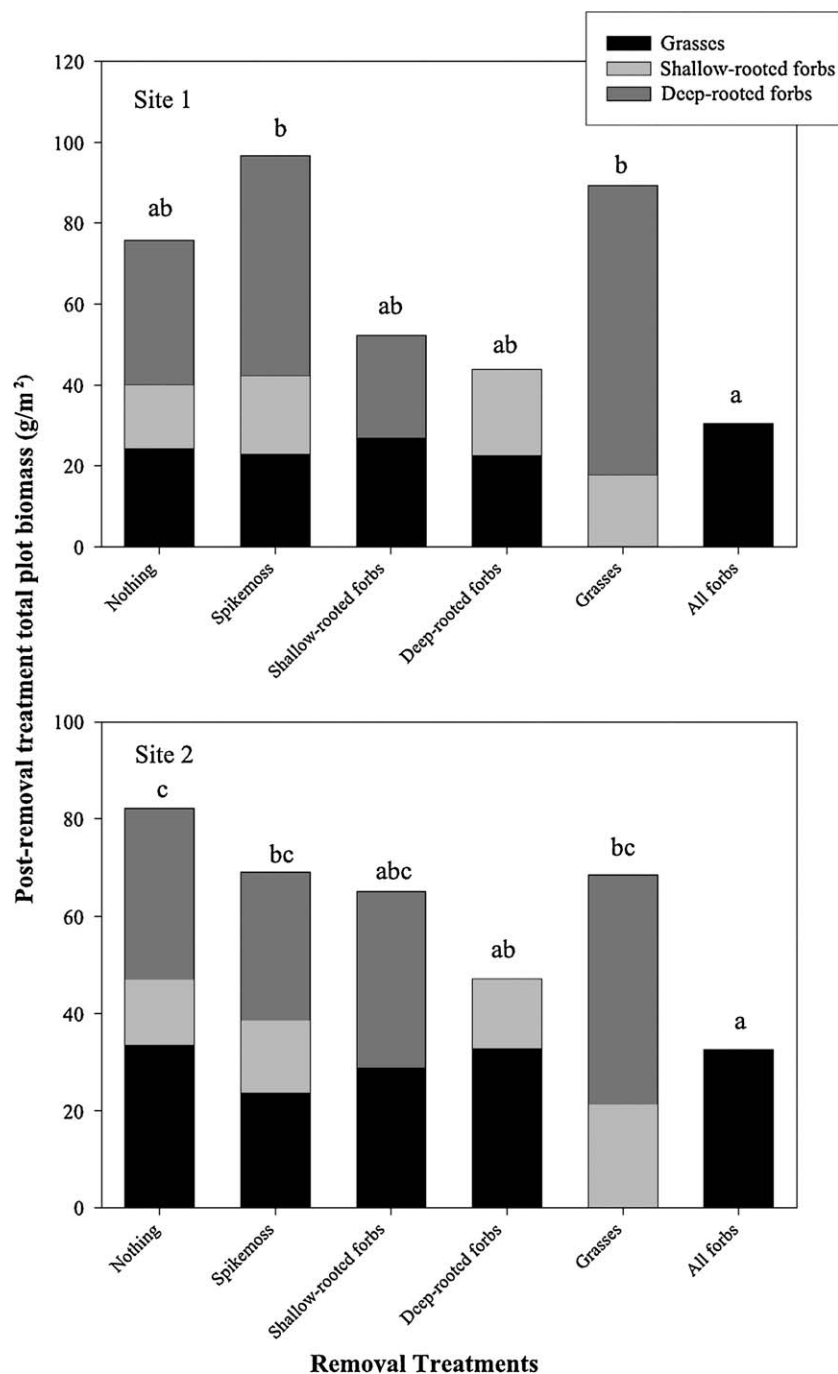
Figure 3. Postremoval treatment total plot biomass of indigenous species per removal treatment at two sites west of Bozeman, Montana, U.S.A. Removal treatments were initiated in spring 2000, and means represent the 2001 seasonal average. *Centaurea maculosa* was seeded in removal treatments during fall 2000. Letters represent significant differences within a site at the 0.05 level. We do not account for spikemoss biomass in each removal treatment. Spikemoss removal treatment averaged 168 and 366 g/m^2 removed for sites 1 and 2, respectively. Spikemoss biomass on other plots was not altered.

