



The creation of diverse prairie-like communities

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Abstract: We tested the prediction that we are more likely to create persistent, species-rich plant communities by increasing the number of species sown and allowing communities to assemble over six or seven growing seasons. Treatments consisted of four initial seed mixtures comprising 4, 8, 12 and 16 species that represent four functional groups (C_3 graminoids, C_4 grasses, N-fixing species, and late-flowering composites) that predominate within North American prairies. Once seeded, half of the plots were left alone to develop without subsequent reseeding. To provide multiple opportunities for establishment, we reseeded the remaining plots with any target species that failed to establish after two growing seasons. There were two 16 x 16 m (256 m²) replicates per treatment established in 1994 and 1996 on former agricultural land. Annually, we measured total species richness and evenness, total cover, and establishment success defined as target species richness and total percentage cover by target species, collectively. In some instances, significant treatment x year interactions indicated that treatment effects on variables varied among years. Both richness and rate of establishment of target communities were higher in the more species-rich mixtures. Moreover, richness of resident species in the plots declined with increasing target species richness. Reseeding had no measurable effect on any of the variables, nor on the eventual establishment of target communities or individual target species. Our results, indicating that establishment of species-rich plant communities can be enhanced by starting with larger numbers of species at the outset, have implications for projects in which community biodiversity creation and maintenance are key goals.

Nomenclature: Great Plains Flora Association (1986) except where otherwise noted.

Introduction

Community construction involves the development of a target community that performs specific, desired functions (Jordan et al. 1987). Such communities may consist of novel combinations of native or even introduced species. Restoration, a type of construction, in its ideal form is the reconstruction of an assemblage that possesses all the species and functions of the original pre-degraded state. The goals for a constructed assemblage may in turn be *functional* or *structural* (i.e., compositional) in nature. Functional goals include such ecosystem processes as a target primary productivity, water clarity, or nutrient retention. Some functional goals (e.g., soil erosion control) may not require the return of a specific set of original species. Structural goals, on the other hand, involve some measure of species or functional group composition (Smith et al. 1997).

Practitioners perceive that it appears relatively easy to restore such functions as water quality, a habitat structure suitable for an endangered animal species, or a sustainable rate of soil loss (Lockwood and Pimm 1999). In con-

trast, restoration projects that aim to re-create a community containing all the species of the original community are less successful. Lockwood and Pimm (1999) reviewed 87 published restoration projects and found, on the one hand, that successful recovery of such properties as water quality or erosion reduction are commonplace (61% successful) as are the restoration of small subsets of target species (66% successful). Yet, very few studies (6%) reported the successful restoration of their stated goals of original species diversity. In short, once a choice has been made regarding which species will be deliberately used in a restoration, it is a challenge to get all of them to establish and maintain populations over some prescribed time frame. Restoring the original biodiversity of a site seems elusive, even if data from pristine sites are available.

In addition to biodiversity, persistence is often an important goal for created communities. Persistent communities are those in which little species turnover occurs, or at the least richness varies within some prescribed range. From a practical perspective, persistent communities are those which should require minimal time constantly replacing target species and weeding out undesired species.

There are two general methods whereby practitioners may mimic the history of natural community development to create diverse and persistent communities. The first involves varying the size of the initial species pool, which can alter subsequent community development and its eventual persistent state (Case 1990, 1991, Drake 1990, 1991). Persistent, diverse communities may be created more efficiently by starting with a relatively large number of species, and allowing the community to sort itself to a stable endpoint, than by experimenting with many mixes of the target species (Tregonning and Roberts 1978, Roberts and Tregonning 1981).

Secondly, the timing and sequence of species colonization can be critical to community development, and even lead to alternative final states (Wilbur and Alford 1985, Robinson and Dickerson 1987, Drake 1991, Drake et al. 1993). Thus, varying the sequence of species introductions may be important to the success of restoration and construction attempts (Post and Pimm 1983, Drake 1990). For example, timely invasion by a particular species, or set of species, may modify resource levels that inhibit or facilitate invasion by other species (Connell and Slatyer 1977, Robinson and Dickerson 1987, Tilman 1994, Brown and Bugg 2001).

Constructed plant communities, modeled on natural grassland systems typical of the central Plains of the United States, should comprise mixtures of herbaceous perennial species. As structural and functional analogs of prairie plant communities they should be composed predominantly of representatives from four major plant functional groups: perennial C_4 grasses, C_3 graminoids (grasses and sedges), N-fixing species (primarily Fabaceae and Mimosaceae), and late summer flowering, drought-hardy composites (Asteraceae) (Kindscher and Wells 1995). Collectively, species within these four groups can constitute as much as 83 to 98% of the above-ground biomass (Piper 1995) and well over 90% of the total cover (Piper, unpublished data) in Kansas prairie vegetation.

We documented the development over several growing seasons of stands of grassland perennials starting from four initial seed pools. Our goal was not prairie restoration *per se*, but to examine a set of methods for creating synthetic communities with the idea that, if successful, variants of these methods would be widely applicable. We expected that persistent communities would eventually develop, although they would contain fewer target species than were sown. One method broadly corresponded to a plan of letting relatively species-rich systems collapse to persistent endpoints (Tregonning and Roberts 1979, Roberts and Tregonning 1981). A second method aimed

to allow both invasion and local extinction during assembly (Post and Pimm 1983, Drake 1990). We had four hypotheses.

Our first hypothesis was that higher initial seeding diversity would increase the likelihood of establishing a species-rich target community. ('Target' species are defined as those intentionally seeded into the research plots. As such, they are contrasted with 'resident' species, which are present as seeds or perennating organs in the soil at the start of the experiment.) Here, success may be determined at the point at which there is no net decrease in the number of target species in the community (i.e., persistence). Or, success may be measured as the percentage of target species sown that eventually establish and persist in each treatment.

The second hypothesis was that treatment species richness would shorten the time required to achieve 100% cover by the target community. In other words, richer treatments should lead to persistent communities that establish sooner than those resulting from less diverse treatments.

