



Plant species richness increases resistance to invasion by non-resident plant species during grassland restoration

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Keywords

diversity; dominance; early succession; *Elymus virginicus*; evenness; functional type; grassland restoration; invasion resistance

Nomenclature

Gleason and Cronquist (1991)

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Abstract

Questions: During restoration of bare subsoil, are planted grassland communities with low species richness more susceptible to invasion by non-residents than communities augmented by additional species? What are the mechanisms of invasion resistance in early succession?

Location: Lexington, Virginia, USA (37.8°N, –79.4°W).

Methods: We planted 62 3 × 3 m plots on compacted clay subsoil with 20–21 replicates of three, 12 and 24 native species. Plots were sampled non-destructively using a stratified random point-intercept method each summer for 5 yr to determine number of species and percentage cover per species, which were classified as residents (planted), internal non-residents (planted in other plots) or external non-residents.

Results: A negative relationship between planted species richness and invasion developed by the fourth year after planting and strengthened thereafter. Plots consisting of a single, highly dominant, resident C₃ grass species were vulnerable to invasion. With the exception of one species, which seems to have overcome resistance with a high seed rain, external non-resident species were less diverse and less abundant in higher diversity plots.

Conclusions: Increased planted species richness was correlated with increased resistance to invasion by non-residents, and we attribute this effect to a combination of the sampling effect and species complementarity, potentially augmented by high species dominance/low evenness in the low species richness plots.

Introduction

Considerable interest exists in whether there is a positive or negative correlation between resident species richness and invasibility by non-resident species, and if so, what the mechanisms of invasion resistance might be (reviewed in Fridley et al. 2007). Invasibility studies have focused upon non-resident species that are not native, since many examples suggest that exotic species are contributing to the decline of native species' populations in ways that lead to species extinctions (Simberloff 2005, 2006). Generally, where co-varying factors have been controlled or standardized in experimental studies carried out at a fine scale (i.e. plots ≤ 10 m²) distributed over a modest spatial extent, a negative relationship has been found between resident species richness and invasibility in grassland com-

munities (Levine 2000; Naeem et al. 2000; Hector et al. 2001; Kennedy et al. 2002; Van Ruijven et al. 2003; Fargione & Tilman 2005) and small (10 × 10 cm) synthetic marine invertebrate communities (Stachowicz et al. 1999).

Much effort and argument has been directed toward distinguishing between the possible mechanisms controlling invasibility. The principal mechanisms discussed are the sampling effect, the species complementarity effect, facilitation, species dominance/evenness and the species-neutral null model (summarized in Fridley et al. 2007). Increasing resident species richness, particularly when species are chosen to be structurally and functionally complementary, should increase resistance to invasion through the operation of one or more of the mechanisms of sampling, complementarity or the species-neutral model, and

might also increase resistance where cases of facilitation occur that involve positive interactions between resident species. A negative relationship between resident richness and invasibility at the fine scale, mediated through biotic interactions, is expected to be large when resource availability is low, when the habitat fluctuates little temporally and spatially, and where resident richness is high (Davies et al. 2005; Stachowicz & Byrnes 2006).

In the mid-Atlantic United States, restoration of roadsides and other large construction sites is usually accomplished by seeding with a mix of exotic herbaceous species, with the objective of establishing perennial herbaceous cover as quickly as possible to reduce erosion. Recognizing the growing threat that exotic species pose to native species, applied scientists who specialize in roadside restoration are making efforts to find methods of restoration that use native species (Booze-Daniels et al. 1998). We tested the hypothesis that increasing resident plant species richness beyond early-successional grass species increases resistance to invasion by non-residents in temperate grasslands, doing so under conditions that simulate an actual roadside or construction site restoration. We chose plants native to our region that were known to grow well on clay soil and would represent different structural and functional types to increase the probability of achieving complementarity.

Methods

Our study is similar to many other studies of invasibility in using many of the same species and constructing fine-scale experimental plots distributed over a limited area; species richness was the main variable among treatments. This study differs, however, from other published studies in two important ways that make the results more applicable to actual restoration efforts. We studied invasibility during the establishment of plant communities from seeds, without weeding plots and without interfering with spontaneous invasions that might occur from the time of planting, and we planted our plots on a compacted clay subsoil that resembled the substrate that is often encountered after heavy construction, improving the soil only by disking and tilling in leaves 5 mo before planting.

