

A TEST OF THE EFFECTS OF FUNCTIONAL GROUP RICHNESS AND COMPOSITION ON GRASSLAND INVASIBILITY

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Abstract. Although many theoretical and observational studies suggest that diverse systems are more resistant to invasion by novel species than are less diverse systems, experimental data are uncommon. In this experiment, I manipulated the functional group richness and composition of a grassland community to test two related hypotheses: (1) Diversity and invasion resistance are positively related through diversity's effects on the resources necessary for invading plants' growth. (2) Plant communities resist invasion by species in functional groups already present in the community. To test these hypotheses, I removed plant functional groups (forbs, C₃ graminoids, and C₄ graminoids) from existing grassland vegetation to create communities that contained all possible combinations of one, two, or three functional groups. After three years of growth, I added seeds of 16 different native prairie species (legumes, nonleguminous forbs, C₃ graminoids, and C₄ graminoids) to a 1 × 1 m portion of each 4 × 8 m plot. Overall invasion success was negatively related to resident functional group richness, but there was only weak evidence that resident species repelled functionally similar invaders. A weak effect of functional group richness on some resources did not explain the significant diversity–invasibility relationship. Other factors, particularly the different responses of resident functional groups to the initial disturbance of the experimental manipulation, seem to have been more important to community invasibility.

Key words: *Cedar Creek Natural History Area, Minnesota, USA; community assembly; community composition; disturbance; diversity; ecosystem properties; grassland; invasion; plant functional groups.*

INTRODUCTION

The long-distance dispersal of species via human activities is a major component of global change (Vitousek 1994) and can profoundly affect populations, communities, and ecosystems (Mooney and Drake 1986, Drake et al. 1989, D'Antonio and Vitousek 1992, Vitousek et al. 1997). As a result, considerable work has been done to understand the properties of species that determine their invasive potential (e.g., Newsome and Noble 1986, Rejmánek and Richardson 1996, Reichard and Hamilton 1997) and the properties of communities that determine their resistance to invasion (e.g., Elton 1958, Robinson and Dickerson 1984, Fox and Fox 1986, Robinson et al. 1995, Tilman 1997). Much of this work has been based on computer modeling (Case 1990, 1991), correlational analyses (e.g., MacDonald and Frame 1988, Planty-Tabacchi et al. 1996, Wisser et al. 1998), or microcosm studies (Robinson and Dickerson 1984, McGrady-Steed et al. 1997). Studies investigating community assembly rules (sensu Diamond 1975; e.g., Drake et al. 1993, Wilson and Roxburgh 1994, Law and Morton 1996) have also con-

tributed to the debate about which, if any, traits characterize the relationships between invulnerable communities and the species that invade them. Direct, experimental tests of hypotheses concerning such traits are necessary to resolve this debate.

One commonly cited characteristic of invulnerable communities is that they have a low diversity of resident species (Elton 1958, Lodge 1993). Various causes of the relationships between diversity and invasibility have been suggested but not experimentally tested. Elton (1958) suggested that greater community diversity caused greater invasion resistance and explained it through the concept of "ecological resistance," particularly for plant communities. According to this concept, competition for the resources required by all plants is greater in diverse plant communities compared to communities with fewer species. This more intense competition for resources tends to prevent newly introduced species from becoming established in the species-rich communities.

The mechanisms for this hypothetical competitive resistance have only recently been explored in experiments (Naeem et al. 1994, 1995; Tilman et al. 1996, 1997a; Hooper and Vitousek 1997, Hooper 1998) and theory (Tilman et al. 1997b, Loreau 1998) investigating the relationship between biodiversity and ecosystem functioning. Recent experiments have shown negative

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relationships between plant species or functional group richness and resource availability (Naeem et al. 1994, 1995; Tilman et al. 1996, 1997a; Hooper and Vitousek 1997, Hooper 1998). One hypothesized mechanism for these relationships is that diverse communities have a greater variety of methods for capturing resources than do simple communities (Naeem et al. 1994, Tilman et al. 1997b). Another possible mechanism for the negative correlation between diversity and resource availability is that the probability of having the most highly competitive species for a given resource increases as community diversity increases (Tilman et al. 1997b). In this case, the composition of a community is important because of the influence of individual species on resources (Tilman 1982, Wedin and Tilman 1990, Naeem et al. 1996, Symstad et al. 1998). Extending either of these hypotheses into invasion theory suggests that greater resident diversity confers resistance to invasion due to lower resource availability for an invading species. Resource availability within a given ecosystem, however, is affected by factors other than plant diversity. Disturbance in particular can temporarily un-hinge the relationship between resident plant species and ecosystem properties, thus potentially weakening the relationship between community diversity and invasibility.

Associated with the diversity–invasion hypothesis is another commonly cited characteristic of invulnerable communities; they lack species that are ecologically similar to the invader (Mooney and Drake 1989, Lodge 1993). This notion of niche limitation is a central tenet of community assembly theory (e.g., Wilson 1995 and references therein) and is related to Elton's "ecological resistance," in that if two species' ecological characteristics are too similar, one may competitively exclude the other (Case 1990, 1991, Pacala and Tilman 1994). Even if the invader is the superior competitor, the resident community may "repel" the invader because of the priority effect that established residents have over invaders (Case 1990, 1991). Because functional definitions of plants (sensu Vitousek and Hooper 1993) are often based on similarities in the manner in which species use and compete for resources, the invasion resistance of a plant community may depend on the functional group composition of the community and the functional type of the potential invader.