The third hypothesis was that higher initial species richness of the seed mixes would result in a higher diversity of resident species in the plots. This could occur if richer seed mixtures provide a greater variety of niches for non-target species (Palmer and Maurer 1997, Palmer and Chandler-Ezell 2001). The alternative hypothesis was that resident species richness could decrease if target species occupy more niches, thus outcompeting residents. This would have a practical benefit in that undesirable (i.e., weedy) species would be overcome faster in more species-rich mixes. The null hypothesis, of course, was that resident species richness would be invariable or would vary independently of treatment.

Our final hypothesis was that we would be more likely to establish a persistent, diverse community by reseeded target species in subsequent years than by one initial seeding. Any reseeded effects on community structure or establishment success would then be attributed to the process of allowing multiple invasion opportunities, or allowing invasion in the more favorable year, for target species. The premise here was that conditions for establishment (e.g., shading, dormancy requirements) may vary among species, and may be better met in some years than in others.

Materials and methods

A total of 32 plots, established at two sites and in two different years, were located on former agricultural land at The Land Institute, ~3 km SE of Salina, Kansas (T15S

Table 1. Species composition of the four richness level treatments. Species used in the 1994 and 1996 plantings were identical except *S. heterolepis* was substituted for hybrid *Sorghum* in 1996.

Treatment	C ₄ grasses	C ₃ grasses	N-fixing species	Composites
4-species	* <i>Tripsacum dactyloides</i>	‡ <i>Leymus racemosus</i>	* <i>Desmanthus illinoensis</i>	* <i>Helianthus maximiliani</i>
8-species: add	† <i>Sorghum bicolor</i> / <i>S. halepense</i> or * <i>Sporobolus heterolepis</i>	* <i>Elymus glaucus</i>	* <i>Dalea purpurea</i>	* <i>Helianthus mollis</i>
12-species: add	* <i>Panicum virgatum</i>	† <i>Agropyron intermedium</i>	‡ <i>Lotus corniculatus</i>	* <i>Ratibida pinnata</i>
16-species: add	* <i>Eragrostis trichodes</i>	* <i>Agropyron smithii</i>	* <i>Amorpha canescens</i>	* <i>Liatrix pycnostachya</i>

*Native to the Great Plains, †Naturalized, ‡Introduced.

R2W, Section 5, Hutchinson Quadrangle), USA. The soil type for both sites was a Longford silt loam (fine, montmorillonitic, mesic udic Argiustolls) with 3 to 7% slope.

Treatments consisted of four seed mixtures of herbaceous perennial species that represent the four functional groups that predominate within North American tallgrass prairie. The initial seed mixtures comprised 4, 8, 12, and 16 species (Table 1) chosen for their general adaptation to grassland environments and their availability from the Natural Resources Conservation Service or commercial suppliers. Most species used are native to the Great Plains; four taxa are introduced or naturalized in the region (Great Plains Flora Association 1986). Each lower diversity treatment was a subset of its higher diversity counterpart (see Naeem et al. 1994). Hence, the treatments varied the size of the species pool, while keeping representation by functional groups constant. Because species richness of our treatments was confounded with species identity, as designed the study does not avoid the problems of 'sampling effect' or 'hidden treatments' (Huston 1997, Wardle 1999). Hence, conclusions can not be drawn unambiguously about diversity effects *per se* on community establishment in this study.

There were four plots per treatment. Once seeded, half the plots within each treatment were left alone to assemble without further intervention. The other group of plots was reseeded with any species that failed to establish or that disappeared after having established initially. This meant that, for some species in some plots, reseeding was repeated for several years.

A first set of 16 plots was established in 1994. This area, an old field, was occupied by a five-year-old degraded stand of *Medicago sativa* L. with considerable invasion by annual and perennial volunteers. Ground was plowed in the fall of 1993 in preparation for planting the following March. Except for disking and harrowing in early 1994 to prepare the soil for seeding, there was no

Table 2. Seeding rates (gm⁻²) for 17 species used in the 1994 and/or 1996 plantings.

Species	Seeding rate
<i>Agropyron intermedium</i>	0.32
<i>Agropyron smithii</i>	0.34
<i>Amorpha canescens</i>	0.38
<i>Dalea purpurea</i>	0.54
<i>Desmanthus illinoensis</i>	0.30
<i>Elymus glaucus</i>	0.59
<i>Eragrostis trichodes</i>	0.12
<i>Helianthus maximiliani</i>	0.18
<i>Helianthus mollis</i>	0.21
<i>Leymus racemosus</i>	0.66
<i>Liatrix pycnostachya</i>	0.11
<i>Lotus corniculatus</i>	0.26
<i>Panicum virgatum</i>	0.18
<i>Ratibida pinnata</i>	0.22
<i>Sorghum bicolor</i> X <i>S. halepense</i>	0.38
<i>Sporobolus heterolepis</i>	0.59
<i>Tripsacum dactyloides</i>	0.72

weed control attempted either at the start or at any time during the course of the study. Initial soil properties at this site are shown in Table 2.

In March 1994, we laid out square plots, each 16 x 16 m (256 m²), with plots at least 3.7 m apart to help reduce dispersal of target species between adjacent plots. Treatments were distributed randomly across the study area. Seed of *Tripsacum dactyloides* (L.) L., *Desmanthus illinoensis* (Michx.) MacM., *Leymus racemosus* (Lam.) Tsvelev (Barkworth and Dewey 1985), and hybrid perennial *Sorghum* (see Piper and Kulakow 1994) were obtained from research plots harvested at The Land Institute in 1992 and 1993. *Helianthus maximiliani* Schrad. and *Agropyron intermedium* (Host) Beauv. seeds were obtained from the Kansas Plant Materials Center in Manhattan. Seeds of the other species were purchased from commercial sources. To keep within-species seeding density constant across treatments, we used a seeding rate (gm⁻²) for each species, obtained from the United States Department of Agriculture (1948) or the seed supplier, that was

Table 3. Initial soil properties^a at three depth increments for 32 restoration plots established in March 1994 and 1996. Except for organic matter (o.m.), nutrient concentrations are expressed in $\mu\text{g g}^{-1}$. Values are means \pm 1 SE ($n=16$).

