Soil Heterogeneity Effects on Tallgrass Prairie Community Heterogeneity: An Application of Ecological Theory to Restoration Ecology

Sara G. Baer,[1,2,3] Scott L. Collins,[3,4] John M. Blair,[3] Alan K. Knapp,[3,5] and Anna K. Fiedler[3,6]

Abstract

Spatial heterogeneity of resources can influence plant community composition and diversity in natural communities. We manipulated soil depth (two levels) and nutrient availability (three levels) to create four heterogeneity treatments (no heterogeneity, depth heterogeneity, nutrient heterogeneity, and depth + nutrient heterogeneity) replicated in an agricultural field seeded to native prairie species. Our objective was to determine whether resource heterogeneity influences species diversity and the trajectory of community development during grassland restoration. The treatments significantly increased heterogeneity of available inorganic nitrogen (N), soil water content, and light penetration. Plant diversity was indirectly related to resource heterogeneity through positive relationships with variability in productivity and cover established by the belowground manipulations. Diversity was inversely correlated with the average cover of the dominant grass, Switchgrass (*Panicum virgatum*), which increased over time in all heterogeneity treatments and resulted in community convergence among the heterogeneity treatments over time. The success of this cultivar across the wide range of resource availability was attributed to net photosynthesis rates equivalent to or higher than those of the native prairie plants in the presence of lower foliar N content. Our results suggest that resource heterogeneity alone may not increase diversity in restorations where a dominant species can successfully establish across the range of resource availability. This is consistent with theory regarding the role of ecological filters on community assembly in that the establishment of one species best adapted for the physical and biological conditions can play an inordinately important role in determining community structure.

Key words: grassland, *Panicum virgatum*, restoration, soil heterogeneity, Switchgrass, tallgrass prairie.

Introduction

Tallgrass prairie is a floristically diverse and formerly extensive ecosystem in North America. Since the 1830s the extent of the tallgrass prairie has declined 82–99%, representing the greatest post-European settlement loss of any terrestrial ecosystem in North America (Samson & Knopf 1994). Reintroduction of tallgrass prairie species into former cropland is a common restoration practice. However, plant diversity is generally slow to recover in these restorations, even in the presence of nearby native prairie as a seed source (Kindscher & Tieszen 1998) or with extensive efforts to introduce native forbs (Warkins & Howell 1983; Thompson 1992; Sperry 1994).

Both the availability and heterogeneity of resources influence plant community composition and species distri-

butions in natural systems (Grime 1979; Huston 1979; Tilman 1984, 1987; Robertson et al. 1988). Several studies have demonstrated a positive relationship between soil resource heterogeneity and plant species diversity in native grasslands (Fitter 1982; Silvertown et al. 1994; Inouye & Tilman 1995; Rusch & Fernandez-Palacios 1995; Steinauer & Collins 1995). Spatial variability of soil resources results from the presence and composition of plants (Gibson 1988; Hook et al. 1991; Milchunas & Lauenroth 1995; Vinton & Burke 1995), topography (Burke et al. 1999), and disturbances such as grazing, fire, and small mammal activity (Robertson et al. 1993; Collins et al. 1998; Knapp et al. 1999). Conversion of prairie to row-crop agriculture homogenizes the soil environment through repeated mixing, leveling, monospecific crop production, and uniform application of nutrients (Rover & Kaiser 1997). Thus, reduced heterogeneity of the soil environment at the onset of prairie restorations in former long-term cultivated soils may act to slow recovery of species diversity.

We established replicated experimental plots to examine the effects of soil heterogeneity on plant diversity in a prairie restoration. Previously, we documented that nitrogen (N) availability was inversely related to plant diversity and the similarity of the restored community to native tallgrass prairie (Baer et al. 2003, 2004). Here we examine temporal changes in the restored plant community to

[1] Address correspondence to S. G. Baer, email sgbaer@siu.edu
[2] Present address: Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901, U.S.A.
[3] Division of Biology, Kansas State University, Manhattan, KS 66506, U.S.A.
[4] Present Address: Department of Biology, University of New Mexico, Albuquerque, NM 87131, U.S.A.
[5] Present Address: Department of Biology, Colorado State University, Fort Collins, CO 80523, U.S.A.
[6] Present Address: Center for Integrated Plant Systems, Michigan State University, East Lansing, MI 48824, U.S.A.

altered resource heterogeneity. We altered soil N availability and soil depth to create four levels of resource heterogeneity within a long-term cultivated field. N was chosen because it is a limiting nutrient in grasslands (Owensby et al. 1970; Seastedt et al. 1991) that modulates plant community structure and diversity in both native prairie and successional systems (Carson & Barrett 1988; Gibson et al. 1993; Steinauer & Collins 1995; Collins & Wein 1998; Foster & Gross 1998). Soil depth was altered because soil depth varies with topographic position in nearby native prairie, which influences soil N availability (Turner et al. 1997), plant productivity (Briggs & Knapp 1995), and plant diversity (Gibson & Hulbert 1987). We varied these two resources at the onset of a restoration to test the following hypotheses: (1) increasing resource heterogeneity will promote divergence in plant community structure among the heterogeneity treatments as a result of differences among communities established under different soil depth and nutrient conditions and (2) increasing heterogeneity of soil resources will increase species diversity by providing a greater variety of suitable microsites for different species with varying resource requirements or by mediating competition and providing competitive release of subordinate species (i.e., forbs) from dominant species (i.e., grasses). In the third year of restoration, we examined ecophysiological characteristics of the dominant species to determine if leaf-level responses to altered resource availability could explain community patterns in response to varied heterogeneity of soil resources.

Methods

Study Site

The restoration was conducted in a recently abandoned agricultural field (cultivated for >50 years) at the Konza Prairie Biological Station (KPBS), located near Manhattan, Kansas (lat 39°05′N, long 96°35′W). The field contained a 0–1% slope and silt loam soil (mesic Typic Arguidoll) formed by colluvial and alluvial deposits. The elevation at the site was approximately 340 m. In the 3 years of study (1998, 1999, and 2000), total precipitation was 944, 825, and 628 mm, of which 593, 693, and 390 mm fell from April through September, respectively. The 30-year mean annual and growing season precipitation were 835 and 622 mm/year, respectively.

Historically, the vegetation at the site would likely have been representative of lowland areas at KPBS, dominated by the native warm-season grasses of Big bluestem (*Andropogon gerardii* Vitman), Little bluestem (*Schizachyrium scoparium* Michx. (Nash)), Indiangrass (*Sorghastrum nutans* (L.)), and Switchgrass (*Panicum virgatum* L.). Lowland prairie at KPBS is also interspersed with a variety of forbs and less common grasses (Freeman 1998). Knapp et al. (1998) provide a complete description of physical and biological characteristics of KPBS.

Experimental Design and Restoration Approach

In the summer of 1997, we established sixteen 6 × 8–m plots (with 6-m buffer strips between plots) delineated in four blocks (4 plots/block). Plots within each block were randomly assigned to heterogeneity treatments of control, soil depth heterogeneity, soil nutrient heterogeneity, or maximum heterogeneity containing both the depth and nutrient heterogeneity treatments (Fig. 1). The soil depth and nutrient manipulations were assigned to strips within each plot. The soil depth heterogeneity plots contained alternating 2 × 6–m strips of buried native limestone. The nutrient heterogeneity plots contained three 2 × 8–m strips with low, ambient, and high N availability. The maximum heterogeneity plots contained both the soil depth and soil nutrient heterogeneity treatments. All plots were subdivided into twelve 2 × 2–m subplots for sampling.