In this paper, I report on an experimental test of the effects of two aspects of plant functional group diversity, the number of functional groups (richness) and the types of functional groups (composition), on the invasibility of a grassland. I also examine the possibility of "ecological resistance" as the mechanism through which diversity affects invasion resistance. Specifically, I asked three questions: (1) Are communities with more functional groups more resistant to invasion? (2) If functionally diverse communities are more resistant to invasion than simple communities, does variation in ecosystem functioning account for

this relationship? (3) Do species more readily invade communities that lack species similar to them? I addressed these questions by experimentally manipulating plant functional group richness and composition in a series of plots for three years, after which I added a mixture of species to them as seed and measured their success for the following two growing seasons. For brevity, the species added as seed will henceforth be referred to as "invaders."

METHODS

Field site

This experiment was conducted at Cedar Creek Natural History Area, which lies on a glacial outwash sand plain in east-central Minnesota. The soils are nutrient poor and nitrogen limited (Tilman 1987). The experimental plots were in an old field last cultivated in 1934 and now dominated by the prairie species *Schizachyrium scoparium* (25% of plant cover), *Ambrosia psilostachya* (15%), *Poa pratensis* (12%), *Helianthus pauciflorus* (7%), *Solidago nemoralis* (7%), and *Artemisia ludoviciana* (5%). (Nomenclature follows Gleason and Cronquist [1991].) Although the research site was an old field, previous work has shown that the vegetation at this site is fairly stable and nonsuccessional (Tilman 1987).

Experimental design

The three functional groups defined for this experiment, C₃ graminoids (including grasses and sedges), C₄ graminoids (including grasses and sedges), and forbs, comprised >99.9% of the biomass in the experimental field. Legumes were not distinguished as a separate group because they were uncommon (<1% of plant cover). I classified the species into functional groups based on their phenology and morphology, assuming that these characteristics are also related to temporal and spatial patterns in nutrient use. C₃ graminoids, mainly *Poa pratensis*, *Panicum oligosanthos*, and *Elytrigia repens*, grow primarily during the cool part of the growing season (spring thaw to mid-June, and September to snow cover), set seed by early summer, and tend to be shallow rooted. C₄ graminoids, mainly *Schizachyrium scoparium* and *Sorghastrum nutans*, are warm-season plants, generally growing from June through August and setting seed in August and September. Although all forbs in this experiment have the C₃ photosynthetic pathway, they tend to differ from the graminoids in their growth form, rooting depth, and allocation to seed.

During the summer of 1993, nine treatments were applied in a completely randomized fashion to 4 × 8 m plots. The treatments consisted of all possible combinations of zero, one, or two plant functional groups removed at a time, plus two extra control treatments in which 25% and 55% of the biomass was removed. These extra controls were included in order to separate

the potential effects of biomass removal from the effects of functional group composition. Each treatment had four replicates except for the totally unmanipulated plots, which had six, yielding a total of 38 plots. Initially (1993), biomass was "removed," or killed, by hand-painting a nonselective herbicide (Roundup, Monsanto Company, St. Louis, Missouri) on leaves of individual plants to kill only C₃ or only C₄ graminoids or to kill biomass in random spatial patterns, or by spraying the appropriate selective herbicide (Amine 4, Platte Chemical Company, Fremont, Nebraska, to remove forbs; Poast Plus, BASF Corporation, Research Triangle Park, North Carolina, to remove all graminoids). After limited herbicide use in early 1994, all treatments were maintained by hand weeding from elevated, movable walkways, to avoid any possible herbicide or trampling effects.

All plots were burned in early May 1994 and late April 1996. Although spring burning is part of a normal maintenance regime for *Schizachyrium*-dominated grassland, both burns had a specific purpose. The experimental field was burned in 1994 in order to remove the aboveground tissues of plants killed by herbicides during the previous growing season and therefore reduce their impact on ecosystem processes such as nitrogen cycling. The 1996 burn was performed to reduce thatch levels, and hopefully improve germination rates of experimentally added seeds above the low levels expected in an unburned field.

After the treatments had been established for three field seasons and the desired levels of functional composition and richness had been reached, seeds of potential invaders were added to previously established, permanent 1 × 1 m subplots within each plot. I had surveyed these subplots annually, via cover estimates, since 1994. Seeds of 16 species of native prairie plants, four each in four functional groups, were added on 8 May 1996. The functional groups and species added were: C₃ graminoids, *Elymus canadensis*, *Koeleria pyramidata*, *Stipa comata*, and *Stipa spartea*; C₄ graminoids, *Andropogon gerardii*, *Bouteloua gracilis*, *Panicum virgatum*, and *Sporobolus cryptandrus*; legumes, *Baptisia lactea*, *Dalea purpureum*, *Lupinus perennis*, and *Vicia villosa*; and nonleguminous forbs, *Asclepias tuberosa*, *Coreopsis palmata*, *Echinacea purpurea*, and *Liatris aspera*.