1994 Planting										
Depth	pH	P	K	Ca	Mg	% o.m.	NH ₄ -N	NO ₃ -N	Total N	Sand:Silt:Clay
0-30 cm	6.44 \pm 0.05	3.3 \pm 0.2	193 \pm 13	2000 \pm 70	328 \pm 17	2.16 \pm 0.06**	2.79 \pm 0.27	0.324 \pm 0.075	850 \pm 30	43.9:39.5:16.6
30-60 cm	6.97 \pm 0.05	2.2 \pm 0.2	191 \pm 5	1940 \pm 110	317 \pm 22	1.59 \pm 0.10**	2.49 \pm 0.12	0.130 \pm 0.010	550 \pm 20	39.5:41.0:19.4
60-100 cm	7.56 \pm 0.07	2.7 \pm 0.2	161 \pm 5	2320 \pm 150	346 \pm 23	1.12 \pm 0.04***	2.41 \pm 0.16	0.222 \pm 0.105	410 \pm 10	41.9:39.4:18.7
1996 Planting										
0-30 cm	6.29 \pm 0.08	18.1 \pm 1.0***	321 \pm 20***	2550 \pm 100***	577 \pm 38***	1.97 \pm 0.03	3.32 \pm 0.12	0.719 \pm 0.033***	1080 \pm 20***	24.7:46.6:29.6
30-60 cm	7.03 \pm 0.11	6.6 \pm 0.7***	283 \pm 12***	3430 \pm 100***	782 \pm 41***	1.28 \pm 0.03	3.78 \pm 0.19***	0.488 \pm 0.020***	830 \pm 20***	24.6:41.6:33.1
60-100 cm	7.54 \pm 0.10	8.6 \pm 0.8***	241 \pm 8***	3420 \pm 130***	686 \pm 55***	0.88 \pm 0.04	2.68 \pm 0.12	0.494 \pm 0.021*	580 \pm 20***	29.1:40.1:30.8

For each depth increment, site mean higher at * $p < 0.0016$ ($\alpha = 0.05/30$), ** $p < 0.0003$ ($\alpha = 0.01/30$), *** $p < 0.00003$ ($\alpha = 0.001/30$); d.f.=30; Student's *t* test using a Bonferroni correction to reduce the likelihood of Type I error.

^a Soil cores were collected in March 1994 and March 1996, respectively. Sampling consisted of collecting four representative cores from each plot to a depth of 100 cm. Samples were then composited by depth increment, returned to the laboratory, and air-dried at 30°C to constant mass. The samples were ground, then analyzed for pH (potentiometrically in a 1:1 soil/water slurry), Bray P (P-1 method), 1 M KCl-extractable NO₃ and NH₄, and exchangeable K, Ca, and Mg (1 M ammonium acetate extractant). Total N and % o.m. were measured colorimetrically. Details of procedures are in Technicon Industrial Systems (1977) and North Dakota Agricultural Experiment Station (1988). Analyses were performed at the Soils Testing Laboratory at Kansas State University, Manhattan, Kansas.

25% of the rate recommended to achieve a solid monoculture stand (Table 3). Seed was weighed to ± 1 g and parceled into individual bags for each plot before planting. Seeds of all species were then hand-broadcasted onto the soil and lightly raked in.

We established an additional set of 16 256 m² plots 0.8 km NE of the 1994 site in March 1996, but on the same soil type (Longford silt loam) as the 1994 planting. Until autumn 1995, this second site supported an eight-year-old patchy stand of restored native tallgrasses (primarily *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash) grazed by cattle in a rotational grazing scheme. Relative to the 1994 plots, soil at the 1996 site was finer and higher in all soil nutrients tested, but lower in organic matter ($P < 0.05$, *t* test, $N=32$; Table 3). As for the 1994 plots, ground was plowed the previous fall, then disked and harrowed in February 1996. Before seeding, the site was fenced to exclude cattle. We used the same four diversity treatments, reseed/no-reseed option, seeding rates, and maintenance protocol as in the 1994 plots. Because of seed supply limitations, however, we substituted another C₄ grass, *Sporobolus heterolepis* (A. Gray) A. Gray for hybrid perennial *Sorghum* in the 8-, 12-, and 16-species treatments in the 1996 plantings (see Table 1).

Beginning in late July of the establishment year, and annually to the cessation of the study, we monitored the vegetation with twelve 75 x 75 cm sample frames per plot. The quadrats were arranged randomly throughout each plot, and cover classes were estimated visually by species. To avoid possible edge effects, we did not sample within 1 m of plot borders. We estimated species composition

and relative abundance using cover class estimates (Daubenmire 1959), where 1=1-5%, 2=6-25%, 3=26-50%, 4=51-75%, 5=76-95%, and 6=96-100% cover. Cover classes were converted to median values (i.e., 1=2.5%, 2=15%, 3=37.5%, etc.), then averaged for each species per plot. We measured species richness and derived species evenness ($H'/\ln[\text{richness}]$, where H' is the information index), total cover (sum of mean% cover for each species), and percentage cover for target and resident species. We expected that richness would not change dramatically after the first two establishment years because whole species would be unlikely to be added to or eliminated from the communities. However, we expected that large shifts in relative dominance, which can greatly affect evenness, would be more likely year-to-year. The mid-summer sampling period was scheduled to optimize our diversity estimate by coinciding with the phenological overlap of early summer (e.g., C₃ grasses and spring ephemerals) with late summer species (e.g., composites and C₄ grasses) (Piper 1995).

Our criterion for presence was if a species was found within at least one of the twelve quadrats per plot (frequency $\geq 8.3\%$). Any target species missing from the eight randomly preassigned 'reseed' plots were then re-sown annually in March 1996-2000 for the 1994 planting and in March 1998-2001 for the 1996 planting. For each variable measured, we tested for differences among treatments and years using a three-way repeated measures ANOVA (SPSS 2000), in which seed mix treatment, year, and reseeding versus no reseeding were the main effects. The significance level for all tests was $P < 0.05$.