Following the assignment of the heterogeneity treatments, plots were excavated to a depth of 25 cm. Limestone slabs (3–6 cm thick and 40–70 cm in width and length) were pieced together to fill the 6 × 8–m strips, and the soil was replaced and leveled across the site. In autumn, the field was lightly disked (2–3 cm deep) to reduce weeds.
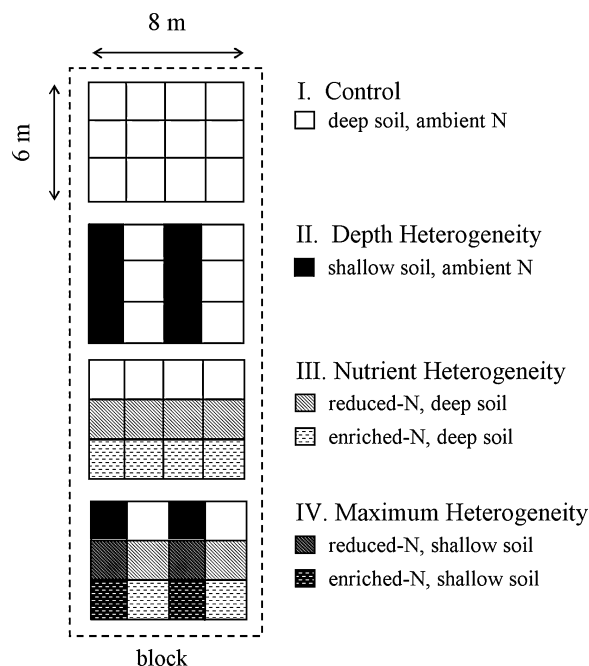

Figure 1. Experimental design of control, depth heterogeneity, nutrient heterogeneity, and maximum heterogeneity whole-plot treatments. Each whole-plot treatment was randomly assigned to a location within each of the four blocks (n = 4 per treatment, 16 plots total). Soil depth (deep and shallow) and nutrient availability (reduced, ambient, and added N) were assigned to widthwise 2 × 6–m and lengthwise 2 × 8–m strips, respectively. Maximum heterogeneity plots contained all levels of soil depth and nutrient treatments. Each plot was divided into twelve 2 × 2–m subplots for sampling.

In February of 1998, sawdust (49% carbon) was added to the strips assigned to the reduced N availability treatment. Sawdust was applied at a rate of 5.5 kg/m² (dry weight) to increase existing soil carbon (C) to a level representative of prairie soil ($\approx$3% C, or two times the existing C content) based on total soil C (0–15 cm) content of 1.5% and bulk density of 1.2 g/cm³. All plots were tilled following the C addition to promote similar conditions prior to planting. Strips with increased N availability were fertilized with ammonium nitrate at a rate of 5 g N/m². Fertilizer was applied following germination of plants in July 1998 and in early to mid-June of years 2 (1999) and 3 (2000).

Native prairie vegetation was reintroduced to the site in spring of 1998 by seeding grasses with a grass drill and hand broadcasting forbs over each plot. All plots were seeded with 42 native prairie species at rates selected to achieve a lognormal species distribution representative of prairie habitats at KPBS. Each species was assigned to one of four seeding categories: dominant grass (160 seeds/m²), common (16 seeds/m²), frequent (10 seeds/m²), or uncommon (5 seeds/m²) species. The dominant grasses were also planted at the same density in buffer strips between the experimental plots to minimize potential edge effects. Grass seed was obtained from a local commercial producer (Star Seed, Inc., Beloit, KS, U.S.A.) and forbs were either locally collected or purchased from Midwestern nurseries. Seed treatments and preparation for planting were followed according to Rock (1981), Packard & Mutel (1997), and Shirley (1994). Baer et al. (1999) provide a complete description of species, seeding rates, and sources of seed used.

Following seeding, each plot was covered with native prairie hay to promote soil–seed contact, maintain soil moisture, reduce loss of seeds by wind, and further promote a lognormal distribution of species from any seed sources within the hay. Deer were excluded from the plots with an electrical fence. Management of the site included burning in the spring prior to the second growing season to reduce standing dead biomass of early successional native and non-native species that accumulated during the first growing season. The site was not burned prior to the third growing season so as not to further promote the dominance of the seeded warm-season grasses.

Resource Heterogeneity Measures

A relative index of inorganic N availability was obtained using buried ion exchange resins (Binkley & Matson 1983). Bags constructed from nylon material were filled with 20 g of a 1:1 mixture of strongly acidic cation (Dowex 50 WXZ, Sigma Chemical, St. Louis, MO, U.S.A.) and strongly basic anion (Dowex 1 × 8-50) resins preloaded with H^+ and Cl^-, respectively. One resin bag was placed in the surface 10 cm of soil in each subplot in July and harvested in November each year. Following collection, resin bags were rinsed with deionized water to remove excess soil, extracted with 75 mL of 2 M KCl by shaking for 1 hour at 200 rpm, and

then filtered through 0.4-μm polycarbonate membranes. Inorganic N was analyzed colorimetrically on an Alpkem Flow Solution autoanalyzer (Clackamas, OR, U.S.A). Ammonium (NH_4–N) was measured using the phenol blue method, and nitrate (NO_3–N) was determined by diazotization with sulfanilamide after reduction through a cadmium coil (Keeney & Nelson 1982). Due to high H^+ ion concentration in resin bag extracts, all samples were neutralized prior to analysis.

Soil water content was measured one time in mid–growing season each year from the surface 10 cm of soil. Two soil cores (2-cm diameter) were removed from each subplot, one from directly under plants and the other from the area between plants. In the laboratory, soil samples were homogenized through a 4-mm sieve and stored at 4°C. Following sieving, gravimetric soil water content was determined from approximately 50 g field moist soil that was weighed, dried for 2 days at 105°C, and reweighed. In 1998, soil moisture was only measured in the control and maximum heterogeneity plots, whereas all treatments were sampled for soil moisture in 1999 and 2000. Soil moisture was only sampled 7–9 days after the last precipitation event (>3 cm).

Photosynthetically active radiation (PAR) was measured in every subplot during mid–growing season of the third restoration year. Percentage of maximum PAR at the soil surface was determined on a sunny day between 1030 hr and 1530 hr. Five integrated measurements of photosynthetic photon flux density (PPFD) were taken with a 0.5-m ceptometer (Decagon Devices, Inc., Pullman, WA, U.S.A.) and averaged from each position (soil surface and above the canopy).

Plant Community Responses to Heterogeneity

At the end of each growing season, a 20 × 50–cm frame was randomly placed outside of the permanent species composition monitoring quadrats in each subplot. All vegetation rooted within the 0.1-m² area was clipped at the soil surface and sorted into planted and volunteer classes of grasses and forbs. In the third growing season, when the site was not burned in the spring, live and dead biomass produced in that year was separated from the previous year's dead biomass. Biomass was dried for 10 days at 60°C and weighed to estimate aboveground net primary production (ANPP) (Briggs & Knapp 1991).