These species were chosen for several reasons. First, logistical constraints of performing an experiment in a field with other active, ecological experiments prevented the use of non-native, aggressive species more typically thought of as invaders. Instead, I used species that occurred in the near vicinity, either in the same old field as the experimental plots, in other old fields, or in undisturbed, native vegetation at Cedar Creek Natural History Area (Tilman 1997; A. Symstad, *personal observation*). The species chosen were rare or nonexistent in the experimental plots and had never been recorded in the permanent survey subplots. This

local rarity was most likely due to seed source limitations (Tilman 1997), as the location of the experiment was in a small (4-ha) grassland surrounded by forest and wetland. Thus, natural recruitment within the time frame of the study was unlikely to occur. In addition to occurring in the region, these species had successfully established in other experiments in the same sandy-soiled ecosystem (Tilman et al. 1996, 1997a, Tilman 1997) and were therefore adapted to the local environment.

Equal mass (1.8 g) of each species, adjusted for inert matter, based on data provided by the commercial seed sources (Prairie Restorations, Incorporated, Princeton, Minnesota and Prairie Moon Nursery, Winona, Minnesota) was added to each plot. I used this method, as opposed to using equal numbers of seeds, because germination rates of the individual species were not available. I assumed, based on a general trend for seed mass and viability to be positively correlated (e.g., Eriksson 1997), that adding equal masses of species would result in approximately equal numbers of viable seed per plot.

Measurements of invasion success and community and ecosystem properties

I measured invasion success in late August 1997 by counting the number of individual invader plants and estimating the total, vertically projected cover of each of the invader species in the 1-m² subplots. In addition, I estimated the cover of all plant species, bare ground, and litter (summed to 100 %) in the same subplots.

On 23 August 1996, transmittance of light through the canopy was measured with a Decagon 2000 Sunflecks Ceptometer (Decagon, Pullman, Washington). Percent transmittance was calculated as the average ratio of light below the vegetation (2 cm from ground level) to that above the canopy along three transects in each plot. On 16 May, 27 June, 17 July, and 12 August 1996, extractable NO₃⁻ and NH₄⁺ (henceforth, nitrogen) in the surface soil (0–18 cm) were measured by pooling and homogenizing four 2.5 cm diameter cores per plot, which were then extracted in 0.01 mol/L KCl overnight and analyzed on an Alpkem autoanalyzer (O. I. Analytical, College Station, Texas). Soil gravimetric moisture content was also determined on these dates and on 25 April, 2 June, and 1 July 1997. Aboveground biomass was measured in August of both years by clipping a 10 × 100 cm strip on two outside edges of each permanent subplot so that no invaders were removed. Clipped biomass was sorted into live and dead material, dried, and weighed.

Data analysis

Three measures of invasion success were recorded. The first two, number of invader species in a plot and number of invader individuals in a plot, are basically measures of germination and survival success. The third, absolute percent cover of the invader species, additionally measures the growth success of the in-

vaders. Although all of these are inextricably related, the number of invader species and individuals in a plot are most closely related. Invader species richness could simply be a function of the number of individuals in a plot and a random draw from the individuals that germinated in the experiment. I tested this hypothesis by counting the number of individual invaders of each species present in the whole experiment in 1997. From this pool of possible individuals, n individuals were drawn randomly, without replacement, and the number of species drawn was recorded. This procedure was repeated 1000 times for each value of n , which is the number of invader individuals in a plot. From this information, the probability of having p species in a plot with n individuals was calculated and compared to the actual data.

All statistical analyses were done with SYSTAT 7.0 for Windows (SPSS 1997). ANOVAs, MANOVAs, and analyses of covariance were done with the GLM procedure and least-squares regressions were performed with the linear regression procedure. Regression models were checked for multicollinearity problems using variance inflation factor, eigenvalue, and condition index criteria (Freund and Littell 1991). Invasion success measures were log-transformed for most analyses to improve compliance with equal variance and normality assumptions. A separate analysis was performed for each measure of success. When applicable, significance tests were adjusted for multiple comparisons by using the sequential Bonferroni correction, which controls experiment-wide error (Rice 1989).

One plot in the treatment with just C_4 graminoids was excluded from all analyses because it was an extreme outlier (studentized residual > 2). This plot had much higher percent cover of all added species (14%) compared to other plots, in which cover of the added species was generally low ($< 7\%$). The outlier plot was also unusual in that its soil nitrogen, soil moisture, and bare ground cover were ≥ 7 –17% higher than all other plots.

RESULTS

Of the 16 invader species added as seed, four (*Andropogon gerardii*, *Liatrus aspera*, *Stipa comata*, and *Stipa spartea*) appeared only in a set of plots not included in this report but planted in the same manner and at the same time as the plots discussed here. Thus, although the seeds of these species were viable, the species did not occur in the analysis for this report. One species, *Vicia villosa*, germinated and grew in six plots in 1996 but did not survive to 1997. Only *Echinacea purpurea* apparently failed to germinate at all. All other added species were present in at least one plot in 1997, yielding 10 out of 16 species for data analysis.