Results

Overall richness, evenness, and percentage cover

Because there was no attempt to control the number of species emerging from the seed bank, total species richness for each plot was always higher than the number of target species sown. There was a general shift in composition with time, however, as the plots were dominated initially by annual and biennial ‘weedy’ species (especially *Setaria* Beauv. spp., *Coryza canadensis* (L.) Cronq., and *Helianthus annuus* L.), and by such perennial weeds as *Convolvulus arvensis* L., then, later, increasingly by target perennials. In the 1994 plots, we sampled a total of 70 species in the establishment year, 90 species in 1995, 80 species in 1996, 79 species in 1997, 76 species in 1998, 72 species in 1999, and 68 species in 2000 summed across all 16 plots. Total species richness across the 1996 set of plots was similar, with 79, 75, 80, 56, 64, and 63 species, respectively, in the first through sixth year of the study. Woody species (e.g., *Ulmus* L. spp. and *Cornus drummondii* C. A. Mey.) never represented >1% cover in any year.

All four target functional groups were maintained in each treatment, although both C₃ graminoids and N-fixing species were represented by relatively low covers in the 1994 planting (C₃: mean=4.58%, N-fixing species: mean=6.21%), and C₃ graminoids by low cover in the 1996 planting (mean=2.22%). Species functional group assignments, and their status as native, naturalized, or introduced, are shown in the Appendix.

In the 1994 plots, there were no treatment effects on total species richness (i.e., combined target and resident species) (Fig. 1A). Significant treatment x year interactions, however, showed that treatment effects differed among years, with total species richness tending to be higher in the 12- and 16-species treatments than in the 4-

species treatment in the first two years. This pattern was reversed in years 4 and 7. In the 1996 planting, total species richness was lower in the 4-species treatment than in the other three treatments (Fig. 1B). In addition, total richness was higher in the establishment year than in all subsequent years.

There were no treatment effects on evenness in the 1994 planting, although there was a general decrease in evenness in years 6 and 7 in these plots (Fig. 2A). In contrast, in the 1996 planting, evenness was greater in the 16-species treatment than in either the 4- or 8-species treatment (Fig. 2B).

In both sets of plots, total percentage cover varied considerably among years. For the 1994 planting, total cover was highest in the first two years, then lower in later years (Fig. 3A). In the 1996 planting, there was a treatment x year interaction on total cover (Fig. 3B). In three years, total cover was higher in the 16-species treatment than in the 4-species treatment. Variation in precipitation among years probably accounted for some of the year-to-year changes we observed. Previous 12 months’ (July-June) precipitation was positively correlated with total percentage cover at both sites (1994 planting: $r=0.95$, 12 d.f., $P<0.01$; 1996 planting: $r=0.68$, 10 d.f., $P<0.05$; Pearson’s correlation). Precipitation during the current growing season (May-July), however, was not correlated with total cover for either planting (1994 planting: $r=0.47$, 12 d.f., n.s.; 1996 planting: $r=-0.45$, 10 d.f., n.s. Pearson’s correlation).

There was no relationship between species richness and total percentage cover in any year for the 1994 planting ($P>0.05$, Pearson’s correlation). In the 1996 plots, however, total species richness was positively correlated with total cover in three of six years (1996: $r=0.53$, $P<0.05$; 1997: $r=0.51$, $P<0.05$; 1999: $r=0.67$, $P<0.01$; d.f.=14, Pearson’s correlation).

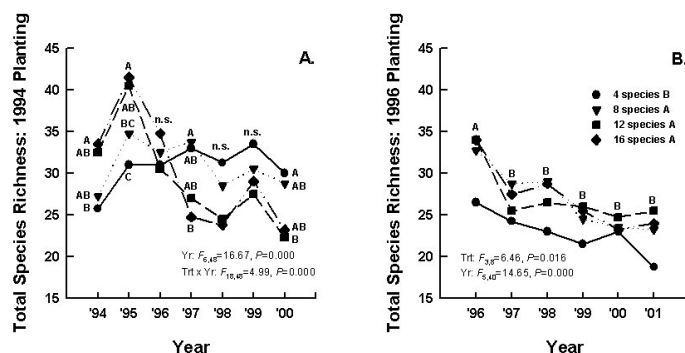


Figure 1. Total species richness of 16 plots planted to four richness treatments in A. 1994 and B. 1996. Within a year (A.), symbols with the same letter indicate that means do not differ at $P<0.05$ (ANOVA, Tukey’s HSD procedure). Years or treatment designations (B.) with the same letter indicate that means do not differ at $P<0.05$ (ANOVA, Tukey’s HSD procedure).

Hypothesis 1: Treatment vs target species richness

Resultant target communities were similar for both sets of plots (Fig. 4A & B), with strong treatment effects occurring. Target species richness of the plots increased directly with the number of species in the initial seed mix, and seemed to reach a stable point by the third year or so. Lack of significant year effects indicated that target species richness changed little within each treatment over the course of the study.

In the 1994 planting, mean percentage establishment of target species (i.e., number of species establishing as a percentage of the number of species sown) ranged from 62.5% in the 8- and 16-species treatments to 70.8% in the 12-species treatment, but these differences were not significant ($F_{3,12}=1.44, P=0.28$, ANOVA). Similarly, in the 1996 plots, the range of percentage establishment was 75.0% (4-species) to 83.3% (12-species), with no treatment differences ($F_{3,12}=0.99, P=0.43$, ANOVA).

Hypothesis 2: Treatment vs target species percentage cover

In the 1994 planting, percentage cover by the target community was greater in the 12- and 16-species treat-

ments than in the 4- and 8-species treatments (Fig. 5A). The target community for the 16-species treatment achieved a mean 100% cover by year 5, and the 12-species target community reached 100% cover by year 6. In the 1996 planting, total target species cover showed a significant treatment x year interaction (Fig. 5B). In every year, however, percentage cover by the target community was generally higher in the 12- and/or 16-species treatments than in the 4-species treatment. In this planting, the target community of the 16-species treatment reached 100% cover by the second year, and the target communities of the 8- and 12-species treatments followed suit in the third year. The target community of the 4-species treatment never achieved a mean 100% cover during the course of the study.