Shallow-rooted forbs and deep-rooted forbs had a high percent N, which differed from that of spikemoss and grasses on both sites in the spring and summer (Table 2). In the fall, N concentration was greater in *C. maculosa* than in any functional group at site 1. Percent N was lower in grasses than in other groups, except deep-rooted forbs on site 2 in the fall.

In the spring, shallow- and deep-rooted forbs had a higher P concentration than the grass and spikemoss groups at site 1 (Table 2). Shallow-rooted forbs had the

Table 2. Variations in mean plant tissue nutrient concentrations among functional groups.

| | | | Tissue Nutrient Concentration (%) | | | | | | | | | | | |
| | | | Nitrogen | | | Phosphorus | | | Potassium[a] | | | Sulfur[b] | |
Site	Functional Group	N	Spring	Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall	Spring	Fall
1	Spikemoss	60	1.57a	1.59ab	1.66c	0.14a	0.09a	0.10c	0.27a	0.27a	0.46a	0.14a	0.14bc
	Shallow forbs	48	2.15b	1.76bc	1.11b	0.22b	0.14b	0.09bc	2.18c	2.05c	1.42c	0.30b	0.13bc
	Deep forbs	48	2.96c	1.91c	0.89ab	0.28c	0.10a	0.07ab	2.91c	2.04c	1.18c	0.26b	0.12b
	Grass	60	1.75a	1.45a	0.82a	0.16a	0.10a	0.06a	1.23b	1.01b	0.73b	0.15a	0.10a
	Centaurea maculosa	4	n/a	n/a	2.14d	n/a	n/a	0.13c	n/a	n/a	1.39bc	n/a	0.18c
2	Spikemoss	60	1.46a	1.53a	1.59d	0.10a	0.09a	0.10c	0.40a	0.34a	0.34a	0.13a	0.14c
	Shallow forbs	48	2.30b	1.91b	1.21bc	0.19b	0.14c	0.09bc	2.22c	1.95c	1.52c	0.32b	0.14c
	Deep forbs	48	2.81c	1.94b	0.98ab	0.21b	0.11b	0.08ab	2.23c	1.75c	1.20c	0.25b	0.12b
	Grass	60	1.58a	1.52a	0.92a	0.11a	0.10ab	0.06a	1.16b	1.00b	0.60b	0.12a	0.08a
	Centaurea maculosa	4	n/a	n/a	1.56cd	n/a	n/a	0.10bc	n/a	n/a	1.74c	n/a	0.13bc

For each functional group, the seasonal nutrient value is averaged over all removal treatments where the functional group was present. Plant biomass was collected in 2001. Values in each column, within a site, which do not share the same letter are significantly different ($\alpha < 0.05$, ANOVA followed by Tukey post hoc test).
[a] Test results represent the natural log transformation for site 1 and the reciprocal transformation for site 2. Nontransformed means are presented.
[b] Test results for the column represent the square root transformation. Nontransformed means are presented.

highest summer value of percent P, which differed from that of all other groups on both sites. In the fall, *C. maculosa* percent P was similar to that of shallow-rooted forbs and spikemoss on both sites, and deep-rooted forbs on site 2.

Percent K in grasses differed from all other groups in each season, except for *C. maculosa* in the fall (Table 2). Percent K for shallow- and deep-rooted forbs was similar during all seasons. In the fall, percent K in *C. maculosa* was similar to that in shallow- and deep-rooted forbs on both sites, and grasses on site 2.

On both sites, percent S in shallow- and deep-rooted forbs was similar and differed from that in the spikemoss and grass functional groups (Table 2). Grasses had the lowest percent S in the fall. *Centaurea maculosa* had a similar percent S as spikemoss and shallow-rooted forbs on both sites and deep-rooted forbs on site 2.