Based on the pool of invaders present in 1997, invader species richness in a plot was not significantly different than would be expected from a random draw ($P > 0.05$ [experiment-wide] for all plots). Invader

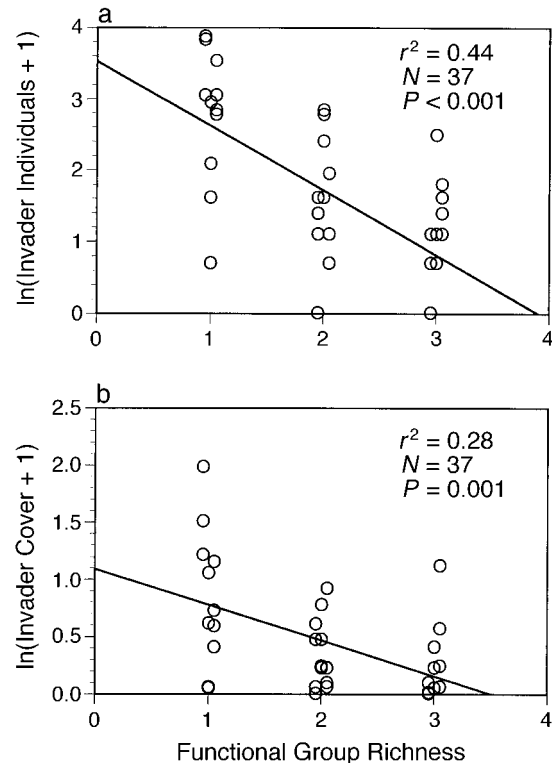


FIG. 1. Least-squares regression of invasion success on community functional group richness using two measures of invasion success. Open circles represent individual plots and have been slightly offset from actual functional group richness to improve visibility of each data point. Data were log-transformed. (a) Number of invader individuals: $y = 3.54 - 0.91x$. (b) Percent cover of invaders: $y = 1.09 - 0.31x$.

species richness was therefore apparently not affected by the experimental manipulations any differently than was the number of invader individuals. Thus, only the number of invader individuals and percent cover of invaders will be considered in the rest of the paper.

Factors influencing overall community invasibility

Both the total number and cover of invaders were significantly, negatively related to functional group richness of the community (Fig. 1 and Table 1). Functional group composition also significantly affected both measures of community invasibility (Table 1). The effect of functional group composition was strongest in the single functional group treatments, in which communities with just C_4 graminoids had significantly higher invasion success than did communities with just C_3 graminoids (Fig. 2b). Based on F values, however, community invasibility was more strongly related to functional group richness than to functional group composition.

Because the treatment with just C_4 graminoids had considerably higher invasion rates than other treatments (Fig. 2), it may have driven the significant relationship between functional group richness and in-

TABLE 1. Dependence of invasion success on functional group richness and composition.

Response variable (log-transformed)	F values			Overall r^2
	Functional group richness (df = 2, 30)	Functional group composition (df = 4, 30)	Overall model (df = 6, 30)	
Number of invader individuals	23.59***	5.48**	11.01***	0.69
Cover of invaders	13.56***	4.94**	7.08***	0.59

Notes: The combined effect of functional group composition and richness on community invasibility was tested by two-way ANOVAs in which functional group composition, nested within functional group richness, and functional group richness were the independent variables. Functional group composition was represented by assigning a unique value to each of the seven possible functional group compositions.

** $P < 0.01$; *** $P < 0.001$.

vasion resistance. To investigate this possibility, I reran the simple regressions of community invasibility on functional group richness but excluded this treatment. The relationship between invasibility and functional group richness remained significant and qualitatively similar [$\ln(\text{number of invaders} + 1) = 3.11 - 0.75 \times (\text{functional group richness})$, $r^2 = 0.35$, $N = 34$, $P < 0.001$; $\ln(\text{cover of invaders} + 1) = 0.73 - 0.18 \times (\text{functional group richness})$, $r^2 = 0.16$, $N = 34$, $P = 0.02$]. As a result, all other analyses were done using all treatments.

Community invasibility remained significantly, negatively related to functional group richness when the measured ecosystem properties were accounted for, as shown by backwards stepwise multiple regressions (Table 2). Both measures of invasion success increased significantly with increasing bare ground cover. In addition, when bare ground cover and functional group richness were accounted for, the number of invaders decreased with increasing light transmittance, and invader cover increased with increasing 1997 soil moisture. The curious relationship between invader numbers and light availability was a result of that relationship in the treatments with two functional groups, in which the number of invader individuals decreased significantly with increasing light levels ($r = -0.60$, $N = 12$, $P = 0.038$). At other levels of functional group richness, there was no relationship between light transmittance and invader success ($P > 0.10$).

Analysis of covariance showed that the relative importance of functional group composition and ecosystem properties on community invasibility varied with the measure of invasion success (Table 3). This analysis, which did not include functional group richness, used categorical variables for the presence or absence of each of the three manipulated functional groups as predictors and the significant ecosystem properties from the multiple regression analyses as covariates. Germination and survival of the invaders, as measured by their number of individuals, decreased significantly in the presence of forbs and C_3 graminoids, but neither of the ecosystem properties remained as significant predictors. For invader cover, however, 1997 soil moisture remained a significant predictor, as did the categorical variable for forb presence.