During the autumn of 2000 we stockpiled leaves of deciduous plants gathered locally from residential yard waste and deposited the biomass on a 0.6-ha 'barren' (37° 47'41.92" N, 79°26'32.28" W) located in the Washington and Lee University Forest in Lexington, Virginia. The site had been strip-mined of topsoil in 1994, leaving a level compacted subsoil of red clay that remained barren for 7 yr, despite the abundance of ruderal and forest species growing in a surrounding old field and forest. In June 2001 we used a farm tractor to mix, spread to a thickness

of about 10 cm, and disc the accumulated compacted leaves into the barren clay subsoil to begin to form a soil. The pH of the subsoil rose from 5.5 to 7.2 over the following 4 mo as soil developed. The following autumn we tilled the site to further mix the developing topsoil to prepare for planting. We planted 62 plots, each 3 × 3 m, and each surrounded by a 1.5-m walkway of about 5 cm of stone over landscape cloth. The study site was surrounded with a 3.4-m tall wire fence to exclude deer but not smaller herbivores. Between the plots and the fence were several meters of buffer that had been prepared with leaves, disced and tilled, but not planted. Outside the fenced research site was a disturbed buffer area supporting a plant community of ruderal volunteer herbaceous species, beyond which was a plantation of *Pinus taeda* and *P. strobus* interspersed with native hardwoods.

In mid-November 2001 we planted approximately 9000 seeds per plot at three levels of species richness (Table 1): 21 plots with three species (low species richness), 21 plots with 12 species (medium species richness) and 20 plots with 24 species (high species richness). Each richness treatment was seeded with approximately equal numbers of seeds of the species planted (e.g. at a richness of 24 species, there were approximately 375 seeds per species, while at a richness of three species, each species was planted with about 3000 seeds). Note that species planted were not randomized per plot, i.e. all low species richness plots were planted with the same species. The number of seeds planted was determined by weight. We mixed all seeds to be planted in a plot with eight handfuls of sphagnum before raking the mix into the plot to distribute the seeds evenly across the 9-m² area. The species composition of treatments was nested, with species in the lower richness plots also planted in the higher richness plots. A stratified random method was used to assign treatments. An erosion control blanket was placed over each plot after planting and compressed with a seed roller.

Species (Table 1) were chosen for being herbaceous perennials native to the region, complementary in structure and function and known to grow well on clay soil. *Elymus virginicus* was selected because it is known to be an aggressive pioneer C₃ grass (Rudgers & Swafford 2009). Four other grass species were chosen because they are C₄ species that are slower than *E. virginicus* to establish, but expected to become dominants in later succession, particularly at warmer and drier parts of the growing season. In addition to the grasses we chose many aggressive early successional forbs, two legumes and two aggressive clonal species capable of dominating later stages of succession.

Recruitment of plants in the plots began in spring 2002. We began plant sampling in July 2003, continuing sampling each June or July thereafter through the summer of 2007. We completed each season's sampling within 2 wk

Table 1. Species planted in plots by treatment.

Species planted	Species richness (No. species planted)		
	Low (3)	Medium (12)	High (24)
<u>Andropogon gerardii</u>		*	*
<u>Asclepias syriaca</u>			*
<u>Asclepias tuberosa</u>		*	*
<u>Aster novae-angliae</u>		*	*
<u>Dalea purpurea</u>	†	†	†
<u>Datura stramonium</u>			*
<u>Echinacea purpurea</u>		*	*
<u>Elymus virginicus</u>	*	*	*
<u>Eupatorium fistulosum</u>			*
<u>Helianthus mollis</u>			*
<u>Liatris spicata</u>		†	†
<u>Lupinus perennis</u>		*	*
<u>Monarda fistulosa</u>		*	*
<u>Panicum virgatum</u>			*
<u>Penstemon digitalis</u>			*
<u>Phytolacca americana</u>			*
<u>Rudbeckia hirta</u>		*	*
<u>Schizachyrium scoparium</u>	*	*	*
<u>Smilax pulverulenta</u>			†
<u>Solidago canadensis</u>			*
<u>Sorghastrum nutans</u>		*	*
<u>Verbesina alternifolia</u>			*
<u>Vernonia noveboracensis</u>			*
<u>Zizia aurea</u>			*

Grasses are underlined. A total of about 9000 seeds were planted in each plot, with 3000 seeds per species in low species richness plots, 750 seeds per species in medium species richness plots, and 375 seeds per species in high species richness plots.