Species identity and maximum percent cover were recorded in spring (June) and summer (August) of each year from two permanently located, 50 × 50–cm quadrats in the center of each subplot. The maximum seasonal cover value for each species was retained, and the replicate 0.25-m² quadrats in each subplot were then averaged prior to further analyses. Species richness was determined from the total number of species recorded from each whole-plot. Whole-plot diversity was calculated from the average percent cover of each species over all 12 subplots using Shannon's diversity index ($H' = -\sum p_i \ln p_i$, where p_i

represented the relative contribution of each species to total percent cover). Richness and diversity were also determined from four plots (of the same dimensions) that were randomly delineated in nearby lowland native prairie on the same soil type in the third year of this study. Plant community similarity was compared among the heterogeneity treatments each year. Proportional similarity was calculated according to Whittaker (1975): $PS = 1 - 0.5 \sum |p_a - p_b|$, where p_a represented the proportional cover of species p in treatment a, and p_b was the proportional cover of the same species in treatment b.

We used nonmetric multidimensional scaling (NMDS; Kruskal 1964) to determine how community composition changed among the heterogeneity treatments over time. NMDS is a flexible, iterative ordination technique that uses ranked distances to maximize the similarity between representation in species space and representation in a reduced, ordination space. NMDS has been shown to perform well on complex nonlinear datasets (Clarke 1993). Each plot in each year was considered a sample unit. Species with fewer than three occurrences were deleted from this analysis. We used Sorenson's index as a measure of dissimilarity. The final ordination was constrained to two axes. Ordinations were performed with PC-ORD (McCune & Mefford 1999).

Ecophysiological Characteristics of the Dominant Species

By the end of the second year, *P. virgatum* was the most abundant species in the restoration. In year 3, we measured leaf-level gas exchange and foliar N concentration of *P. virgatum* from one randomly selected subplot of each soil depth and nutrient treatment from the nutrient and depth heterogeneity plots in each block, and one randomly selected subplot of the shallow soil, reduced-N treatment from the maximum heterogeneity plots in two of the blocks. We also sampled two randomly selected subplots from each of the four native prairie plots.

Leaf-level gas exchange in *P. virgatum* was measured every 2 weeks (five times) from June to September in 2000. Net photosynthesis and stomatal conductance were quantified using a Li-Cor 6200 portable closed-flow gas exchange system (Lincoln, NE, U.S.A.). Gas exchange was measured from three sets of two leaves from different tillers in each subplot under full sunlight (PPFD > 1,800 μmol m^{-2} s^{-1}). Foliar N concentrations were determined 1 month after fertilization from the midsections of three leaf samples from different tillers within a treatment. Leaves from each subplot were composited, dried at 60°C, finely ground, and analyzed for percent N through dry combustion on a CN analyzer (Carlo Erba, Milan, Italy).

Statistical Analyses

Coefficients of variation, or CVs (%, [SD ÷ mean] × 100), were calculated for all variables measured from the 12 subplots within each heterogeneity treatment (i.e.,

inorganic N, soil moisture, light, cover, and productivity). Resource heterogeneity (CVs of soil moisture, N and light), vegetation heterogeneity (CVs of plant cover and productivity), community structure (cover, diversity, and richness), and ecophysiological measurements (net photosynthesis and foliar N) were analyzed according to a randomized complete block design. Plant community responses to the heterogeneity treatments were measured for 3 years, and statistical analyses included repeated measures. The five biweekly measurements of net photosynthesis rates and foliar N content in year 3 were averaged prior to statistical analyses. N and soil moisture were not analyzed as repeated measures because resin-collected N varies with the timing and amount of rainfall over the growing season and soil water content also varies with recent precipitation. All analyses were performed using the mixed model procedure in SAS (1999) in order to specify error terms for random effects (blocks) and specify a covariance structure for repeated measurements that minimized Akaike's Information Criterion and Schwartz's Bayesian Criterion (Littell et al. 1996). Tests of fixed effects (treatment, time, and treatment × time interaction) were conducted with denominator degrees of freedom estimated according to Satterthwaite's method (Littell et al. 1996). All means were compared using the differences in least squares means comparison procedure (SAS 1999), with alpha value ≈ 0.05 (p values <0.10 also reported). All CVs were log transformed to normalize the data prior to statistical analyses (Zar 1984). Relationships between plant diversity and resource heterogeneity, biomass heterogeneity, and average vegetative biomass and cover were examined using correlation analyses (r = Pearson's correlation coefficients) in SAS, alpha value = 0.05.

Results

Resource and Vegetation Heterogeneity

The soil treatments were effective at increasing resource heterogeneity (Table 1). The addition of limestone limited plant rooting depth to an average of 25 ± 3 cm (Baer et al. 1999). The pulse amendment of sawdust to the soil reduced the availability of NO$_3$–N for 3 years by increasing the microbial biomass and immobilization of N in the soil (Baer et al. 2003). Annual fertilization increased the availability of NO$_3$–N throughout the 3 years of study (Baer et al. 2003). The N treatments increased the heterogeneity of inorganic N availability relative to plots without N manipulations in the first 2 years of study. In year 3, only the maximum heterogeneity plots exhibited greater variability in N. This variability was largely a result of heterogeneity in soil nitrate, which may be a more sensitive indicator of N available to plants over the growing season because resin-collected NO$_3$–N reflects soil N availability better than resin-collected NH$_4$–N due to the greater mobility of nitrate in the soil (Binkley 1984).

Table 1. Average CV (CV ± SE) in resin-collected inorganic N, soil water content, and PAR in the heterogeneity treatments ($n = 4$ per treatment).

	Treatment	Year 1 (1998)	Year 2 (1999)	Year 3 (2000)
Total inorganic N	control	60.0 (8.7) a	37.1 (13.0) a	43.4 (8.7)
	depth	65.3 (7.0) a	47.0 (5.0) a	38.9 (5.7)
	nutrient	107.7 (10.5) b	118.7 (32.0) b	50.4 (12.4)
	maximum	125.6 (17.2) b	114.8 (19.8) b	80.9 (11.3)
		$p = 0.002$	$p = 0.008$	$p = 0.078$
Resin NH$_4$–N	control	63.3 (6.2) a	58.0 (28.7)	47.8 (12.6)
	depth	72.6 (9.5) ab	34.9 (2.0)	34.7 (3.8)
	nutrient	96.4 (13.3) b	40.3 (2.8)	42.8 (5.3)
	maximum	117.6 (22.6) b	42.1 (3.1)	72.2 (13.9)
		$p = 0.057$	$p > 0.10$	$p = 0.072$
Resin NO$_3$–N	control	74.2 (11.6) a	44.2 (5.1) a	41.9 (4.6) a
	depth	76.1 (3.9) a	67.2 (5.2) a	61.3 (11.9) ab
	nutrient	121.2 (13.2) b	152.8 (32.0) b	79.3 (19.6) b
	maximum	129.9 (15.5) b	143.5 (24.4) b	126.1 (15.3) c
		$p = 0.004$	$p = 0.001$	$p = 0.009$
Soil water content	control	5.5 (0.8) a	5.6 (1.2) a	8.3 (1.2)
	depth	—	6.9 (1.4) a	9.5 (1.3)
	nutrient	—	12.5 (1.5) b	13.5 (3.2)
	maximum	12.0 (1.9) b	14.6 (1.7) b	10.7 (1.5)
		$p = 0.016$	$p = 0.007$	$p > 0.10$
Light (PAR)	control	—	—	82.3 (10.3) ab
	depth	—	—	64.7 (6.3) a
	nutrient	—	—	109.9 (8.1) b
	maximum	—	—	100.2 (12.3) b
				$p = 0.028$

Means within a year with the same letter were not significantly different ($\alpha \approx 0.05$); all p values <0.10 reported.