Invasion success was apparently also related to the amount of disturbance associated with the experimental manipulations. Both the number and cover of invaders were significantly higher in the high-level random biomass removal plots, compared to the controls in which no vegetation had been killed at the outset of the experiment (Fig. 2). Paired t tests were used to compare invasion success in the experimental treatments to the random biomass controls that corresponded to the amount of biomass killed in 1993. Invasion success in the treatments in which one functional group was killed (those with two functional groups remaining) did not differ from invasion success in the corresponding, low random biomass removal treatment ("RBH," Fig. 2). However, the C_4 graminoid and forb treatments (in which two functional groups had been killed) had significantly higher numbers of invaders than did the corresponding, high random biomass removal treatment ("RBH," Fig. 2a) and the C_4 graminoid treatment had significantly higher percent cover (Fig. 2b).

Ecosystem properties

The ecosystem properties measured for this experiment were only weakly, if at all, related to functional group richness. Simple regressions on functional group richness showed that light transmittance decreased as functional group richness increased ($r^2 = 0.10$, $N = 37$, $P = 0.05$; Fig. 3a). All other variables included in the multiple regressions (bare ground cover, soil moisture, extractable soil N, aboveground biomass, and resident species richness) were not related to it ($P > 0.10$; Fig. 3). The relationship between functional group composition and some of these ecosystem properties was slightly stronger than the effect of functional group richness, as shown by ANOVAs on treatment within each level of functional group richness. For the treatments with just one resident functional group, light transmittance and bare ground cover were higher in plots with just C_4 graminoids compared to plots with just C_3 graminoids (Fig. 3a, b). Light transmittance and bare ground cover also varied among treatments with two functional groups; plots with forbs and C_3 graminoids had significantly lower levels than plots with forbs and C_4 graminoids (Fig. 3a, b). Soil moisture in 1997 varied little among treatments (Fig. 3c). There

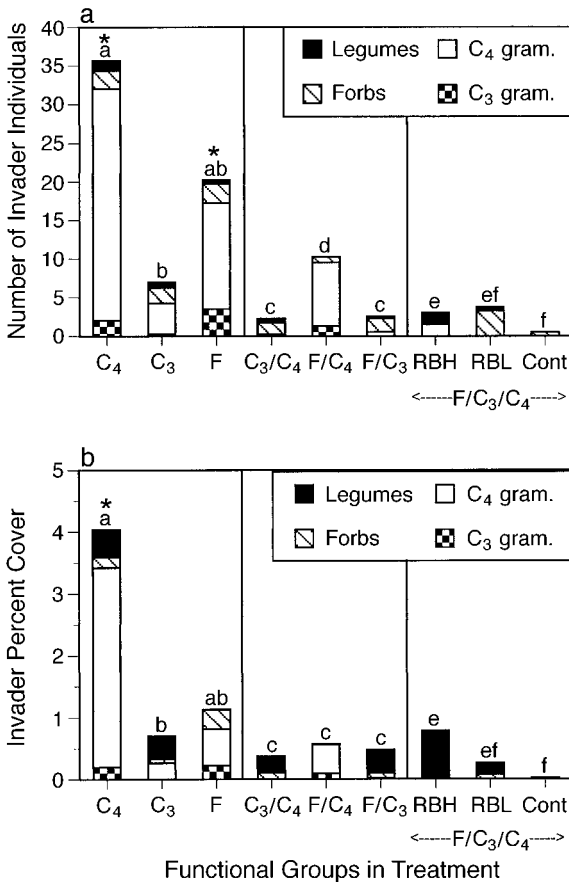


FIG. 2. Mean success of invaders, by functional group, in individual treatments: (a) number of invader individuals; (b) percent cover of invaders. Treatments are designated on the horizontal axis by the functional groups they contain, not including invader species: C₄ = C₄ graminoids, C₃ = C₃ graminoids, F = forbs, Cont = control (nothing removed), RBL/H = random biomass removal at low and high levels, respectively. Stacked bars show the average functional group composition of the invader species. Significant (experiment-wide error, $P < 0.05$) differences in total invasion success among treatments within each level of functional group richness are indicated by different letters above bars (Tukey comparison of means). A different set of letters is used for each level of functional group richness but does not necessarily indicate differences in invasion success across functional group richness levels. An asterisk above a bar indicates a significant difference between that treatment and its respective random biomass removal treatment. Data were log-transformed for analysis but are shown untransformed.

were no significant effects of random biomass removal on any of these ecosystem properties (treatments with three functional groups in Fig. 3).

Effect of community composition on invader species composition

Both measures of invader success were used to address the effects of ecological similarity between the invader and resident species with multivariate analyses of variance. In these, the presence or absence of the

three experimentally manipulated functional groups (forbs, C₃ graminoids, and C₄ graminoids) were the predictor variables, and the performance of the invaders in each of four functional groups (legumes, other forbs, C₃ graminoids, and C₄ graminoids) were the response variables. The only resident functional group to have a significant ($P < 0.05$) effect on the composition of the successful invader species was the C₃ graminoids (Table 4A). The presence of this functional group decreased the number of invaders and their cover in both the C₃ graminoid and C₄ graminoid groups but had little effect on the forb or legume invaders (Table 4B). A weak effect ($0.05 \leq P < 0.10$) of the presence of forbs on invader community composition (Table 4A) reflected a decrease in the number and cover of C₄ graminoid invaders when forbs were present (Table 4B). Thus, given the power of this experiment, the only evidence for resident species' repelling invaders from the same functional group was in the C₃ graminoid group.