*The species that grew.

†The species that did not grow.

to minimize seasonal effects. Throughout the study we did not walk in the plots, nor did we weed plots or sample destructively, with the exception of removal of woody species taller than 1.5 m in 2006 and 2007, which were cut at ground level and the stumps painted with herbicide.

We refer to species planted in plots as residents, while those not planted are non-residents. We distinguish internal non-residents (species that were not planted in a plot but were residents in another treatment) from external non-residents (species not planted in any of the treatments). To estimate the cover of each common plant species in a plot non-destructively, we used a point-intercept method, sampling 45 random points per plot along five random parallel transects from an overhead aluminium bleacher seat, on which the observer sat, suspended between step ladders that stood outside the plot on the walkways. A 2-m long, 3-cm diameter plastic PVC pipe 'pin' was used to establish sampling points, and each species touching the pin was recorded just once at each of the 45 random pin 'drops' sampled within each plot. The shortest plants touched (<5 cm) were probably under-

counted because of the difficulty of the sampler seeing them in dense taller vegetation. Additional, brief qualitative surveys of all species present were conducted simultaneously with quantitative sampling.

We measured both the number of species of each category per plot detected by the point-intercept method and the percentage cover of each species. Cover was calculated as the percentage of 45 random points per plot at which a species was touched by the sampling pin. Non-resident species percentage cover, P , was normalized to total species percentage cover using the following formula:

$$P = \frac{(E + I)}{(E + I + R)}$$

where E is the sum of the percentage cover of all external non-resident species, I is the sum of the percentage cover of all internal non-residents and R is the sum of the percentage cover of all resident species. External non-resident species percentage cover, P_{ext} , was calculated similarly:

$$P_{\text{ext}} = \frac{E}{(E + I + R)}$$

P and P_{ext} for each plot were then arcsine-square-root transformed to reduce heterogeneity of variance. All data sets (species counts, P and P_{ext}) for all plots of each treatment in each year were subjected to repeated measures analysis [autoregressive(1) covariance structure with Tukey-Kramer adjustment using SAS 9.2; SAS Institute, Cary, NC, US]. The threshold for significance (alpha) was set at 0.05.

Results

In 2003 and 2004 the mean number of non-resident species sampled did not differ significantly among treatments ($P = 1.00$). By 2005 a pattern of substantial decreases in the number of non-resident species sampled with increasing planted species richness was established, and this pattern was amplified in 2006 and 2007 (Fig. 1). From 2003 through 2007 the mean number of non-resident species sampled rose in low ($P < 0.001$) richness plots, while the number of non-resident species sampled did not change significantly for the duration of the experiment in the medium ($P = 0.430$) and high ($P = 0.474$) richness plots.

The percentage cover data largely echoed the species count results. The percentage cover of non-resident species rose in the low ($P < 0.001$) and medium ($P < 0.001$) planted species richness plots from 2003 to 2007 (Fig. 2). In 2003 and 2004, non-resident cover was low and did not differ significantly between any treatments. By 2005 a pattern had begun to emerge of a negative relationship between resident richness and non-resident cover, and

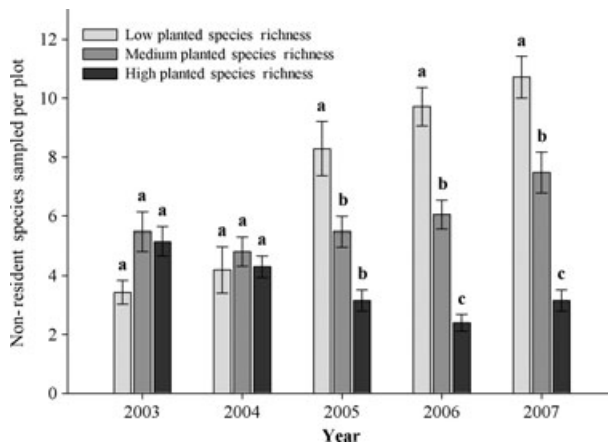


Fig. 1. Mean \pm SE number of non-resident species sampled by point intercept per plot by treatment and year. Bars with different letters above within each year are significantly different ($P < 0.05$).