Hypothesis 3: Treatment vs resident species richness

Although this study was not designed explicitly to address the question of whether diversity promotes or inhibits within trophic level diversity, there were nevertheless some significant differences in resident species richness among treatments in the 1996 planting, and treatment effects in some years in the 1994 planting (Fig. 6A-B). In the 1994 planting, by the fourth year, the number of resi-

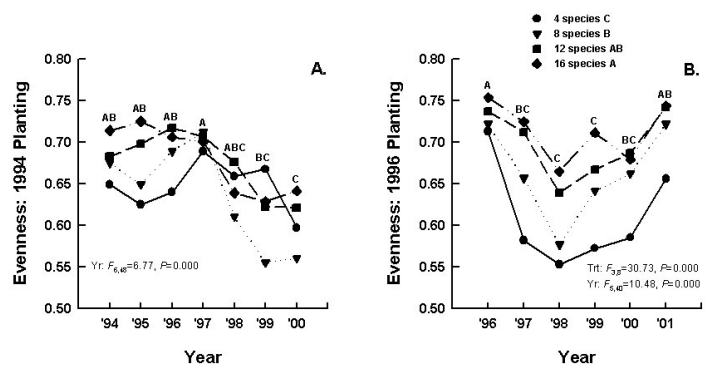


Figure 2. Species evenness of 16 plots planted to four richness treatments in A. 1994 and B. 1996. Years or treatment designations with the same letter indicate that means do not differ at $P<0.05$ (ANOVA, Tukey's HSD procedure).

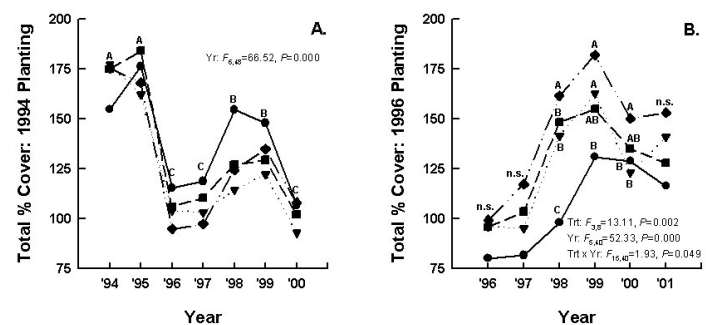


Figure 3. Total percentage cover of 16 plots planted to four richness treatments in A. 1994 and B. 1996. Year designations (A.) with the same letter indicate that means do not differ at $P<0.05$ (ANOVA, Tukey's HSD procedure). Within a year (B.), symbols with the same letter indicate that means do not differ at $P<0.05$ (ANOVA, Tukey's HSD procedure).

dent species was lower in the 12- and 16-species plots than in the 4- or 8-species plots. In the fourth year, for example, annual and biennial cover in the most diverse treatment was ~1/10 that of the least diverse treatment (7 vs. 65%). Even *Convolvulus arvensis*, a perennial weed, had consistently lower cover in the 16-species treatment than in the 4-species treatment (e.g., 16.1 versus 34.7% cover in the second year) in this planting. Moreover, there

was some indication that resident species richness was trending downward with time in the 12- and 16-species treatments but remaining steady in the 4- and 8-species plots (Fig. 6A). The 1996 planting showed an overall general decrease in number of resident species with time, with fewer resident species supported in the 16-species plots than in the 4- or 8-species treatments (Fig. 6B).

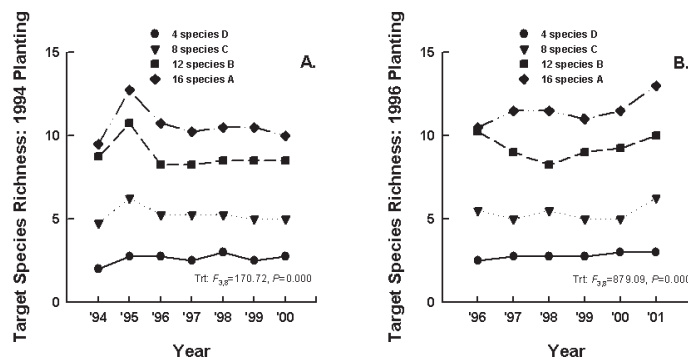


Figure 4. Richness of target species in 16 plots planted to four richness treatments in A. 1994 and B. 1996. Treatment designations with the same letter indicate that means do not differ at $P < 0.05$ (ANOVA, Tukey's HSD procedure).

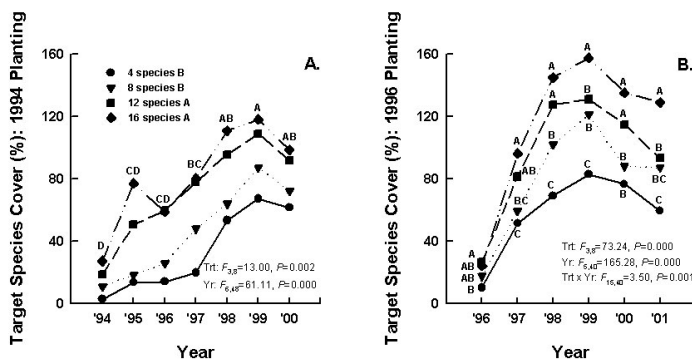


Figure 5. Total percentage cover by target species in 16 plots planted to four richness treatments in A. 1994 and B. 1996. Treatment designations or years with the same letter indicate that means do not differ at $P < 0.05$ (ANOVA, Tukey's HSD procedure). Within each year (B.), symbols with the same letter indicate that means do not differ at $P < 0.05$ (ANOVA, Tukey's HSD procedure).

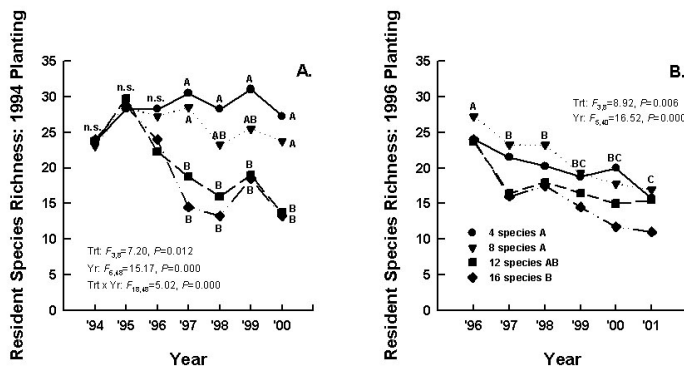


Figure 6. Richness of resident species in 16 plots planted to four richness treatments in A. 1994 and B. 1996. Within each year (A.), symbols with the same letter indicate that means do not differ at $P < 0.05$ (ANOVA, Tukey's HSD procedure). Treatment designations or years (B.) with the same letter indicate that means do not differ at $P < 0.05$ (ANOVA, Tukey's HSD procedure).