DISCUSSION

This experiment tested the effects of plant community functional group richness, functional group composition, and ecosystem properties on community invasibility, as well as the relationship between the functional group identity of the resident species and the species that could successfully invade. Overall invasion resistance increased significantly as community functional group richness increased and was also related to community functional group composition. Some of this relationship may have been caused by diversity's effects on ecosystem properties, or by resident species' repelling functionally similar invaders. However, the greatest effect of functional group richness and composition on invasion resistance was apparently due to an interaction between functional group composition and disturbance.

Ecological resistance of functionally diverse communities?

The hypothesis that diverse communities are more resistant to invasion than are simple communities because they have fewer resources available for the invaders was only weakly supported in this experiment. Bare ground cover, soil moisture, and light availability at ground level did help explain some variability in the number and cover of invaders (Table 2). However, the effect of functional group richness on these ecosystem properties was weak, if existent at all (Fig. 3). In fact, only one resource, light, significantly decreased with increasing functional group richness in this experiment, and its relationship with invasion success (as measured by the number of invaders) was negative when other factors were accounted for. I cannot explain this relationship, which was the opposite of the expected effect. Given the weak effects of functional group richness on ecosystem properties, the first link in the diversity-

TABLE 2. Stepwise regressions of the effects of functional group richness and ecosystem properties on community invasibility. Response variables were log-transformed. The *t* values are for the test that each regression parameter is different from 0.

Variable	Number of invader individuals§			Cover of invaders		
	Parameter estimate	Partial <i>r</i> ²	<i>t</i>	Parameter estimate	Partial <i>r</i> ²	<i>t</i>
Intercept	4.20	...	6.13***	NS
Functional group richness	-1.04	0.60	-7.05***	-0.26	0.29	3.64**
Bare ground†	0.05	0.29	3.69**	0.02	0.22	3.07**
Light transmittance	-0.02	0.15	2.38*	NS
1997 soil moisture‡	NS	0.28	0.25	3.27**
Extractable soil nitrogen‡	NS	NS
1996 soil moisture‡	NS	NS
Aboveground biomass†	NS	NS
Resident species richness	NS	NS

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = $P \geq 0.05$.

† Values averaged over 1996 and 1997.

‡ Values averaged over four sampling times in 1996, over three sampling times in 1997.

§ Overall model: $F_{3,34} = 33.89$, $P < 0.001$, $r^2 = 0.75$.

|| Overall model: $F_{4,33} = 21.29$, $P < 0.001$, $r^2 = 0.72$.

ecosystem properties–invasion resistance hypothesis was weak. In addition, accounting for the ecosystem properties did not eliminate the significant relationship between functional group richness and community invasibility (Table 2), as would be expected if the second link in the hypothesis were strong.

The connection between diversity and invasibility through resistance to invaders functionally similar to the residents was also only weakly supported in this study. C₃ graminoids were the only functional group in which there was a negative relationship between the presence of a functional group in the resident community and the invasion success of that functional group. The C₃ graminoids were not a large component of the successful invaders (Fig. 2), however, and the C₄ graminoids, which were the most successful invaders, were also negatively affected by the presence of resident C₃ graminoids. This lack of interactions within

functional groups may have been caused by the relatively young age and small size of the invader plants. For example, the hypothesized competitive mechanisms that limit the similarity between successful colonizers and resident species may not have been strong enough yet to limit the growth of the species added in this experiment. Specifically, although nitrogen is the limiting resource for established communities at Cedar Creek (Tilman 1987), soil moisture, light transmittance, and bare ground cover were the ecosystem properties related to the success of the invaders (Table 2). More time, however, will not necessarily change the results of this experiment. For example, in a 23-yr study of the invasion of a forest by an exotic perennial herb, Wisner et al. (1998) found that the invading species occurred in plots with more resident species in the same morphological guild. These studies suggest that if niche limitation does occur, it may only happen when the definitions of functional groups or guilds are more refined.

Disturbance, diversity, and invasibility

Given the weak relationship between functional group richness and ecosystem properties, additional explanation for the significant relationship between functional group richness and community invasibility in this experiment is needed. The disturbance imposed on the plant communities in the process of creating the variation in functional group richness seems to be the primary candidate for this additional explanation for two reasons. First, invasion success was greater in the high random biomass removal plots than in the unmanipulated control plots (Fig. 2). Although there were no significant differences in the ecosystem properties among these treatments, there was a trend for bare ground cover to increase with increasing disturbance (Fig. 3b). Since bare ground cover was a property im-

TABLE 3. Dependence of community invasibility on functional group composition and significant factors from the multiple regressions, according to analysis of covariance.

Source	Number of invader individuals		Cover of invaders	
	<i>F</i>	df	<i>F</i>	df
Forbs	7.20*	1, 32	6.65*	1, 31
C ₃ graminoids	23.38***	1, 32	4.11 ^{NS}	1, 31
C ₄ graminoids	5.16*	1, 32	1.12 ^{NS}	1, 31
Bare ground	2.88 ^{NS}	1, 32	3.68 ^{NS}	1, 31
Light transmittance	1.50 ^{NS}	1, 32	N/A	...
1997 soil moisture	N/A	...	7.22*	1, 31
Overall model	13.93***	4, 32	7.27***	5, 31

Notes: "Forbs," "C₃ graminoids," and "C₄ graminoids" are categorical variables indicating the presence or absence of the functional group in the plot prior to seed addition. Response variables were log-transformed. "N/A" indicates that the predictor variable was not significant in multiple regression.