Variability in soil water content and light were affected more by the nutrient treatments than by soil depth (Table 1). Although a single sampling for soil water content does not reflect seasonal patterns of soil water availability, the results did provide some insight into the availability of this resource during periods of soil drying (i.e., when the site received <3 cm of precipitation 7–9 days prior to sampling). Variability of soil water content was highest in the nutrient and maximum heterogeneity plots in the first two growing seasons. This pattern was not maintained into the third year of restoration due to the presence of a thick layer of detritus that accumulated in the absence of burning. Variability in PAR (measured only in year 3) was greatest in the nutrient and maximum heterogeneity plots.

Aboveground heterogeneity was related to variability of resources (Fig. 2). During the first 2 years, heterogeneity in ANPP was not related to variability in N or soil water content. In the third year, the CV of ANPP was correlated with the variability in NO$_3$–N ($r = 0.58$, $p = 0.018$). Variability in total plant cover was correlated with CVs in soil moisture in the first ($r = 0.93$, $p = 0.001$) and second ($r = 0.74$, $p = 0.001$) year but not in year 3 (when variability in soil water content was similar among the whole-plot treatments). As with ANPP, variability in total cover was most highly correlated with variability in NO$_3$–N ($r = 0.50$, $p = 0.057$) in year 3. When all years were combined, variability in ANPP and cover were significantly correlated with heterogeneity in total inorganic N (Fig. 2).

Plant Community Response to Heterogeneity

Total plant species richness and native species richness were similar among the heterogeneity treatments over all years (Table 2). Moderate differences in total Shannon diversity occurred over all years, with the highest diversity generally occurring in control and maximum heterogeneity plots (Table 2). A similar pattern was observed for diversity of native species ($p = 0.095$). In general, Shannon diversity tended to decrease with time in all heterogeneity treatments (Table 2).

There were no direct relationships between Shannon diversity (or richness) and resource heterogeneity (N, soil moisture, or light availability). Diversity was, however, correlated with CV of ANPP ($r = 0.43$, $p = 0.002$) and CV of plant cover ($r = 0.54$, $p < 0.001$), particularly that of the dominant species *P. virgatum* ($r = 0.63$, $p < 0.001$) (Fig. 3). Diversity was strongly negatively correlated with the average cover of this species ($r = -0.91$, $p < 0.001$) (Fig. 3). Variability of ANPP and plant cover decreased over time as a result of increasing cover of *P. virgatum* over time across all heterogeneity treatments (Table 3) and contributed to declining diversity in the all the treatments.
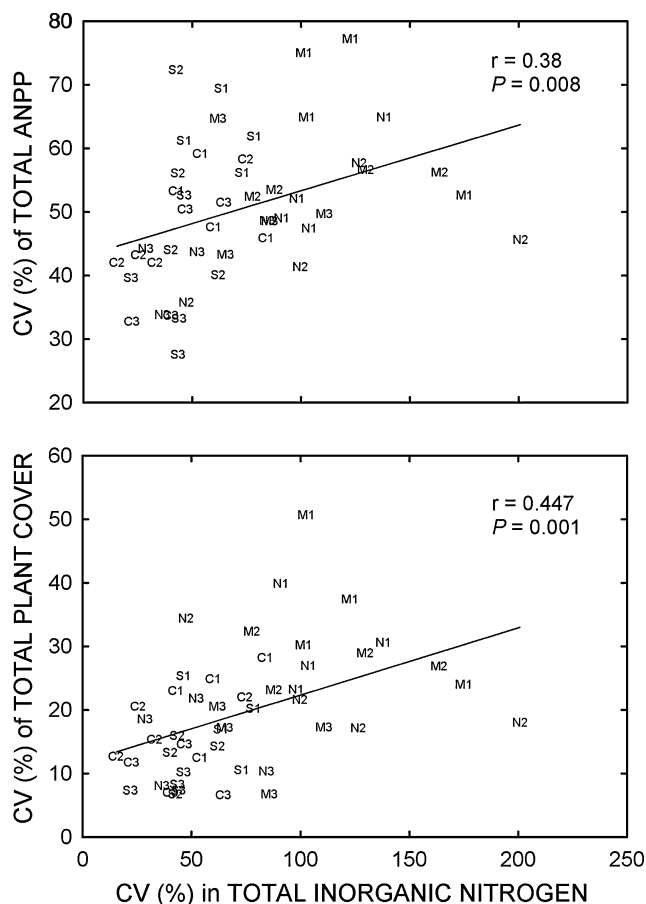
Figure 2. Relationship between heterogeneity (CV) in total ANPP and total plant cover with CV of inorganic N collected on ion exchange resins over the growing season. All plots and years included in analyses, *r* = Pearson's correlation coefficient (α = 0.05). Labels represent the treatment (C = control; D = soil depth heterogeneity; N = nutrient heterogeneity; and M = maximum heterogeneity) and year (1 = 1998; 2 = 1999; 3 = 2000).

There were also no differences in community similarity (or dissimilarity) among the heterogeneity treatments. All heterogeneity treatments increased in similarity over time ($p < 0.001$). Average proportional similarity among all heterogeneity treatments increased from 0.68 ± 0.021 in year 1 to 0.77 ± 0.020 in year 2 to 0.82 ± 0.015 in year 3. The NMDS ordination showed that all treatment plots had a relatively similar suite of species and followed the same general pattern of change in species composition over time (Fig. 4). Initially, plots were strongly dominated by early successional volunteer species such as Velvetleaf (*Abutilon theophrasti* Medic, non-native), Redroot pigweed (*Amaranthus retroflexus* L., native), Large crabgrass (*Digitaria sanguinalis*, non-native), and Foxtail (*Setaria* spp., non-native), with a minor contribution by native grasses and forbs. By year 2, abundance of non-native and volunteer forbs declined dramatically and representation of native forbs and grasses increased. By year 3, composition among plots converged as dominance by the native C_4 grass *P. virgatum* increased.

Leaf-Level Characteristics of *P. Virgatum*

In year 3, leaf-level gas exchange rates of *P. virgatum* varied among the soil nutrient treatments but were not affected by soil depth (Table 4). Both net photosynthesis ($p < 0.001$) and stomatal conductance ($p < 0.001$, data not shown) increased significantly from the reduced-N to the enriched-N treatments. Foliar N concentrations reflected the same pattern as gas exchange. Gas exchange rates of *P. virgatum* plants in the reduced-N treatment of the restoration were most similar to those of the plants of this species growing in native prairie, despite lower tissue N concentration than the native prairie plants (Table 4).

Table 2. Total plant species richness and diversity (mean ± SE) in the heterogeneity treatments (*n* = 4 per treatment) and native prairie plots (*n* = 4).