Hypothesis 4: Effects of reseeded on establishing target communities

Somewhat surprisingly, there were no reseeded effects on any of the variables measured within either set of plots ($P > 0.05$, ANOVA). Nor were there any reseeded effects on establishment (% cover) by any of the target species.

Discussion

Several important factors must be considered in the construction or restoration of stable and diverse plant communities. From a practical perspective, the 'success' of one's project could be defined in any of several ways. For example, if the purpose is to create a stand composed predominantly of target species, then the concern might be the amount of time following seeding required to achieve high (e.g., 100%) cover by the target species collectively. Related to this objective would be the speed with which undesired, weedy species are supplanted by desired, target species. Or, if the goal is to establish as diverse a community as possible, then a measure of success could be the species richness of the eventual target community as a proportion of the number of species sown. Third, if the cost of seed is a major consideration, then an appropriate goal might be to achieve the maximal level of target species richness with the minimal number of species included in the original mix. Finally, for practitioners facing significant time and labor constraints, community persistence is an important issue where persistence is inversely related to the level of ongoing management required continually to replace target species and weed out undesired species.

The present study aimed to demonstrate that varying the initial species pool, and allowing multiple opportunities for colonization, can have significant effects on subsequent plant community composition. We examine our observations for each of our four predictions in turn.

Hypothesis 1: Treatment vs target species richness

First, we predicted that richer species mixes would eventually produce assemblages containing more species, and more of the species initially sown. Indeed, we found in both sets of plantings (1994 and 1996) that target species richness increased with initial planting richness. It is likely, however, that our plots were undersaturated with target species. Small (122 m²) areas of local tallgrass prairie typically support 30 to 50 perennial species (Piper 1995). It would be interesting, in a follow-up study, to discover the point above which final community diversity no longer increases with initial seeding diversity. It would

also be crucial to separate the effects of species diversity per se from species identity in the various treatments (see Huston 1997, Wardle 1999). For example, since *T. dactyloides*, *L. racemosus*, *D. illinoensis*, and *H. maximillianii* were constants in all plots, another study could randomly select 1 to 4 species from a pool of available species within each functional group to create the various levels of species richness. Otherwise, it is difficult to know to what extent the treatment effects we observed were due to the characteristics of the species present in richer treatments (e.g., possible weed-control effects of a species contained in the 12- and 16-species plots).

Natural systems, of course, operate at scales much greater than the size of the plots used in our study, and maintenance of species diversity may therefore be more important among plots than within plots. At the landscape level, then, changing diversity within plots may not matter as long as overall diversity is maintained across plots.

Hypothesis 2: Treatment vs target species percentage cover

Our second prediction was that persistent communities would establish faster from richer treatments through the collective ability of the target species to occupy a greater range of niches, thereby preempting access to resources by weeds. Because of their canopy, typically deep and extensive root systems, and regrowth in spring from underground perennating organs, grassland perennials should, in general, compete well against annuals and biennials. This pattern corresponds to the commonly observed assembly trajectory typical of old field succession in the central United States, in which an initial period of dominance by weedy annuals is followed by increasing dominance by an array of herbaceous perennials (Holt et al. 1995). We were not surprised by the gradual replacement of annual species with perennials. The question remains, however, whether plant species diversity per se can suppress weeds (Evers 1983, Liebman and Dyck 1993, Brown and Bugg 2001). In the 1994 planting, percentage cover by resident species declined fairly dramatically, an effect that was enhanced in the richer treatments. This treatment effect was not seen in the 1996 planting, although weedy cover in the 1996 plots was significantly lower by the second year. Occupation of a greater variety of niches by members of more diverse target communities may increase a community's resistance to invasion by species present in the seed bank or by species dispersing from outside the plot (Tilman 1997). Because the total seed mass added to the plots increased incrementally from the 4- to 16-species treatment, it is unknown to what extent seeding density itself may have contributed to the results we obtained. Where we defined success in terms of

percentage cover by the intended community, we obtained a successful (i.e., sum of target species cover $\geq 100\%$) establishment remarkably fast in the richer treatments. Target species richness also reached a stable level fairly soon in all treatments. Although the possibility remains that, with sufficient time, the different persistent communities could eventually converge on a single persistent community composition, as of the close of the study, no net species loss was evident.

Hypothesis 3: Treatment vs resident species richness

Several years ago, Palmer and Maurer (1997) conducted a study in which they asked, "Does diversity beget diversity?" Their findings, based on annual crop monocultures and mixtures observed within a single growing season, were that species diversity of weeds was higher in mixture than in monocultures, suggesting that plant diversity somehow increased microhabitat heterogeneity, provided 'diversity-promoters' in the mix, or affected competitive interactions among crops to allow greater coexistence. The results from our study seemed to indicate an opposite effect, that target species richness reduced the number of resident species, especially after the first or second year. This pattern may have resulted from a more thorough occupation of available niches by established target species in high-richness treatments, resulting in a monopolization of resources that prevented seedling establishment in later years.

Hypothesis 4: Effects of reseeded on establishing target communities

Finally, because the biotic micro-environments change greatly from one year to the next in successional communities, we expected that some species, unable to establish in year 1 would find the reduced weed cover, altered microclimate, or other factors prevailing in subsequent years more favorable for their germination and growth. Betz et al. (1999) and Schramm (1992) have proposed long-term successional schemes for tallgrass prairie restoration in which first-stage communities (the 'prairie matrix') are replaced by stages that appear several years (or decades) later. Successional theory and assembly models led us to expect that transitional states would be important. Hence, we tested the idea that we could more readily create a diverse stable community by allowing multiple colonizations by target species than by one initial seeding. Nevertheless, our results showed that target species had one initial opportunity to enter these communities, and plots did not seem to become more favorable for seedling establishment of missing species in later years. Target species that were present in early years, but that disappeared subsequently, could not be re-estab-

lished from seed later on. Our results seem to support Weber (1999), who, in contrast to Schramm (1992) and Betz et al. (1999), advocated including 'late successional' species in initial seed mixes as the best way to create diverse prairie plantings. This may be the most important finding of this study from a restoration perspective, although our 6 to 7 year study is still rather short-term.

Each target species was encountered at least once during the course of the study, demonstrating that each was at least able to germinate and establish for a short time, if not persist, within the plots. This difficulty in permanently establishing some target species may have arisen for two reasons. First, after the establishment year, the environment of the plots was characterized by increasingly dense stands of perennial plants. Seedlings may not have been able to cope with this shaded environment. Second, small mammals (e.g., *Microtus ochrogaster* Wagner) and mound-building ants (*Pogonomyrmex occidentalis* Cresson) became active in these plots in later years and may have removed seeds and seedlings as they appeared following reseeded. Our definition of species presence was fairly conservative. Conceivably, a target species may have been present in a plot, but at too low a frequency for us to sample. The possibility exists, then, that these plots were in fact richer than we measured and, with the passage of enough time, rare target species will manifest themselves.

Comparing the 1994 and 1996 plantings

Because both year of abandonment and nature of the last crop can affect the successional trajectories of old fields (e.g., Pickett 1982), we expected there to be some differences in pattern of community development between the 1994 and 1996 plantings. For instance, the lack of mechanical soil cultivation for eight years prior to establishment at the 1996 site might have reduced the size of its weedy seed bank relative to the 1994 site. Continuous soil disturbance should promote weedy species. Perhaps the most striking difference between the sites was the difference in cover by N-fixing species in the target communities (1994: mean=6.21% versus 1996: mean=36.53%). Otherwise, percentage cover by the various functional groups were similar between sites. Other community attributes were sufficiently robust to transcend site and year effects. These included a similar number of resident species per plot in the establishment year, a faster decline of resident species in the more species-rich treatments, and the greater target community richness and cover obtained with the richer seed mixtures. Our results therefore suggest a positive role for perennial

Table 4. Performance of native vs non-native target species in the various richness treatments in two plantings. Percentage species established and % cover per species were determined in the final year of the study for each planting. Numbers are means of 4 plots per treatment.

Treatment	Number of non-native species used	1994 Planting—7th Year				1996 Planting—6th Year				
		% Established		% Cover per species		% Established		% Cover per species		
		Native	Non-native	Native	Non-native	Native	Non-native	Native	Non-native	
4	1	92	0	22.3	0	1	100	0	19.8	0
8	2	83	0	14.3	0	1	89	0	13.9	0
12	4	88	38	12.7	1.9	3	92	58	10.4	4.0
16	4	73	31	11.0	1.7	3	85	67	10.7	5.8

plant biodiversity in reducing weed incidence and thereby accelerating grassland community establishment.

Establishment of native versus non-native target species

Although this study was not intended as an experiment in prairie restoration, it is nevertheless important to examine whether some species we grouped together functionally (e.g., the introduced C₄ grass *Sorghum bicolor x halepense* with the native prairie perennial C₄ grasses; the introduced *Lotus corniculatus* L. with the native legumes) may not in fact have been ecologically similar. One way to test this is to compare the performance of the non-native species in question relative to other members of its functional group. Here, hybrid *Sorghum* responded like a short-lived perennial, declining in the 1994 plots from 9% cover in 1994, to 5% in 1995, to <1% cover in each of the subsequent years. In contrast, the native C₄ grasses (*T. dactyloides*, *S. heterolepis*, *E. trichodes*, and *P. virgatum*) established well and remained vigorous. This may lead to difficulties interpreting the results obtained from treatments using ecologically dissimilar species. Lotus, on the other hand, acted in concert with the rest of the legumes at each site. In the 1994 planting, its percentage cover rose then fell with time, ranging from 5% in 1994, to 11% in 1995, 3% in 1996, 2% in 1997, and <1% afterward. In the 1996 planting, *Lotus* rose from 2% cover in 1996, to 4% in 1997, 8% in 1998, 13% in 1999, 10% in 2000, and 5% in 2001. These results suggest that it was valid to include *L. corniculatus* in the functional group that also contained *A. canescens*, *D. purpurea*, and *D. illinoensis*.

In general, however, the native species outperformed the naturalized and introduced species in the treatment mixes. This was true both in terms of the percentage of species present in the plots at the end of the study as well as the mean cover per species (Table 4).

Implications of the study

Jordan et al. (1987) declared that ecologists have much to glean, both theoretically and practically, from synthetic approaches to the study community development (see also Munro 1991). During periods of several years, it is possible to observe rates of local extinction, invasion, and changes in relative abundance in ensembles. Such studies may be valuable for gaining insights into the ways natural communities begin, develop, and achieve stability.

Positive relationships between level of biodiversity and functional efficiency of ecosystems have been proposed (e.g., Naemm et al. 1994), and studies of experimental grassland systems have indicated that diversity, productivity, resilience, and sustainability are linked (Tilman et al. 1996). Our study suggested a role for species diversity in assisting the development of persistent, diverse prairie-like plant communities. Such results could contribute to a methodology that could be applied elsewhere and on a larger scale to restore and conserve diversity.

For instance, less than 5% of the original extent the North American tallgrass prairie remains (Samson and Knopf 1994). Many component species exist at low population densities, offering the hope of restoring a nearly original complement to once degraded lands. Across the scale of North America's tallgrass prairies, however, natural, non-assisted recovery may be impossible; the only hope is to re-create the original diversity on lands now remote from any source of natural immigration. Our results, indicating that establishment of species-rich plant communities can be enhanced by starting with larger numbers of species, have implications for the restoration of prairies and other types of ecosystems, mitigation, or

landscaping designs where biodiversity creation and maintenance are goals.

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Appendix. Functional group assignments for identifiable taxa sampled in the 1994 and 1996 assembly plots. Several species occurred as small seedlings, in many instances only once.