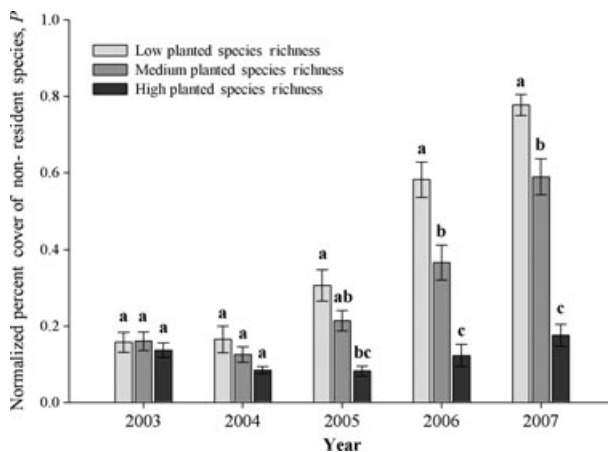


Fig. 2. Mean \pm SE of total percentage cover of non-resident species sampled by point intercept, normalized to total percentage cover of all species (P). Bars with different letters above within each year are significantly different ($P < 0.05$).

that pattern strengthened further in 2006 and 2007 as the cover of non-resident species rose. The pattern was similar for the external non-resident species but took slightly longer to emerge; by 2006 their cover was significantly lower ($P < 0.001$) in high richness plots than in the low and medium richness plots (Fig. 3).

We found differences in the species composition of the dominant plants sampled in different treatments within a year, as well as between the same treatments in 2003 and 2007. We defined 'dominant species' as those that had the highest absolute percentage cover. In 2003 the most dominant plant by far in all plots, regardless of treatment, was the resident grass *E. virginicus* (Table 2). This was the only species that recruited in the low richness plots, making all other species in these plots non-residents. The percentage

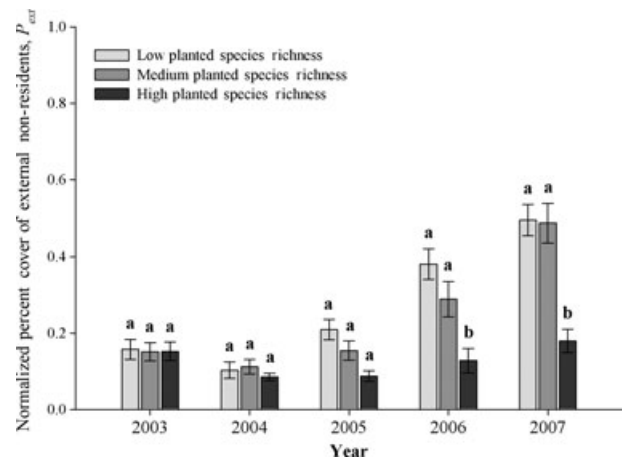


Fig. 3. Mean \pm SE of total percentage cover of external non-resident species sampled by point intercept, normalized to total percentage cover of all species (P_{ext}). Bars with different letters above within each year are significantly different ($P < 0.05$).

cover of *E. virginicus* was above 95% in all the individual plots in 2003, regardless of treatment. Percentage cover of *E. virginicus* declined from 2003 to 2007 in all treatments ($P < 0.001$), and in no year was it significantly different between medium and high species richness plots ($P > 0.05$). By 2006, the percentage cover of *E. virginicus* was less than 30% in medium ($\bar{x} = 25.1 \pm 4.0\%$) and high ($\bar{x} = 24.4 \pm 9.5\%$) species richness treatments, and less than 50% in all treatments by 2007. By 2007, internal non-residents had emerged among the top 10 dominant species in low and medium richness plots. That year, four internal non-resident species were among the 10 dominant species in the low richness plots, as was one internal non-resident species in the medium richness plots.

As *E. virginicus* grew tall and flowered, it often lodged, falling on other species and causing them also to lodge. The denser the cover of *E. virginicus*, the greater was the frequency of lodging. The impact of lodging was evident in the significantly lower mean height measured for the tallest standing vegetation in low richness plots in 2004 ($\bar{x} = 68.8 \pm 3.1$ cm) and 2006 ($\bar{x} = 87.6 \pm 3.9$ cm), compared to the other treatments in 2004 ($\bar{x} = 102 \pm 3.2$ cm for medium richness; 111 ± 1.8 cm for high richness) and 2006 (93.2 ± 3.5 cm for medium richness; 105.7 ± 4.2 cm for high richness).