	Year 1 (1998)	*Year 2 (1999)*	*Year 3 (2000)*	*Overall Years*
Richness				
Control	24.8 (0.9)	23.5 (1.9)	23.8 (1.2)	
Depth heterogeneity	24.3 (1.0)	25.3 (0.6)	24.8 (1.9)	
Nutrient heterogeneity	21.0 (1.4)	23.8 (1.8)	21.0 (1.1)	
Maximum heterogeneity	22.3 (1.0)	22.5 (1.3)	26.0 (0.4)	
Native prairie			19.5 (1.2)	
Diversity (*p* < 0.001)				
Control	2.25 (0.09)	2.02 (0.07)	1.57 (0.13)	1.94 (0.05) b
Depth heterogeneity	2.15 (0.06)	1.80 (0.06)	1.33 (0.09)	1.76 (0.06) ab
Nutrient heterogeneity	2.12 (0.06)	1.67 (0.11)	1.30 (0.10)	1.70 (0.05) a
Maximum heterogeneity	2.15 (0.06)	1.82 (0.11)	1.51 (0.14)	1.82 (0.09) ab
Overall treatments (*p* = 0.086)	2.17 (0.03)	1.83 (0.05)	1.43 (0.06)	
Native prairie			1.83 (0.12)	

No significant effects occurred in richness; significant main effects of treatment and time occurred in diversity. Means with the same letter were not significantly different (α ≈ 0.05); all *p* values <0.10 reported.
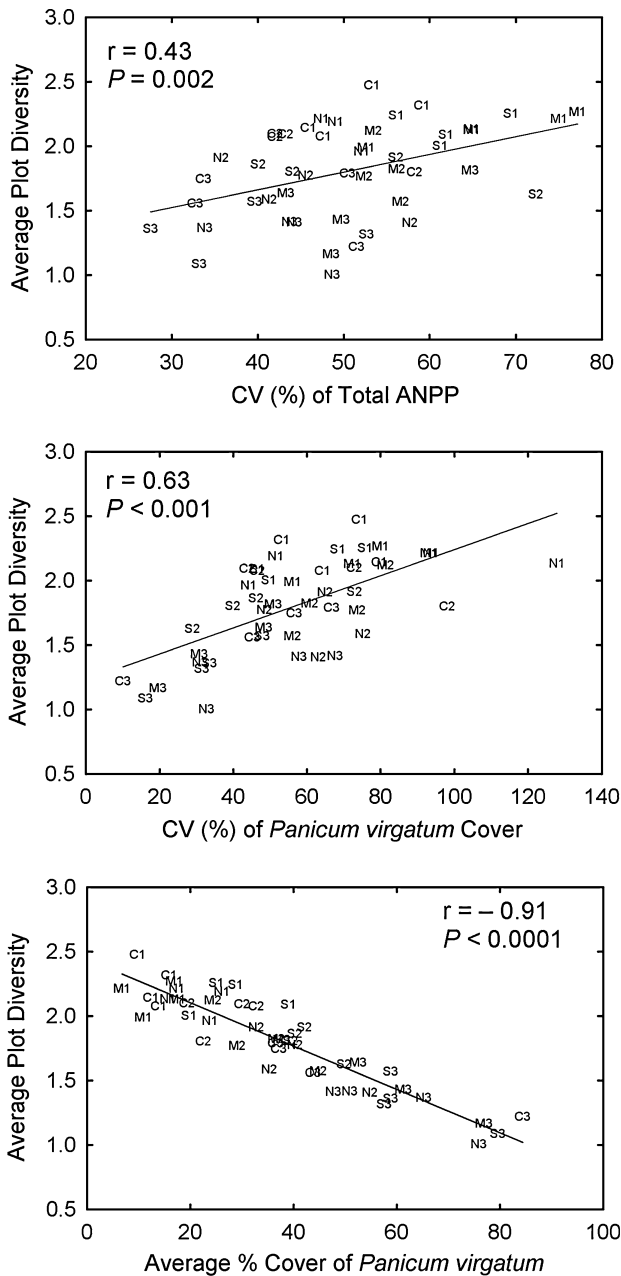
Figure 3. Correlations between average plot diversity and CV of total ANPP, CV of *P. virgatum* cover, and the average cover of *P. virgatum*. All plots and years included in analyses, r = Pearson's correlation coefficient ($\alpha = 0.05$). Labels represent the treatment (C = control; D = soil depth heterogeneity; N = nutrient heterogeneity; and M = maximum heterogeneity) and year (1 = 1998; 2 = 1999; 3 = 2000).

Discussion

Environmental heterogeneity has been invoked as a potential mechanism for the maintenance of diversity by facilitating coexistence of species (Grime 1979; Huston 1979; Tilman & Pacala 1993; Caldwell & Pearcy 1994), and this mechanism has received convincing support from studies

Table 3. Average variability in aboveground vegetation (CV $\pm$ SE) and average cover of the dominant species in the heterogeneity treatments ($n = 4$ per treatment).

	Year 1	Year 2	Year 3	Overall Years
CV of ANPP				($p = 0.069$)
Control	51.5 (3.0)	46.4 (4.0)	42.1 (5.1)	46.7 (2.7)
Depth	62.2 (2.8)	53.1 (7.3)	38.3 (5.4)	51.2 (2.4)
Nutrient	53.3 (4.0)	45.2 (4.7)	42.6 (3.1)	47.0 (3.2)
Maximum	67.4 (5.6)	54.7 (1.0)	51.6 (4.6)	57.9 (2.0)
Overall	58.6 (2.5) x	49.8 (2.4) y	43.6 (2.4) z	
($p < 0.001$)				
CV of total plant cover				($p < 0.001$)
Control	22.1 (3.4)	17.6 (2.2)	10.0 (1.9)	16.5 (2.3) a
Depth	18.2 (3.1)	12.5 (2.0)	8.3 (0.7)	13.0 (1.7) a
Nutrient	30.1 (3.6)	22.8 (4.0)	14.7 (3.3)	22.5 (1.6) c
Maximum	35.5 (5.7)	27.8 (1.9)	15.4 (3.0)	26.2 (3.1) c
Overall	26.5 (2.5) x	20.2 (1.9) y	12.1 (1.3) z	
($p < 0.001$)				
CV of *Panicum virgatum* cover				($p > 0.10$)
Control	67.8 (5.9)	65.3 (12.7)	44.6 (12.3)	59.2 (9.8)
Depth	60.1 (7.1)	47.0 (9.4)	32.2 (6.5)	46.4 (6.4)
Nutrient	79.3 (19.5)	62.9 (5.5)	47.3 (9.2)	63.1 (2.4)
Maximum	75.4 (7.7)	68.0 (5.8)	37.4 (7.4)	60.2 (6.5)
Overall	70.6 (5.5) x	60.8 (4.5) x	40.4 (4.4) y	
($p < 0.001$)				
Average % cover of *P. virgatum*				($p = 0.017$)
Control	13.0 (1.3)	26.2 (3.1)	50.4 (11.4)	29.8 (11.0) a
Depth	28.1 (4.1)	42.9 (2.4)	63.7 (5.3)	44.9 (10.3) c
Nutrient	20.7 (2.5)	40.7 (5.0)	59.9 (6.5)	40.4 (11.3) bc
Maximum	13.0 (2.6)	33.7 (4.5)	57.1 (8.2)	34.6 (12.7) ab
Overall	18.7 (2.0) x	35.9 (2.4) y	57.8 (3.9) z	
($p < 0.001$)				

Differences among years (over all treatments) and among treatments (over all years) indicated by a letters x–z and a–c, respectively. Means with the same letter were not significantly different ($\alpha \approx 0.05$); all p values <0.10 reported.

where the structural heterogeneity of plant communities promoted diversity of associated animal communities (MacArthur & MacArthur 1961; Pianka 1967). Our study tested a potential application of the "environmental heterogeneity hypothesis" to increasing plant diversity in a grassland restoration.