* $P < 0.05$; *** $P < 0.001$; NS = $P \geq 0.05$.

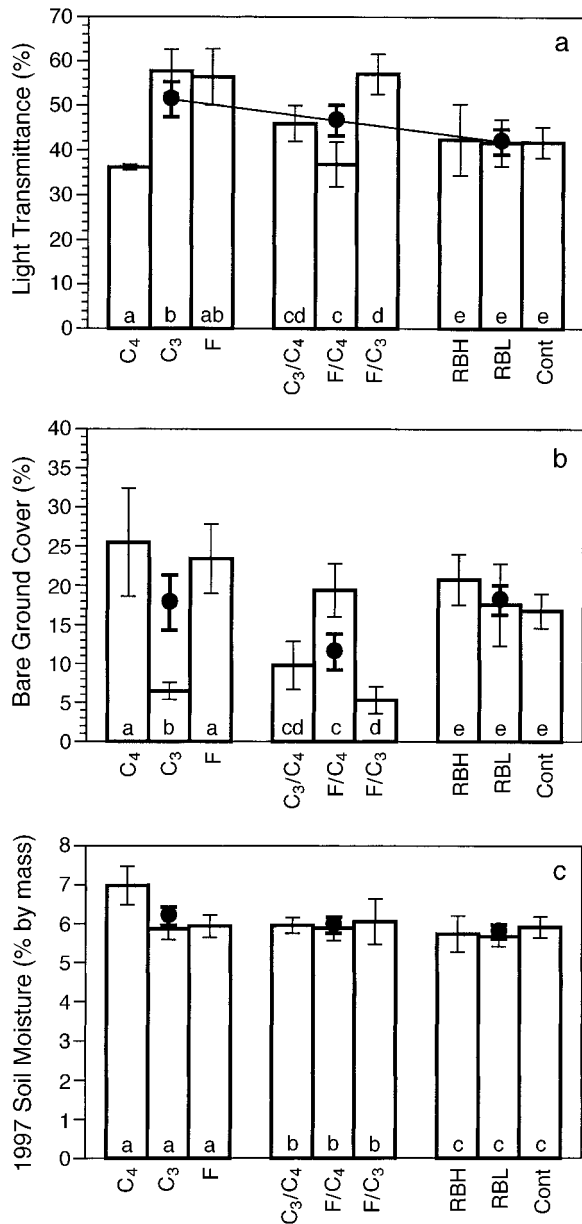


FIG. 3. Means (± 1 SE) of ecosystem properties significantly related to invasion success in multiple regressions (Table 2): (a) light transmittance; (b) bare ground cover; (c) 1997 soil moisture. Bars represent means for individual treatments, whereas circles indicate means for functional group richness levels. See Fig. 2 for explanation of treatment labels. The regression line in (a) indicates a significant relationship between functional group richness and light transmittance: light transmittance = $56.1 - 4.7 \times$ (functional group richness). No other regression of an ecosystem property on functional group richness was significant ($P > 0.10$). Significant (experiment-wide error, $P < 0.05$) differences in an ecosystem property among treatments within each level of functional group richness are indicated by different letters above bars (Tukey comparison of means). A different set of letters is used for each level of functional group richness but does not necessarily indicate differences in invasion success across functional group richness levels.

portant to both measures of invasion success (Table 2), the disturbance caused by killing any biomass, regardless of functional group, probably contributed to the relationship between functional group richness and invasion success found in the experiment as a whole.

Second, significantly higher invasion success in two of the treatments with a single functional group, compared to the high random biomass removal treatment (Fig. 2), suggests that the reactions of the different functional groups to the initial disturbance were at least as important as the random disturbance. For example, plots that contained C₃ graminoids had significantly lower bare ground cover than did plots without them (Fig. 3b), because the dominant species in this functional group, *Poa pratensis*, spreads vigorously across bare soil via vegetative growth (Tilman and Wedin 1991). As a result, open space created by the removal of other functional groups was quickly filled when C₃ graminoids remained in a plot. In contrast, *Schizachyrium scoparium*, the dominant C₄ graminoid in this system, does not readily colonize either vegetatively or by seed (Tilman and Wedin 1991), so that plots with just C₄ graminoids may not have reached equilibrium cover when the seeds of invader species were added. The lower bare ground cover in plots with C₃ graminoids was probably the main reason for their significant effect, but other factors may have contributed. For example, the timing of the experimental seed addition, in May when the C₃ graminoids are most active, might also have added to the significant C₃ effect.

This difference in how the functional groups responded to the experimental manipulation could have translated into a relationship between functional group richness and community invasibility because richness and composition are inextricably linked. In this experiment, C₃ graminoids were the functional group with the greatest effect on the number of invaders (Table 3, Fig. 2a) and on invader species composition (Table 4). The probability of a treatment's having this functional group inevitably increased with increasing functional group richness. Thus, the significant, negative effect of C₃ graminoids on invasion success, through their reaction to the initial disturbance, is likely partly responsible for the significant diversity-invasibility relationship.