Among the external non-resident species sampled were many that are exotic to North America. In 2003 more exotic species were sampled among the ten most dominant species in plots planted at low richness compared to plots planted at higher richness (Table 2). By 2007, the number of exotic species among the ten most dominant species had dropped in the low and high richness plots, and the composition of those species had changed as well. Over these

Table 2. Species composition and mean percentage cover of ten species with highest mean percentage cover in 2003 and 2007 in the three treatments.

Low species richness (3)	Medium species richness (12)	High species richness (24)
2003		
<i>Elymus virginicus</i> 99.9	<i>Elymus virginicus</i> 99.5	<i>Elymus virginicus</i> 98.4
<i>Centaurea maculosa</i> 6.7*	<i>Monarda fistulosa</i> 14.2	<i>Helianthus mollis</i> 19.8
<i>Trifolium</i> spp. 5.2*	<i>Trifolium</i> spp. 11.9*	<i>Monarda fistulosa</i> 16.2
<i>Plantago</i> sp. 1.5*	<i>Aster novae-angliae</i> 7.9	<i>Echinacea purpurea</i> 8.6
<i>Ambrosia artemisiifolia</i> 1.3	<i>Echinacea purpurea</i> 7.4	<i>Centaurea maculosa</i> 5.7*
<i>Chrysanthemum leucanthemum</i> 1.2*	<i>Sorghastrum nutans</i> 6.2	<i>Aster novae-angliae</i> 4.6
<i>Medicago</i> sp. 1.1*	<i>Centaurea maculosa</i> 5.8*	<i>Trifolium</i> spp. 4.5*
<i>Daucus carota</i> 0.9*	<i>Asclepias tuberosa</i> 5.5	<i>Solidago canadensis</i> 4.1
<i>Duchesnia indica</i> 0.3*	<i>Ambrosia artemisiifolia</i> 3.1	<i>Asclepias syriaca</i> 3.7
<i>Verbascum thapsus</i> 0.3*	<i>Chrysanthemum leucanthemum</i> 2.9*	<i>Zizia aurea</i> 3.5
2007		
<i>Elymus virginicus</i> 41.6	<i>Dipsacus laciniatus</i> 25.7*	<i>Helianthus mollis</i> 57.9
<i>Solidago canadensis</i> 28.2	<i>Elymus virginicus</i> 25.2	<i>Solidago canadensis</i> 29.9
<i>Dipsacus laciniatus</i> 21.7*	<i>Sorghastrum nutans</i> 21.9	<i>Penstemon digitalis</i> 18.7
<i>Rubus</i> sp. 12.8	<i>Monarda fistulosa</i> 13.7	<i>Dipsacus laciniatus</i> 15.8*
<i>Centaurea maculosa</i> 11.1*	<i>Solidago canadensis</i> 12.5	<i>Elymus virginicus</i> 11.9
<i>Monarda fistulosa</i> 9.9	<i>Rubus</i> sp. 11.4	<i>Verbesina alternifolia</i> 9.4
<i>Bromus commutatus</i> 6.2*	<i>Aster novae-angliae</i> 8.4	<i>Asclepias syriaca</i> 5.9
<i>Verbesina alternifolia</i> 6.2	<i>Lonicera japonica</i> 7.8*	<i>Sorghastrum nutans</i> 5.1
<i>Sorghastrum nutans</i> 4.3	<i>Coronilla varia</i> 6.2*	<i>Monarda fistulosa</i> 4.8
<i>Parthenocissus quinquefolia</i> 3.2	<i>Vitis</i> sp. 4.9	<i>Aster novae-angliae</i> 3.5

Resident species are in bold. Internal non-residents are underlined.

*Exotic species.

five growing seasons, four internal non-residents rose from 0% cover in 2003 to join the ten most dominant species in low richness plots in 2007. In contrast, in high richness plots, by 2007, only one external non-resident, the exotic *Dipsacus laciniatus*, was among the ten most dominant species. Two exotic non-resident species (*Centaurea maculosa* and *Trifolium* sp.) that were formerly among the ten most dominants in high richness plots in 2003 had experienced steep drops in cover by 2007 (Table 2).