The soil treatments increased heterogeneity of N availability, soil moisture, and light penetration. Despite this increase in variability of resources, plant diversity only differed between the control and nutrient heterogeneity treatments, and this difference was counter to expectations. Collins & Wein (1998) also tested whether heterogeneity in soil nutrient enrichment affected vegetation composition by varying the patch size of nutrient enrichment and found no evidence that diversity increased with nutrient heterogeneity. As in our study, Collins & Wein (1998) observed that plots with the most coarse-grained heterogeneity in enrichment were the least similar to unenriched plots due to greater dominance of a perennial species and lower richness within fertilized subplots (Collins & Wein 1998). Relative to the ambient N subplots within the nutrient heterogeneity treatments, the N-addition treatment reduced plant diversity to a much greater extent than the carbon addition increased plant diversity (Baer et al. 2003, 2004), suggesting asymmetric
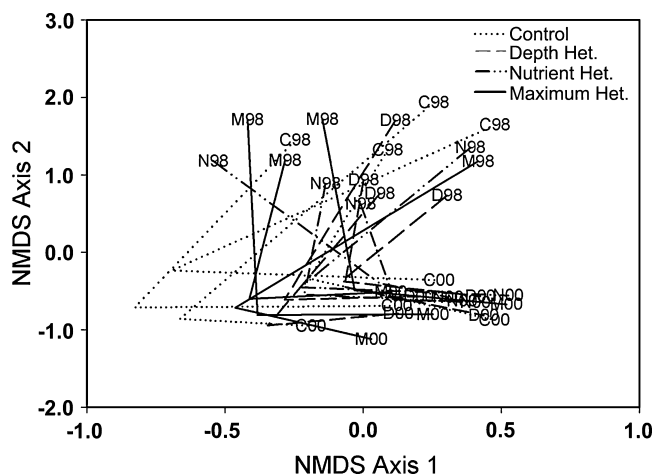
Figure 4. NMDS ordination showing change in species composition among the heterogeneity treatments over time (98, 99, 00). Labels represent the treatment (C = control; D = soil depth heterogeneity; N = nutrient heterogeneity; and M = maximum heterogeneity) and year (98 = 1998; 99 = 1999; and 00 = 2000).

competition for N by *Panicum virgatum* and that N is an important ecological "filter" in community assembly (Pimm 1991) through its effect on one species that was a strong determinant of community structure. N addition to individual *P. virgatum* plants at KPBS has been shown to increase the number of tillers that flowered and produced seed but not to affect the rate of increase in clonal growth of this species (Hartnett 1993). Increased seed production from supplemental N addition may have also contributed to the higher cover of this species in our restoration. Demographic consequences of N availability on species used in restorations and among different seed stock (e.g., cultivars and native sources) deserve further investigation.

We hypothesized that increased heterogeneity in plant rooting depth would promote species diversity through

competitive release of forbs from the dominant grasses in shallow soils. van Auken et al. (1994) demonstrated that the growth of C_4 grasses increased with soil depth and functional niche differences promoted the coexistence of grassland species. Fitter (1982) also showed that heterogeneity in plant rooting depth increased diversity, supported by a decrease in the number of species per unit area with increased root density ratio in shallow soil depths (0–10 cm). Despite higher cover of *P. virgatum* in the depth heterogeneity treatment relative to the control plots, there was no difference in diversity between these two treatments. The limestone was likely buried too deep to impose an effect of this treatment on diversity within the first 3 years of restoration, when root systems were developing. Unlike the N treatments, the reduced plant rooting depth treatment represented a continuous manipulation expected to indirectly affect community composition (through soil moisture limitation) over a longer time frame than labile resources required for growth (i.e., N availability) and for which there is direct and immediate competition for by plants.

Although diversity did not track resource heterogeneity in the experimental treatments, our results demonstrated that resource heterogeneity influenced aboveground heterogeneity in vegetation structure and was indirectly related to diversity. Variability in inorganic N was positively related to variability in total plant cover and cover of *P. virgatum*. Plant diversity was positively correlated with variability in ANPP and plant percent cover. Silvertown et al. (1994) found a similar result when testing whether variability in rainfall affected heterogeneity of plant community composition. In their study, plant community composition responded more to the heterogeneity in biomass (rather than directly to heterogeneity in precipitation) because high precipitation favored grasses and resulted in asymmetric competition for light (Silvertown et al. 1994). In our restoration, native grass biomass increased in response to N enrichment (Baer et al. 2003), which reduced light levels below the canopy. Thus, diversity in our experiment depended more on heterogeneity of the biomass in response to the soil N treatments, rather than the direct effects of heterogeneity on N availability.

A strong inverse relationship existed between diversity and the average cover of *P. virgatum*, which increased over time across all treatments. *Panicum virgatum* is a common warm-season perennial grass with broad niche requirements (inhabiting open woods, prairies, dunes, shores, and marshes from Canada to Texas). This species is commonly used in restorations due to its ability to successfully establish in highly disturbed environments such as roadsides, eroded croplands, and mine tailings (Choi & Wali 1995; Corbett et al. 1996; Skeel & Gibson 1996). Demand for native grass seed has promoted the commercial production of *P. virgatum* (as well as other prairie grasses), and cultivar development commonly selects for vigorous plants with high viable seed production (Knapp & Dyer 1998; Kolliker et al. 1998). We used the recommended "Blackwell"

Table 4. Average net photosynthesis rate and foliar N content of *Panicum virgatum* in the soil N and depth treatments in the third year of restoration.

N Treatment	Soil Depth	Net Photosynthesis ($\mu mol\ m^{-2}\ second^{-1}$)	Foliar N (% N)
Reduced N (+carbon)	deep	15.1 (0.88) a	0.92 (0.04)
	shallow[a]	14.0 (0.97) a	0.96 (0.14)
Ambient N	deep	17.3 (0.49) b	1.05 (0.04)
	shallow	17.3 (0.69) b	1.04 (0.05)
Enriched N (+fertilizer)	deep	20.0 (0.28) c	1.36 (0.23)
Native prairie[b]		15.5 (0.92)	1.24 (0.03)

Photosynthesis was measured biweekly from June to September in 2000. Foliar N was measured in mid–growing season, after fertilization. Means accompanied by the same letter were not significantly different ($p > 0.05$).
[a] Net photosynthesis was measured four times over the growing season.
[b] Not included in statistical analyses.

cultivar of *P. virgatum* in our restoration, which was developed by the United States Department of Agriculture Plant Materials Center (Manhattan, KS, U.S.A.) from a single plant collected in 1934. Although the seeds of all native grasses used in our restoration were obtained commercially, *P. virgatum* was the most dominant species in all treatment combinations (Baer et al. 2004). Several factors may have contributed to the success of this species across all heterogeneity treatments. First, *P. virgatum* produces a heavy seed that would be more likely to disperse and establish near a parent plant, whereas other C_4 grasses (*Sorghastrum nutans*, *Andropogon gerardii*, and *Schizachyrium scoparium*) produce hairy to villous inflorescences that are more susceptible to wind dispersal. Although native grasses primarily reproduce vegetatively in native prairie, seed production may be more important in the early stages of restoration, where open sites for colonization exist, especially if there is a higher proportion of viable seed from cultivars than from native source populations. Second, *P. virgatum* is strongly rhizomatous, often forming large, dense stands. The combination of high seed production and viability in cultivars, seed rain into open sites, and clonal capabilities of this species may have promoted its rapid spread and the decline in species diversity under the dense shading of tall plants.