Aboveground Plant Nutrient Uptake. Aboveground plant nutrient uptake depended on functional group and season

main effects for N at both sites, K and S at site 1, and P at site 2 ($F_{[N, 3,159]} = 11.5$, $F_{[K, 3,159]} = 22.6$, $F_{[S, 2,108]} = 18.6$; for all nutrients $p < 0.0001$). We focus on the functional group results. In general, the grass and shallow-rooted forb functional groups had consistently lower nutrient uptake compared to other functional groups at both sites (Table 3). Total N, P, and S uptake by deep-rooted forbs was greater than that by all other groups on site 1 and greater than that by the shallow-rooted forb and grass groups on site 2. On site 2, *C. maculosa* had the greatest N and P uptake.

Net nutrient uptake was affected by the interaction of functional group and season for P on site 1, and K and S on site 2 ($F_{[P, 4,159]} = 3.3$, $p_P = 0.014$; $F_{[K, 4,159]} = 3.1$, $p_K = 0.017$; $F_{[S, 2,108]} = 3.3$, $p_S = 0.04$). In general, shallow-rooted forbs and grass had low nutrient uptake compared to other functional groups (Table 4). In the fall, although *C. maculosa* and deep-rooted forbs had higher K and S uptake than the other groups, the nutrient uptake did not differ between these groups.

Table 3. Significant differences in plant net nutrient uptake among functional groups.

| | | Plant Net Nutrient Uptake (mg/m^2) | | | | |
| | | Site 1 | | | Site 2 | |
Functional Group	N[a]	Nitrogen[b]	Potassium[c]	Sulfur[b]	Nitrogen[b]	Phosphorus[b]
Shallow forbs	48	434a	492b	47a	315a	25a
Deep forbs	48	787b	1,000c	73b	659b	47b
Grass	60	352a	258a	31a	381a	26a
Centaurea maculosa	4	242a	186a	22a	1,468c	91c

A functional group's uptake values are the mean of spring, summer, and fall 2001 data. Values in each column that do not share the same letter are significantly different ($\alpha < 0.05$, ANOVA followed by Tukey post hoc test).
[a] The N for sulfur in grass: 40, shallow- and deep-rooted forbs: 32, and *C. maculosa*: 4 due to spring and fall samples only.
[b] Test results for the column represent the square root transformation. Nontransformed means are presented.
[c] Test results for the column represent the natural log transformation. Nontransformed means are presented.

Table 4. Significant results for plant net nutrient uptake for functional group by season interaction.

| | | Plant Net Nutrient Uptake (mg/m^2) | | | | | | | |
| | | Phosphorus[a] | | | Potassium[b] | | | Sulfur[a] | |
Functional Group	N	Spring	Summer	Fall	Spring	Summer	Fall	Spring	Fall
Shallow forbs	48	32a	47a	41a	276a	363a	376a	38a	34a
Deep forbs	48	98b	52a	43a	483a	761b	912b	45a	76b
Grass	60	23a	30a	22a	255a	296a	217a	27a	31a
Centaurea maculosa	4	n/a	n/a	17a	n/a	n/a	1653b	n/a	122b

Values in each column that do not share the same letter are significantly different ($p < 0.05$, ANOVA followed by Tukey post hoc test). P results are for site 1. K and S results are for site 2. For each functional group, the seasonal nutrient value is averaged over all removal treatments where the functional group was present.
[a] Test results for column represent the square root transformation. Nontransformed means are presented.
[b] Test results for column represent the natural log transformation. Nontransformed means are presented.