Dipsacus laciniatus emerged among the ten dominant species in all treatments by 2007 (Table 2). It was the only non-resident species among the ten most dominant species in high richness plots in 2007. There was no significant difference in the cover of *D. laciniatus* among treatments in 2007 (single-factor ANOVA, $P > 0.05$). A waste dump outside one end of the fenced research site had a large, rapidly growing population of *D. laciniatus* from which seed rain into the plots is likely to have occurred. The mean cover of *D. laciniatus* in invaded plots nearest the dump was significantly higher ($\bar{x} = 43.94 \pm 6.2\%$; $P = 0.006$ Mann–Whitney) than in invaded plots further from the dump ($\bar{x} = 11.66 \pm 5.5\%$).

Discussion

No relationship between planted species richness and invasibility was found in the first 2 yr of sampling (2003 and

2004). By 2005, a negative relationship developed and strengthened through the following summers of 2006 and 2007, as shown by a negative trend between planted species richness and both the number and cover of non-resident species sampled (Figs 1 and 2). Species observed to be present in the qualitative surveys but of insufficient abundance to be detected by the point intercept technique reflected a similar trend (data not shown).

We observed a large decline in cover of what was initially the dominant species in all plots, the resident *E. virginicus* (Table 2). We suspect that, in 2003, it limited invasion of non-residents in all plots by more completely occupying space and other resources. In 2004, *E. virginicus* cover was beginning to fall in all plots as other species rose in cover. Since the only resident species that recruited in low richness plots was *E. virginicus*, any increases in other species in low richness plots was the result of non-resident recruitment. As the dominance of *E. virginicus* fell steeply in the high and medium richness plots in 2005, the cover of other resident species continued to rise; a negative relationship between resident species richness and invasibility emerged, and this pattern strengthened through 2006 and 2007 (Figs 1 and 2). If our hypothesis for the early invasion resistance conveyed by *E. virginicus* is correct, it fits the mechanism described as the ‘sampling effect,’ in that resistance resulted from the identity and performance of the species selected for

planting. The tendency of *E. virginicus* to lodge may have reinforced this effect. Unfortunately, our ability to attribute a strong sampling effect is confounded by the recruitment of only a single resident species in our low species richness plots.

Another factor potentially affecting invasibility is species evenness, the measure of relative abundance of species. It has been hypothesized that high species evenness may confer resistance to invasion by enhancing niche complementarity. As our low species richness plots only had a single resident species, which was present at very high abundance, such an extreme value might be expected to influence invasibility regardless of other factors. We cannot dismiss this mechanism with this study; some studies have reported finding a correlation between evenness and invasibility (Wilsey & Polley 2002) while others have not (Mattingly et al. 2007). Smith et al. (2004) linked increased abundance of dominant species to increased invasibility, similar to the results of our *E. virginicus*-dominated low species richness plots.

The pattern of a negative relationship between resident richness and invasibility has been frequently observed by others investigating invasion resistance in synthetic grassland plots at a fine scale (Fridley et al. 2007). With few exceptions (Piper et al. 2007), however, other investigators have primarily explored this phenomenon in established, mature grassland plots, whether seeded or natural. Our study is novel in finding the process in primary succession, as the resident community was recruiting from seeds. The negative relationship that we found is consistent with complementary, non-synchronous changes in cover of resident species in our high richness plots over 5 yr (Table 2), similar to the 'temporal complementarity' found by Hobbs et al. (2007) in a long-term study of California grassland dynamics, and Stachowicz et al. (1999, 2002) studying marine invertebrates, where complementary space use was judged to be the mechanism of resistance. The higher number and cover of invasive exotics in our low richness plots presumably resulted from the greater availability of space and other resources than in higher diversity plots, but we are unable to confirm this mechanism with this study. Stachowicz & Byrnes (2006) argue that richness-driven invasion resistance is more likely when resources are limited in a seasonal environment, a description that we think fits our plots, which had been grown on scarcely improved subsoil in a seasonal temperate environment.

Evidence of both sampling and complementarity contributing to a negative relationship between resident richness and invasibility was found in experimental plots planted with prairie species at Cedar Creek in Minnesota (Fargione & Tilman 2005; Fargione et al. 2007). Unlike our study, Cedar Creek plots were planted with resident species, and the community was grown to maturity over

several years with repeated weeding before the plots were allowed to experience invasion. There, the sampling effect was attributed to the presence and long-term persistence of dominant C₄ grasses that had large root systems and were highly efficient at capturing and utilizing nitrogen in the soil. The failure of two of the four C₄ grass species that we planted (Table 1) and the weak development of a third probably reduced the potential for additional invasion resistance in our plots. It is generally recommended that fertilizer be added to nutrient-poor soils when attempting to establish C₄ grasses (Booze-Daniels et al. 1998); however, we chose not to fertilize since that practice is also known to increase invasibility of plant communities by exotics (Booze-Daniels et al. 1998; Leishman & Thomson 2005). Perhaps the trade-off of greater risk of invasion would have been worth the invasion resistance gained by better establishment of C₄ grasses. We might have had greater success in establishing another C₄ grass had we selected and planted a species known to perform well in nutrient-poor, drought-prone sites (Booze-Daniels et al. 1998).

The most aggressive invasive plant species are often exotic species that are suspected to have been released from biotic and abiotic controlling factors existing in other parts of the world where they evolved (Hiero et al. 2005). Exotic invasive species were less diverse and less abundant in our higher richness plots, with the exception of one species, *D. laciniatus*, which by 2007 already ranked among the top four species by percentage cover in all plots and was rapidly increasing in cover in all treatments when we concluded our study (Tables 2 and 3). Since a large population of *D. laciniatus* grew in a waste dump just outside

Table 3. Exotic species that were sampled in the plots in 2007, ranked in categories indicating the level of invasiveness according to the Virginia Division of Natural Heritage (2003), if ranked.

Species	Planted species richness (No. species planted)		
	Low (3)	Medium (12)	High (24)
Highly invasive species			
<i>Ailanthus altissima</i>	0.21 ± 0.2	0	0
<i>Centaurea maculosa</i>	11.1 ± 4.6 ^a	1.2 ± 0.7 ^b	0.8 ± 0.7 ^b
<i>Lespedeza cuneata</i>	1.8 ± 1.0 ^a	1.2 ± 1.2 ^a	0
<i>Lonicera japonica</i>	0	7.8 ± 5.5 ^a	0.1 ± 0.1 ^a
<i>Rubus phoenicolasius</i>	0.2 ± 0.2	0	0
Moderately invasive species			
<i>Dipsacus laciniatus</i>	21.7 ± 0.7 ^a	25.7 ± 7.2 ^a	15.8 ± 5.6 ^a
Occasionally invasive species			
<i>Coronilla varia</i>	0.5 ± 0.4 ^a	6.2 ± 4.4 ^a	1.0 ± 1.0 ^a
<i>Melilotus alba</i>	0.6 ± 0.6	0	0
<i>Melilotus officinalis</i>	0	0	0.4 ± 0.4
<i>Perilla frutescens</i>	2.0 ± 1.7 ^a	0.9 ± 0.9 ^a	0

If the plant was detected by point intercept, the mean ± SE percentage cover is listed. Means with different letter superscripts are significantly different between species richness treatments.

our plots, and the pattern of colonization of plots was from that side of our study area, we suspect that a heavy rain of seeds from the dump overwhelmed the invasion resistance of our plot communities, regardless of their richness. Experimental evidence from other studies (Tilman 1997; Levine 2000; Von Holle & Simberloff 2005) has shown that a heavy propagule rain can overwhelm richness-based invasion resistance; our data fit this view of the importance of propagule pressure.

Conclusion

A seed mixture comprised of 24 native species conferred significantly greater, though incomplete, resistance to invasion compared to low species richness seed mixes, while requiring minimal site preparation and no further intervention. Our method is inexpensive and ecologically attractive as it required no additions of fertilizer or topsoil. We facilitated development of soil only 5 mo before planting by discing and tilling deciduous leaves into the clay. In only 6 yr a barren site of compacted clay subsoil was restored to a native herbaceous plant community with a relatively low abundance and richness of invasive species in the high species richness plots. We attribute this result to a combination of the sampling effect and species complementarity, with a potential contributing effect from low community evenness in the low species richness plots.

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