Community divergence under varying levels of nutrient enrichment has been demonstrated in successional ecosystems (Inouye & Tilman 1995). In our study, plant community composition among the heterogeneity treatments converged over time because the soil depth and nutrient treatments did not limit the establishment of *P. virgatum*. This likely resulted from the ecophysiological and morphological plasticity of this species, especially the cultivars of *P. virgatum* used in our restoration. Physiologically, *P. virgatum* has characteristics considered typical of the native prairie C_4 grasses, such as high photosynthetic efficiency under water stress and low nutrient availability (Byrd & May 2000; Sanderson & Reed 2000). Our results demonstrated that the cultivar of *P. virgatum* we used had higher photosynthetic rates and lower tissue N content than plants of this species growing in native prairie, which may explain the tendency for this species to dominate newly restored grasslands (e.g., the "monocultural Switchgrass syndrome" [Schramm 1992]). Furthermore, *P. virgatum* can yield similar biomass at a variety of seeding densities due to compensatory responses of tiller number and size (Sanderson & Reed 2000). Last, community convergence may also result under different resource availability regimes if the dominant species is present in high frequency among all treatments at the onset of a manipulation because this species will tend to increase in proportional abundance with less establishment of new individuals (Inouye & Tilman 1995).

We seeded the experimental plots using a lognormal distribution of native prairie species. Although the germination rates of each species were not measured, seeding rates were based on pure live seed. Our seeding approach reflected what we considered to be similar to seed rain composition in lowland native prairie based on long-term plant community monitoring at KPBS. The seed composition was advantageous for the dominant grasses, with application rates of these species of at least an order of magnitude greater than forbs and less common prairie grass species. Despite equivalent seeding rates among the four dominant native prairie grasses, one species was clearly capable of preempting resources and establishing dominance. This is consistent with theory regarding the role of ecological filters on community assembly in that environmental (e.g., cultivated soil conditions) and biological (e.g., seeding rates and use of cultivars) filters resulted in the successful establishment of one species (*P. virgatum*) best adapted for the present physical and biological conditions, and this species played an inordinately important role in determining community structure (Pimm 1991; Lockwood & Pimm 1999; Hobbs & Norton 2004). Community assembly models predict highest richness and continuous community change with greater frequency of colonization from the species pool (Lockwood et al. 1997; Lockwood & Samuels 2004). We introduced species only once and not equivocally, which resulted in a continuous loss of species over time in our restoration.

Conclusion

Native tallgrass prairie communities are generally dominated by a few species of perennial grasses but also contain a large number of satellite species with low abundance (Gotelli & Simberloff 1987). Disturbance and environmental heterogeneity affect the temporal and spatial variability of satellite species that contribute to the overall diversity of tallgrass prairie communities (Collins & Barber 1985; Collins & Glenn 1990). Increasing dominance in tallgrass prairie restoration results when a few aggressive species monopolize abundant resources. The absence of any relationship between resource heterogeneity and diversity in our study resulted from the treatments not limiting resource availability below the requirements of a dominant species. The dominant species, *Panicum virgatum*, in the restored prairie had higher photosynthetic rates and lower foliar N content than *P. virgatum* plants growing in native prairie, which suggests that the cultivar of this species has greater nutrient-use efficiency than its native conspecifics and likely contributed to its successful establishment in all the soil treatments. Consequently, plant communities within the different soil treatments and heterogeneity treatments converged over time. Thus, spatial variability of resources was not a sufficient mechanism to promote diversity in a community constrained by a pulse introduction of species in conditions where one species was a successful competitor across the range of resource availability.

Preventing the dominance of native grasses will be required to achieve, maintain, and/or increase diversity in tallgrass prairie restorations. Variable fire regimes, grazing,

and/or mowing can reduce or prevent the dominance of grasses in restored prairie (Howe 1994, 1999). Seed selection (i.e., cultivars vs. noncultivar population sources) may also have important consequences for restoration success (Lesica & Allendorf 1999), but there have been few empirical tests of genetic, physiological, phenological, and ecological differences between cultivar and noncultivar seed sources used in restoration (but see Gustafson et al. 2004*a*, 2004*b* for genetic and competitive variation among population sources of prairie species). This information is clearly needed to better guide the restoration of diverse prairie community assemblages.

Acknowledgments

LITERATURE CITED

Baer, S. G., J. M. Blair, S. L. Collins, and A. K. Knapp. 2003. Soil resources regulate productivity and diversity in newly established tallgrass prairie. Ecology **84:**724–735.

Baer, S. G., J. M. Blair, S. L. Collins, and A. K. Knapp. 2004. Plant community responses to resource availability and heterogeneity during restoration. Oecologia **139:**617–639.

Baer, S. G., J. M. Blair, and A. K. Knapp. 1999. Manipulation of soil resource heterogeneity in a tallgrass prairie restoration. Pages 78–87 in J. T. Springer, editor. Proceedings of the Sixteenth North American Prairie Conference, 26–29 July, University of Nebraska, Kearney, Nebraska.

Binkley, D. 1984. Ion exchange resin bags: factors affecting estimates of nitrogen availability. Soil Science Society of America Journal **48:**1181–1184.

Binkley, D., and P. Matson. 1983. Ion exchange resin bag for assessing forest soil nitrogen availability. Soil Science Society of America Journal **47:**1050–1052.

Briggs, J. M., and A. K. Knapp. 1991. Estimating aboveground biomass in tallgrass prairie with the harvest method: determining proper sample size using jackknifing and Monte Carlo simulations. Southwestern Naturalist **36:**1–6.

Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. American Journal of Botany **82:**1024–1030.

Burke, I. C., W. K. Lauenroth, R. Riggle, P. Brannen, B. Madigan, and S. Beard. 1999. Spatial variability in soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems **2:**422–438.

Byrd, G. T., and P. A. May. 2000. Physiological comparisons of switchgrass cultivars differing in transpiration efficiency. Crop Science **40:**1271–1277.

Caldwell, M. M., and R. W. Pearcy. 1994. Exploitation of environmental heterogeneity by plants. Academic Press, New York.

Carson, W. P., and G. W. Barrett. 1988. Succession in old field plant communities: effects of contrasting types of nutrient enrichment. Ecology **69:**984–994.

Choi, Y. D., and M. K. Wali. 1995. The role of *Panicum virgatum* (switchgrass) in the revegetation of iron-mine tailings in northern New York. Restoration Ecology **3:**123–132.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18:**117–143.

Collins, B., and G. Wein. 1998. Soil resource heterogeneity effects in early succession. Oikos **82:**238–245.

Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetation **64:**87–94.

Collins, S. L., and S. M. Glenn. 1990. A hierarchical analysis of species abundance patterns in grassland vegetation. American Naturalist **135:**633–648.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science **280:**745–747.

Corbett, E. A., R. C. Anderson, and C. S. Rodgers. 1996. Prairie revegetation of a strip mine in Illinois: fifteen years after establishment. Restoration Ecology **4:**346–354.

Fitter, A. H. 1982. Influence of soil heterogeneity on the coexistence of grassland species. Journal of Ecology **70:**139–148.

Foster, B. L., and K. L. Gross. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. Ecology **79:**2593–2602.

Freeman, C. C. 1998. The flora of Konza Prairie: a historical review and contemporary patterns. Pages 69–80 in A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York.

Gibson, D. J. 1988. The maintenance of plant and soil heterogeneity in dune grassland. Journal of Ecology **76:**497–508.

Gibson, D. J., and L. C. Hulbert. 1987. Effects of fire, topography, and year-to-year climate variation on species composition in tallgrass prairie. Vegetatio **72:**175–185.

Gibson, D. J., T. R. Seastedt, and J. M. Briggs. 1993. Management practices in tallgrass prairie: large- and small-scale effects on species composition. Journal of Applied Ecology **30:**247–255.

Gotelli, N. J., and D. Simberloff. 1987. The distribution and abundance of tallgrass prairie plants: a test of the core-satellite hypothesis. American Naturalist **130:**18–35.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, New York.