Perennial C4 grasses	Perennial C3 gram inoids	N-fixing species	Perennial composites	Annuals/biennials	Other perennials
* <i>Andropogon gerardii</i>	† <i>Agropyron intermedium</i>	* <i>Amorpha canescens</i>	* <i>Achillea millefolium</i>	‡ <i>Abutilon theophrasti</i>	* <i>Acer negundo</i>
* <i>A. saccharoides</i>	* <i>Agropyron smithii</i>	* <i>Cassia chamaecrista</i>	* <i>Artemisia ludoviciana</i>	* <i>Acalypha virginica</i>	* <i>Apocynum cannabinum</i>
* <i>A. scoparius</i>	† <i>Bromus inermis</i>	‡ <i>Coronilla varia</i>	* <i>Aster ericoides</i>	* <i>Amaranthus retroflexus</i>	* <i>Asclepias syriaca</i>
* <i>Bouteloua curtipendula</i>	* <i>Carex</i> sp.	* <i>Dalea candida</i>	* <i>Aster novae-angliae</i>	* <i>Amaranthus graecizans</i>	† <i>Campsis radicans</i>
* <i>Bouteloua hirsuta</i>	* <i>Dichanthelium oligosanthe</i>	* <i>Dalea purpurea</i>	* <i>Cirsium undulatum</i>	* <i>Ambrosia artemisiifolia</i>	* <i>Cassia marilandica</i>
* <i>Chloris verticillata</i>	* <i>Elymus glaucus</i>	* <i>Desmanthus illinoensis</i>	* <i>Eupatorium altissimum</i>	* <i>Ambrosia trifida</i>	* <i>Celtis occidentalis</i>
* <i>Eragrostis trichodes</i>	* <i>Elymus virginicus</i>	* <i>Desmodium illinoense</i>	* <i>Helianthus maximiliani</i>	* <i>Arisida oligantha</i>	† <i>Convolvulus arvensis</i>
* <i>Leptoloma cognatum</i>	† <i>Festuca arundinacea</i>	* <i>Lespedeza capitata</i>	* <i>Helianthus mollis</i>	† <i>Bromus japonicus</i>	* <i>Cornus drummondii</i>
* <i>Panicum virgatum</i>	* <i>Hordeum jubatum</i>	‡ <i>Lotus corniculatus</i>	* <i>Hieracium longipilum</i>	† <i>Bromus tectorum</i>	* <i>Cynanchum laeve</i>
* <i>Paspalum laeve</i>	* <i>Koeleria pyramidata</i>	‡ <i>Medicago sativa</i>	* <i>Kuhnia eupatorioides</i>	† <i>Camelina microcarpa</i>	* <i>Fraxinus pennsylvanica</i>
* <i>Schedonnardus paniculatus</i>	‡ <i>Leymus racemosus</i>	‡ <i>Melilotus alba</i>	* <i>Liatris punctata</i>	* <i>Capsella bursa-pastoris</i>	* <i>Geum canadense</i>
* <i>Sorghastrum nutans</i>	† <i>Lolium perenne</i>	‡ <i>Melilotus officinalis</i>	* <i>Liatris pycnostachya</i>	‡ <i>Carduus nutans</i>	* <i>Gleditsia triacanthos</i>
† <i>Sorghum hybrid</i>	* <i>Poa pratensis</i>	* <i>Robinia pseudo-acacia</i>	* <i>Ratibida pinnata</i>	* <i>Cenchrus longispinus</i>	* <i>Gymnocladus dioica</i>
* <i>Sporobolus asper</i>		* <i>Strophosyles leioperma</i>	* <i>Ratibida tagetes</i>	† <i>Chenopodium album</i>	* <i>Juniperus virginiana</i>
* <i>Sporobolus cryptandrus</i>		‡ <i>Trifolium pratense</i>	* <i>Solidago canadensis</i>	* <i>Chenopodium berlandieri</i>	† <i>Lonicera</i> sp.
* <i>Sporobolus heterolepis</i>		‡ <i>Vicia villosa</i>	* <i>Solidago rigida</i>	* <i>Chenopodium desiccatum</i>	† <i>Morus alba</i>
* <i>Tridens flavus</i>			‡ <i>Taraxacum officinale</i>	* <i>Cirsium altissimum</i>	* <i>Oxalis stricta</i>
* <i>Tripsacum dactyloides</i>			* <i>Vernonia baldwinii</i>	* <i>Conyza canadensis</i>	* <i>Oxalis violacea</i>
				* <i>Croton glandulosus</i>	* <i>Physalis heterophylla</i>
				* <i>Cuscuta cuspidata</i>	* <i>Physalis pumila</i>
				† <i>Descurainia pinnata</i>	† <i>Plantago major</i>
				† <i>Digitaria sanguinalis</i>	* <i>Polygonum scandens</i>
				† <i>Echinocloa crusgalli</i>	* <i>Rhus glabra</i>
				† <i>Eragrostis ciliaris</i>	* <i>Rumex altissimus</i>
				* <i>Eriogonum strigosum</i>	‡ <i>Rumex crispus</i>
				* <i>Eriochloa contracta</i>	* <i>Salvia azurea</i>
				* <i>Erysimum asperum</i>	* <i>Solanum interius</i>
				* <i>Euphorbia dentata</i>	* <i>Symphoricarpos orbiculatus</i>
				* <i>Euphorbia maculata</i>	* <i>Teucrium canadense</i>
				* <i>Euphorbia marginata</i>	* <i>Toxicodendron radicans</i>
				* <i>Helianthus annuus</i>	‡ <i>Ulmus pumila</i>
				‡ <i>Hibiscus trionum</i>	* <i>Ulmus rubra</i>
				‡ <i>Lactuca serriola</i>	* <i>Verbena stricta</i>
				† <i>Lamium amplexicaule</i>	* <i>Verbena urticifolia</i>
				* <i>Lepidium virginicum</i>	* <i>Vitis riparia</i>
				† <i>Lolium persicum</i>	
				* <i>Mollugo verticillata</i>	
				* <i>Oenothera laciniata</i>	
				* <i>Panicum capillare</i>	
				* <i>Panicum dichotomiflorum</i>	
				* <i>Plantago lanceolata</i>	
				* <i>Plantago patagonica</i>	
				† <i>Portulaca oleracea</i>	
				† <i>Setaria glauca</i>	
				† <i>Setaria viridis</i>	
				* <i>Silene antirrhina</i>	
				* <i>Solanum rostratum</i>	
				‡ <i>Sonchus asper</i>	
				† <i>Thlaspi arvense</i>	
				‡ <i>Tragopogon dubius</i>	

*Native to the Great Plains (per Great Plains Flora Association 1986)

†Naturalized

‡Introduced