Discussion

Centaurea maculosa Density and Biomass

Our results are consistent with a growing body of evidence suggesting that increased functional diversity decreases invasion possibly through the preemption of available resources (Tilman et al. 1996; Sheley et al. 1998; Davis & Pelsor 2001; Dukes 2001). Work by Stohlgren et al. (1999) and Robinson et al. (1995) found that species-poor communities tend to support lower levels of nonindigenous species than do species-rich communities. Both studies focused on species diversity rather than on functional diversity. We focused on functional group diversity because it accounts for redundancy in ecosystem function among species and may be a better test for measuring invasion resistance. In our study, *Centaurea maculosa* density and biomass were higher at lower levels of functional group diversity on both sites. Similarly, in grassland community microcosms, Dukes (2001) found that high functional diversity decreased an invader's success by decreasing resource availability, and in a tallgrass prairie ecosystem, Symstad (2000) found a negative relationship between functional group richness and invasion success.

Since total biomass production is intimately related to functional group representation (Anderson & Inouye 2001; Tilman et al. 2001) because greater functional group richness can increase overall resource use (Tilman 1997; Brown 1998; Levine & D'Antonio 1999; Carpinelli 2001), it was reasonable to hypothesize that removing one or two functional groups contributing a large portion of the communities' biomass would decrease total indigenous plot biomass and affect community stability (Tilman et al. 1996, 1997; Hooper & Vitousek 1997). It was surprising that based on covariate analyses, a treatment's postremoval indigenous plot biomass and *C. maculosa* density and biomass were unrelated. Based on ANOVA of the postremoval plot biomass, functional groups remaining in a plot were able to recover and/or expand in the plot, except for where spikemoss and, of course, all plant material was removed.

We were not able to completely differentiate between biomass versus functional group as a mechanism for invasion because of their coupled relationship. On the one hand, removing all forbs had low postremoval plot biomass and high *C. maculosa* density and biomass. But, at site 1, the postremoval plot biomass on plots where all forbs were removed was not significantly different from that of the control (Fig. 3). On the other hand, treatments with lower postremoval plot biomass did not correspond to plots having a greater *C. maculosa* biomass and/or density on site 2 (Figs. 1–3). For example, site 2 deep-rooted forb removal decreased postremoval plot biomass relative to the control but still allowed less *C. maculosa* establishment than that of the all-forbs removed treatment.

If only biomass removal influenced invasion success, we would expect plots with the greatest biomass removed to consistently have greater invasion success. Plots with spikemoss removed had the greatest amount of biomass removed, except where all plant material was removed. Spikemoss removal plots did not recover from the spikemoss biomass removed, yet had a *C. maculosa* density and biomass similar to the control on both sites, suggesting no direct link between amount of biomass removed and invasion success. Our overall assessment was that *C. maculosa* establishment and persistence were mainly associated with restructuring functional group diversity and/or composition through functional group removal.

Our data supported the hypothesis that indigenous forbs resist invasion by *C. maculosa* better than grasses because the absence of functionally similar groups was related to the higher *C. maculosa* densities and biomass. These results suggest that the degree of functional diversity may not be as important in *C. maculosa* invasion as the composition of functional groups in the community (Diaz & Cabido 2001; Tilman et al. 2001) because competition may be more intense within functionally similar groups (Lavorel et al. 1999). Although biomass production may play a role, our data suggest that the dominant mechanism for invasion resistance by morphologically similar indigenous and nonindigenous forbs is that they share physiological traits and ecosystem function (Johnson 1985; Smith et al. 1998). The presence of indigenous forbs may increase the intensity of interspecific resource competition with a nonindigenous invader and may inhibit their recruitment success (Brown 1998; Symstad 2000; Carpinelli

2001; Dukes 2001). On site 1, removing nothing, spikemoss, shallow-rooted forbs, deep-rooted forbs, or grasses singularly resulted in low *C. maculosa* densities and biomass. Limited *C. maculosa* establishment into these treatments may be a response of functional groups present that share close traits with the invader. *Centaurea maculosa* density and biomass increased when all forbs were removed from either site. Removing all forbs may have opened complementary niches that may have allowed greater resource acquisition by *C. maculosa* (Hooper & Vitousek 1997) and a higher likelihood of establishment in the grass/spikemoss communities. Therefore, functional group composition is important because a plant community missing an important functional group may have a greater susceptibility of invasion.

Ecological Role of Indigenous Functional Groups and *Centaurea maculosa*

Our plant nutrient results support the hypothesis that indigenous functional groups have different ecological roles because groups differed in N, P, K, and S concentrations and net nutrient uptake (Parrish & Bazzaz 1976; McJannet et al. 1995; Carrera et al. 2000; Duke & Caldwell 2001; Reich et al. 2001). Even functional groups within the same soil strata had different nutrient concentrations. This may indicate that groups have different physiological demands from life history traits, ecological roles, and/or may be acquiring resources differently. Of all the functional groups, shallow- and deep-rooted forbs had the most overlap, which may reflect physiological demands of morphologically similar plants (Chapin 1993; Lambers et al. 1998). Grasses exhibited only partial overlap in resource capture with the other groups and appear to have a unique ecological role.

Centaurea maculosa nutrient concentration for each nutrient examined was similar to at least one of the functional groups, except for N at site 1. However, nutrient concentration of *C. maculosa* tissue was usually similar to that of shallow-rooted forbs. Therefore, our data support the hypothesis that indigenous and nonindigenous forbs have similar ecological demands (Johnson 1985; Thompson et al. 1995; Reich et al. 2001). It could be possible that the presence of one excludes the other through resource preemption (Tilman et al. 1996; Davis and Pelsor 2001; Dukes 2001), but to verify this interpretation, more needs to be known about the location and timing of resource uptake in these groups and the limiting resources for *C. maculosa* establishment and growth. Plant nutrient uptake data also support our hypothesis because *C. maculosa* and indigenous deep-rooted forbs had similar values for nutrient uptake. These two groups had the greatest aboveground biomass of any functional group, and a higher resource acquisition may have been required to meet demands for growth and reproduction (Tilman et al. 1999).

There was a degree of overlap in *C. maculosa* nutrient concentration with other groups, suggesting indigenous and nonindigenous functional groups have similar ecological roles, or that functional groups do not have complete niche differentiation (Bengtsson et al. 1994). It could also be a result of increased nutrient pools due to the decomposition of removed-species roots. The nutrient concentrations provide some evidence that *C. maculosa* may have broad overlap in resource capture with other functional groups (Hoopes & Hall 2002). Plants may avoid competition through niche differentiation (Bengtsson et al. 1994), but all plants have similar resource demands and may draw resources from similar nutrient pools in soil strata, which may lead to overlap in nutrient consumption.

This study provides some evidence for the theory that maximizing niche complementarity decreases invasion, possibly through preemptive use of resources. Diverse grassland communities may be more stable if a separation of resource use reduces the intensity of competition among indigenous plants (Berendse 1979; Fowler 1986, 1990). Thus, preemption of resources by an indigenous group may exclude recruitment of a functionally similar nonindigenous group and may be the mechanism of invasion resistance.

Our study has important management implications for establishing, maintaining, and restoring invasion-resistant plant communities. Grasslands high in functional group diversity, particularly the forb functional group, are important for resisting invasion by nonindigenous forbs. The role of various indigenous functional groups, particularly forbs, needs to be carefully considered in grassland management. Maintaining functional group diversity should be a primary objective of land managers because increased functional group diversity could be related to increased productivity and stability and decreased invasibility through niche differentiation and possibly though resource acquisition. Indigenous forb functional groups may use resources similarly to *C. maculosa* and were a critical component in invasion resistance. The goal of invasive plant management must be to maintain and/or restore these important functional groups.

Diversity can be maintained or restored during management practices. For example, intermediate levels of disturbance, proposed to maintain high levels of diversity, can be obtained by regulating grazing and burning timing and intensity. Diversity can also be maintained through careful planning of herbicide applications. When using herbicides, we recommend carefully calibrating herbicide rates to minimize effects on off-target plants, applying herbicides when the majority of desired vegetation are senescent, spot spraying to maintain diversity where individual weedy plants exist, and reseeding competitive grasses and forbs after herbicide application.

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