Disturbance is often cited as an important precursor for invasion of an ecosystem (Fox and Fox 1986, Crawley 1987, Robinson et al. 1995, Burke and Grime 1996, Case 1996), usually in the context of its causing increases in resource availability. The results of this experiment suggest that this direct effect is only part of the story. Indirect effects of disturbance on invasibility may also occur through changes in community composition and through differences among species in the time course of their resistance and resilience to the disturbance. The generality of the importance of disturbance for invasion is questionable, however, based on the results of other studies that found disturbance

TABLE 4. Relationship between community functional group composition and invader functional group composition. (A) MANOVAs of number of individuals in, or percent cover of, each added functional group on the presence or absence of each of the manipulated functional groups. (B) Mean (± 1 SE) of the invasion success for each functional group in the absence or presence of each resident functional group.

A) Multivariate analysis of variance										
Resident functional group	Number of invader individuals					Percent cover of invaders				
	Pillai's trace	df	<i>F</i>	<i>P</i>	Sq. can. cor.†	Pillai's trace	df	<i>F</i>	<i>P</i>	Sq. can. cor.†
Forbs	0.250	4, 30	2.49	0.06	0.25	0.233	4, 30	2.29	0.08	0.23
C ₃ graminoids	0.676	4, 30	15.64	0.0001	0.68	0.546	4, 30	9.02	0.0001	0.55
C ₄ graminoids	0.076	4, 30	0.62	0.65	0.08	0.221	4, 30	2.13	0.10	0.22
B) Univariate analyses										
Resident functional group	<i>N</i>	Number of invaders				Percent cover of invaders				
		Legumes	Forbs	C ₃ graminoids	C ₄ graminoids	Legumes	Forbs	C ₃ graminoids	C ₄ graminoids	
Forbs										
Absent	11	0.83 (0.22)	2.08 (0.70)	1.23 (0.45)	13.3 (1.9)	0.32 (0.16)	0.14 (0.03)	0.10 (0.04)	1.22 (0.25)	
Present	26	0.39 (0.15)	1.63 (0.48)	1.29 (0.31)	6.62 (1.32)	0.17 (0.11)	0.12 (0.02)	0.09 (0.03)	0.35 (0.17)	
<i>P</i>		NS‡	NS	NS	0.016	NS	NS	NS	0.016	
C ₃ graminoids										
Absent	11	0.64 (0.22)	2.02 (0.70)	2.36 (0.45)	17.7 (1.9)	0.16 (0.16)	0.18 (0.03)	0.18 (0.04)	1.42 (0.24)	
Present	26	0.58 (0.15)	1.69 (0.48)	0.16 (0.31)	2.18 (1.32)	0.33 (0.11)	0.08 (0.02)	0.01 (0.03)	0.16 (0.17)	
<i>P</i>		NS	NS	<0.002	<0.001	NS	0.02	<0.002	<0.001	
C ₄ graminoids										
Absent	12	0.58 (0.21)	2.22 (0.67)	1.61 (0.43)	9.79 (1.83)	0.25 (0.15)	0.18 (0.03)	0.11 (0.04)	0.64 (0.23)	
Present	25	0.63 (0.16)	1.49 (0.51)	0.91 (0.33)	10.1 (1.4)	0.24 (0.11)	0.09 (0.02)	0.08 (0.03)	0.93 (0.18)	
<i>P</i>		NS	NS	NS	NS	NS	0.09	NS	NS	

Note: *P* values for univariate tests for differences between means are shown, adjusted for multiple comparisons using the sequential Bonferroni method; NS indicates $P \geq 0.10$.

† Sq. can. cor. = squared canonical correlation; it is analogous to r^2 in that it is a measure of how much of the total variance the source explains.

was not a prerequisite for invasion (Wiser et al. 1998 and references therein).

Experiments, invasion, and assembly rules

So far, observational and experimental evidence is insufficient to ascertain whether there are generalizable rules for the role of disturbance, diversity, and their interaction in invasibility. Chalk this experiment up as another "yes" in the tabulation of votes for whether disturbance enhances invasion success. Because of the correlation between disturbance and diversity in my experimental design, however, only a "maybe" can be recorded in the vote for whether increased functional group richness enhances invasion resistance. Controlled, well-replicated, long-term experiments will be the only way to adequately understand the influence of either factor and their interactions.

Finally, although the intent and main discussion of this experiment was to investigate how functional group diversity affects community invasibility, the native prairie species used here as "invaders" may seem more pertinent to community assembly theory. Specifically, assembly theory attempts to describe the process of "natural" invasions, that is, colonization of communities by species that have interacted with the species in the existing community over evolutionary time scales. Studies of ecological invasions, on the oth-

er hand, usually concern novel species that colonize communities with which they had no previous interactions. Despite somewhat different focuses, the ecological principles underlying both areas of study are the same (e.g., niche limitation, competition for resources, predator-prey interactions). Thus, experiments using either native, conservative species or exotic, aggressive species as invaders are both pertinent to understanding which traits characterize invulnerable communities and the species that can invade them. Where possible, however, experiments comparing the two types of species would provide extra power for understanding the rules that govern "natural" and human-induced invasions of ecological communities.

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