Gustafson, D. J., D. J. Gibson, and D. L. Nickrent. 2004*a*. Conservation genetics of two co-dominant species in the endangered tallgrass prairie ecosystem. Journal of Applied Ecology **41:**389–397.

Gustafson, D. J., D. J. Gibson, and D. L. Nickrent. 2004*b*. Competitive relationships of *Andropogon gerardii* (big bluestem) from remnant and restored native populations and select cultivated varieties. Functional Ecology **18:**451–457.

Hartnett, D. C. 1993. Regulation of clonal growth and dynamics of *Panicum virgatum* (Poaceae) in tallgrass prairie: effects of neighbor removal and nutrient addition. American Journal of Botany **80:**1114–1120.

Hobbs, R. J., and D. A. Norton. 2004. Ecological filters, thresholds, and gradients in resistance to ecosystem reassembly. Pages 72–95 in V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. Assembly rules and restoration ecology. Island Press, Washington, D.C.

Hook, P. B., I. C. Burke, and W. K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. Plant and Soil **138:**247–256.

Howe, H. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology **8:**691–704.

Howe, H. 1999. Dominance, diversity and grazing in tallgrass prairie restoration. Ecological Restoration **17:**59–64.

Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist **113:**81–101.

Inouye, R. S., and D. Tilman. 1995. Convergence and divergence of old-field vegetation after 11 years of nitrogen addition. Ecology **76:** 1872–1887.

Keeney, D. R., and D. W. Nelson. 1982. Nitrogen-inorganic forms. Pages 643–698 in A. L. Page, R. H. Miller, and D. R. Keeney, editors. Methods of soil analysis. Part II. Microbiological and biochemical properties. American Society of Agronomy and the Soil Science Society of America, Madison, Wisconsin.

Kindscher, K., and L. L. Tieszen. 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. Restoration Ecology **6:**181–196.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience **49:**39–50.

Knapp, A. K., J. M. Briggs, D. C. Hartnett, and S. L. Collins. 1998. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York.

Knapp, E. E., and A. R. Dyer. 1998. When do genetic considerations require special approaches to ecological restoration? Pages 345–363 in P. L. Fiedler and P. M. Kareiva, editors. Conservation biology for the coming decade. Chapman & Hall Publishers, New York.

Kolliker, R., F. J. Stadelmann, B. Reidy, and J. Nosberger. 1998. Fertilization and defoliation frequency affect genetic diversity of *Festuca pratensis* Huds. in permanent grasslands. Molecular Ecology **7:** 1557–1567.

Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika **29:**1–17.

Lesica, P., and F. W. Allendorf. 1999. Ecological genetics and the restoration of plant communities: mix or match? Restoration Ecology **7:**42–50.

Littell, R. C., G. G. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Inc., Cary, North Carolina.

Lockwood, J. L., and S. L. Pimm. 1999. When does restoration succeed? Pages 363–392 in E. Weiher and P. Keddy, editors. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, Massachusetts.

Lockwood, J. L., R. D. Powell, M. P. Nott, and S. L. Pimm. 1997. Assembling ecological communities in time and space. Oikos **80:** 549–553.

Lockwood, J. L., and C. L. Samuels. 2004. Assembly models and the practice of restoration. Pages 55–70 in V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. Assembly rules and restoration ecology. Island Press, Washington, D.C.

MacArthur, R. H., and J. MacArthur. 1961. On bird species diversity. Ecology **42:**594–598.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4.0. MjM Software, Gleneden Beach, Oregon.

Milchunas, D. G., and W. K. Lauenroth. 1995. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. Ecological Applications **5:**452–458.

Owensby, C. E., R. M. Hyde, and K. L. Anderson. 1970. Effects of clipping and supplemental nitrogen and water on loamy upland bluestem range. Journal of Range Management **23:**341–346.

Packard, S., and C. F. Mutel. 1997. The tallgrass restoration handbook: for prairies, savannas, and woodlands. Island Press, Washington, D.C.

Pianka, E. R. 1967. On lizard species diversity: North American flatland deserts. Ecology **48:**333–351.

Pimm, S. L. 1991. The balance of nature? Chicago University Press, Chicago, Illinois.

Robertson, G. P., J. R. Crum, and B. G. Ellis. 1993. The spatial variability of soil resources following long-term disturbance. Oecologia **96:**451–456.

Robertson, G. P., M. A. Huston, F. C. Evans, and J. M. Tiedge. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. Ecology **68:**744–748.

Rock, H. W. 1981. Prairie propagation handbook. 6th edition. Wehr Nature Center, Milwaukee, Wisconsin.

Rover, M., and E. Kaiser. 1997. Spatial heterogeneity within the plough layer: low and moderate variability of soil properties. Soil Biology and Biochemistry **31:**175–187.

Rusch, G., and J. M. Fernandez-Palacios. 1995. The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. Journal of Vegetation Science **6:**417–426.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience **44:**418–421.

Sanderson, M. A., and R. L. Reed. 2000. Switchgrass growth and development: water, nitrogen, and plant density effects. Journal of Range Management **53:**221–227.

SAS, Inc. 1999. SAS/STAT user's manual. SAS Institute, Inc., Cary, North Carolina.

Schramm, P. 1992. Prairie restoration: a twenty-five year perspective on establishment and management. Pages 169–177 in D. D. Smith and C. A. Jacobs, editors. Proceedings of the Twelfth North American Prairie Conference, 5–9 August 1990. University of Northern Iowa, Cedar Falls, Iowa.

Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. Oecologia **87:**72–79.

Shirley, S. 1994. Restoring the tallgrass prairie: an illustrated manual for Iowa and the upper-Midwest. University of Iowa Press, Iowa City, Iowa.

Silvertown, J., M. E. Dodd, K. McConway, J. Potts, and M. Crawley. 1994. Rainfall, biomass variation, and community composition in the Park Grass experiment. Ecology **75:**2430–2437.

Skeel, V. A., and D. J. Gibson. 1996. Physiological performance of *Andropogon gerardii*, *Panicum virgatum*, and *Sorghastrum nutans* on reclaimed mine spoil. Restoration Ecology **4:**355–367.

Sperry, T. M. 1994. The Curtis Prairie restoration, using the-single species planting method. Natural Areas Journal **14:**124–127.

Steinauer, E. M., and S. L. Collins. 1995. Effects of urine deposition on small-scale patch structure in prairie vegetation. Ecology **76:** 1195–1205.

Thompson, J. 1992. Prairies, forests, and wetlands: the restoration of natural landscape communities in Iowa. University of Iowa Press, Iowa City.

Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. Ecology **65:**1445–1453.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs **57:** 189–214.

Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 in R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois.

Turner, C. L., J. M. Blair, R. J. Shartz, and J. C. Neel. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. Ecology **78:**1832–1843.

van Auken, O. W., Bush, J. K., and D. D. Diamond. 1994. Changes in growth of two C4 grasses (*Schizachyrium scoparium* and *Paspalum plicatulum*) in monoculture and mixture: influence of soil depth. American Journal of Botany **8:**15–20.

Vinton, M. A., and I. C. Burke. 1995. Interactions between individual plant species and soil nutrient status in short-grass steppe. Ecology **76:**1116–1133.

Warkins, T. E., and E. A. Howell. 1983. Introduction of selected prairie forbs into an established tallgrass prairie restoration. Pages 147–151 in R. Brewer, editor. Proceedings of the Eighth North American Prairie Conference, 1–4 August 1982. Western Michigan University, Kalamazoo.

Whittaker, R. H. 1975. Communities and ecosystems. MacMillan, New York.

Zar, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey.