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## Plant community responses to resource availability and heterogeneity during restoration

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**Abstract** Availability and heterogeneity of resources have a strong influence on plant community structure in undisturbed systems, as well as those recovering from disturbance. Less is known about the role of resource availability and heterogeneity in restored communities, although restoration provides a valuable opportunity to test our understanding of factors that influence plant community assembly. We altered soil nitrogen (N) availability and soil depth during a prairie restoration to determine if the availability and/or heterogeneity of soil resources influenced plant community composition in restored grassland communities. Plant community responses to three levels of N availability (ambient, enriched by fertilization, and reduced by carbon amendment) and two levels of soil depth (deep and shallow) were evaluated. In addition, we evaluated plant community responses to four whole plot heterogeneity treatments created from the six possible combinations of soil N availability and soil depth. The soil depth treatment had little influence on community structure during the first 3 years of restoration. Total diversity and richness declined over time under annual N enrichment, whereas diversity was maintained and richness increased over time in soil with reduced N availability. Non-native species establishment was lowest in reduced-N soil in the initial year, but

their presence was negligible in all of the soil N treatments by the second year of restoration. *Panicum virgatum*, a native perennial C<sub>4</sub> grass, was the dominant species in all soil N treatments by year three, but the magnitude of its dominance was lowest in the reduced-N soil and highest in enriched-N soil. Consequently, the relative cover of *P. virgatum* was strongly correlated with community dominance and inversely related to diversity. The differential growth response of *P. virgatum* to soil N availability led to a higher degree of community similarity to native prairie in the reduced-N treatment than in the enriched-N treatment. There were no differences in plant community structure among the four whole plot-level heterogeneity treatments, which all exhibited the same degree of similarity to native prairie. Diversity and community heterogeneity in the whole-plot treatments appeared to be regulated by the dominant species' effect on light availability, rather than soil N heterogeneity per se. Our results indicate that a strong differential response of a dominant species to resource availability in a restored community can regulate community structure, diversity, and similarity to the native (or target) community, but the importance of resource heterogeneity in restoring diversity may be dampened in systems where a dominant species can successfully establish across a range of resource availability.

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### Introduction

Chronic disturbance can alter availability and/or spatial distribution of resources (Robertson et al. 1988, 1993; Rover and Kaiser 1997), which can in turn strongly influence vegetation pattern, community structure, and diversity in terrestrial ecosystems (Grime 1979; Huston 1979; Tilman 1984, 1987; Stevens and Carson 2002). Although plant communities recover from disturbance through natural succession, many aspects of community

structure are slow to return without human intervention (Pywell et al. 2002). Thus, steering the rate and direction of recovery is a fundamental aspect of restoration ecology, and restoration presents a valuable opportunity to test ecological theory on community recovery following disturbance (Bradshaw 1987; Ewel 1987; Hobbs and Norton 1996; Palmer et al. 1997).

The role of resource availability and heterogeneity in restoring species-rich communities is poorly understood. In native vegetation, floristic diversity is regulated in part by the availability and heterogeneity of soil resources. Studies have demonstrated inverse relationships between diversity and resource availability, i.e., nutrients (Wilson and Shay 1990; Collins et al. 1998), and positive relationships between diversity and soil heterogeneity (Fitter 1982; Silvertown et al. 1994; Rusch and Fernandez-Palacios 1995; Inouye and Tilman 1995; Steinauer and Collins 1995). Given its key role in natural systems, it seems likely that resource heterogeneity may control the rate and direction of community restoration.

Resource availability and heterogeneity in grasslands are influenced by the spatial distribution of plants (Gibson 1988; Hook et al. 1991; Vinton and Burke 1995), species composition (Wedin and Tilman 1990; Milchunas and Lauenroth 1995), fire frequency (Knapp and Seastedt 1986; Blair 1997), grazing (Collins et al. 1998; Knapp et al. 1999), and topographic position in the landscape (Burke et al. 1999). Conversion of grasslands to row-crop agriculture alters the structure, function, and complexity of grassland soils (Anderson and Coleman 1985; Elliot 1986; Rover and Kaiser 1997). Thus, at the onset of a grassland restoration in formerly cultivated soils, the availability and spatial distribution of resources may not be representative of uncultivated (native) prairie. The re-introduction of native grasses into long-term cultivated soil is often successful (Schramm 1970, 1990; Baer et al. 2002), but the establishment of the less common forb species, critical to the biodiversity of most grasslands, is often inadequate (Clarke and Bragg 1994; Kindscher and Tieszen 1998) and these species are vulnerable to local extinction (Howe 1999). Understanding the relationship between resource availability and heterogeneity and community recovery during grassland restoration may be key to successfully restoring biodiversity in this and other species-rich ecosystems.

We altered the heterogeneity of two factors, soil nitrogen (N) availability and soil depth, known to influence plant community structure in native prairie and other herbaceous systems. Previously, we demonstrated that our soil treatments affected nutrient availability, net primary production, and diversity following three years of restoration (Baer et al. 2003). Here, we examine the role of resource availability on changes in community composition over time and the role of resource heterogeneity in restoring community diversity and similarity to native prairie. We hypothesized that the responses of restored prairie communities to different levels soil depth and N availability would be consistent to those observed in native grasslands and old-field systems: (1) greater plant

diversity in shallow soil with reduced rooting depth (Gibson and Hulbert 1987); (2) lower diversity with increasing nutrient availability (Tilman 1984; Carson and Barrett 1988; Wilson and Shay 1990; Collins et al. 1998; Foster and Gross 1998); and (3) lower abundance of early successional annual species in response to reduced nutrient availability (Redente et al. 1992; Paschke et al. 2000; Blumenthal et al. 2003). To what degree N availability influences diversity and similarity to the target restoration community has not been examined in restored tallgrass prairie. Furthermore, to what extent resource heterogeneity affects the recovery of diversity and community heterogeneity in restored prairie is also unknown. Because spatial variability in resources can increase suitable microsites for colonization of species with different niche requirements (Tilman 1993) and mediate competition for resources (Fitter 1982; Tilman and Pacala 1993), community divergence may increase among patches with varying levels of resource availability (Inouye and Tilman 1995; Collins and Wein 1998).

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## Materials and methods

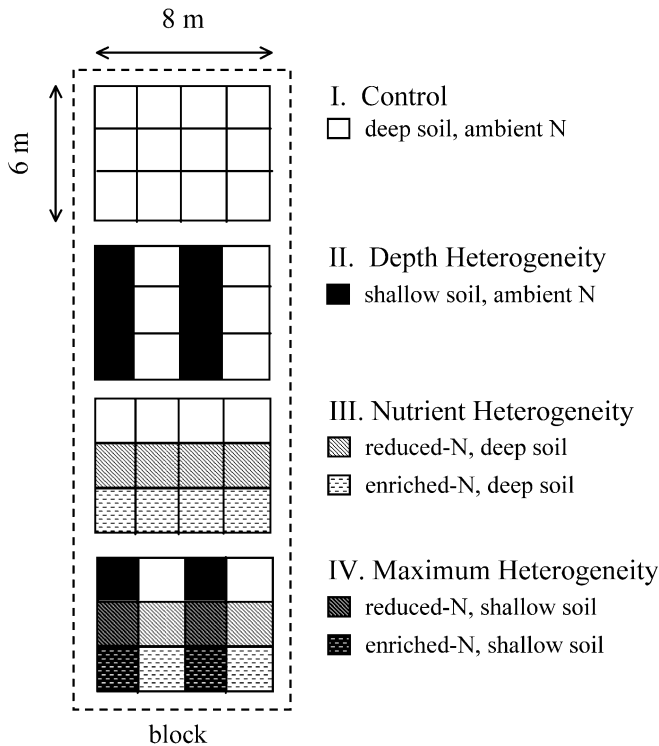
### Site description

The restoration was conducted in a lowland agricultural field that had been cultivated for >50 years at the Konza Prairie Biological Station Long-Term Ecological Research site (KPBS LTER), located ~9 km south of Manhattan, Kansas (340 m asl). The 30-year average annual and growing season precipitation at KPBS were 835 and 620 mm/year, respectively. During the 3 years of this study (1998–2000), total precipitation was 944, 825, and 628 mm, of which 593, 693, and 390 mm fell during the growing season (April through September), respectively. The soil at the site was a gently sloping (0–1%) Reading silt loam (mesic Typic Arguidoll) formed by colluvial and alluvial deposits. Historically, the vegetation of the study site would have been characteristic of lowland native tallgrass prairie at KPBS, dominated by warm-season (C<sub>4</sub>) grasses and interspersed with a variety of less common grass and forb species (Abrams and Hulbert 1987; Freeman 1998).

### Experimental design and restoration approach

In June 1997, we delineated 16 6×8-m plots separated by 6-m-wide buffer strips in the agricultural field. Four whole-plot heterogeneity treatments (WPHTs) were randomly assigned to four plots within each of four blocks (Fig. 1). The control WPHT (I) contained deep soil at ambient N levels. The soil depth WPHT (II) included four alternating 2×6-m strips of deep and shallow soil (see next paragraph for treatment details). The N availability WPHT (III) included three 2×8-m strips randomly assigned to reduced-N, ambient-N and enriched-N treatments. The maximum WPHT (IV) included the soil N treatments crossed with soil depth treatments, resulting in replicated 2×2-m subplots of six possible treatment combinations. All whole plots were subdivided into twelve 2×2-m subplots for sampling.

In August 1997, all plots were excavated to a depth of ~25 cm. Native limestone slabs were pieced together in alternating strips in WPHTs II and IV. The soil was then replaced, leveled, and shallowly disked (2–3-cm deep). Three levels of N availability were randomly assigned to strips in WPHTs III and IV. In February 1998, 5.5 kg sawdust/m<sup>2</sup> was tilled into the top 15 cm of soil in strips assigned to the reduced-N treatment. This application rate increased soil carbon (C) to levels representative of native prairie soil, ~3% C. Following



**Fig. 1** Whole plot heterogeneity treatment designs (I-IV) and resultant six treatment combinations in the prairie restoration experiment (deep and shallow soil at reduced, ambient, and enriched N availability). Each plot was divided into twelve 2×2-m subplots for sampling ( $n=192$ )

the C addition, all plots were tilled to promote similar conditions prior to planting. Strips assigned to the enriched-N treatment were fertilized with ammonium-nitrate (5 g N/m<sup>2</sup>) following germination of plants each year (July 1998, mid-June 1999 and 2000).

In April 1998, all plots were seeded at rates selected to achieve a log-normal distribution of species representative of native prairie (Howe 1994b). Seeds of 42 species were assigned to dominant grass, common, frequent, or uncommon species sowing density categories (Table 1); Baer et al. (1999) provide further details on seed sources and seed preparation procedures. Prior to seeding, all plots were lightly raked. The seeds of common, frequent, and uncommon species were mixed with damp builder's sand and hand broadcast evenly over plots. The dominant grasses were seeded with a grass drill (Truax, Minneapolis, Minn.) over the experimental plots and between the plots at the same seeding rate to reduce potential edge effects. A fence was erected around the site to exclude deer and the study site was burned in early spring following the initial growing season.

#### N and light responses

Heterogeneity of N availability was assessed in the restoration site prior to imposing the experimental treatments and in lowland native prairie occurring on the same soil type in winter of 1998. In each of the 16 restoration plots and 16 plots delineated in native prairie (of the same dimension and spatial configuration), multiple 2-cm diameter by 10-cm deep soil cores were removed and composited by plot. In the laboratory, soil samples were crumbled by hand through a 4-mm diameter sieve and stored at 4°C. A 20-g subsample was removed, weighed, dried at 105°C, and reweighed to determine gravimetric soil moisture. A 10-g subsample was extracted for inorganic N availability (described below). Bulk density of 1.37 and 1.00 g/cm<sup>3</sup> were used to convert inorganic N concentrations in the

restoration site and native prairie to volumetric amounts (mg/m<sup>2</sup>), respectively.

In year three, we used inorganic N captured on ion exchange resins (Binkley and Matson 1983) to quantify relative N availability and heterogeneity in all subplots within all WPHTs (only data for 2000 are presented here). Resin bags were constructed of nylon, and contained 20 g of a 1:1 mixture of cation (Dowex 50 WX2) and anion (Dowex 1X8-50) resins, preloaded with H<sup>+</sup> and Cl<sup>-</sup>, respectively. One resin bag was buried in the surface 10 cm of each subplot in July and retrieved in October each year.

Extractable NO<sub>3</sub>-N for assessment of initial heterogeneity and recovery of NO<sub>3</sub>-N on the resins in year three were determined by agitating the samples at 200 rpm (rotation frequency 3.33 Hz) with 2 mol/l KCl for 1 h, then filtering the solutions through 0.4-μm polycarbonate membranes. Ammonium and nitrate concentrations in the extracts were determined colorimetrically on a Flow Solution autoanalyzer (Alpkem, Clackamas, Or.).

At the midpoint of the third growing season, light availability was measured in two permanently located 50×50-cm quadrats in each subplot. Five measurements of photosynthetic photon flux density (PPFD) were made in each quadrat at the soil surface and above the canopy with a Decagon 0.5-m ceptometer (Decagon Devices, Pullman, Wash.). The five PPFD measurements at the soil surface and above the canopy (maximum PPFD) were averaged for each location in each quadrat, and then PPFD was averaged over the two quadrats.

#### Plant community responses

The percent cover of each plant species was visually assessed in spring (June) and summer (August) surveys of all plants rooted within two permanently located 50×50-cm quadrats in every subplot of all WPHTs. For each species, the maximum cover value from the combined spring and summer surveys was used for further analyses. Cover values from the replicate 0.25-m<sup>2</sup> quadrats in each subplot were then averaged prior to calculating species richness, diversity, and dominance. Diversity was calculated using Shannon's diversity index,  $H' = -\sum p_i \ln p_i$ , where  $p_i$  represented the proportion of total cover contributed by each species. Dominance was calculated using Simpson's index,  $SI = [\sum n_i (n_i - 1)] / [N(N-1)]$ , where  $n_i$  and  $N$  were the percent cover of each species and total cover of all species in a subplot, respectively (Wolda 1981). Community responses to the WPHTs were determined by averaging the cover of each species among 12 subplots within a WPHT. Community heterogeneity in the WPHTs was evaluated by calculating coefficients of variation (CV) among the 12 subplots and the mean dissimilarity in species composition among all possible comparisons of the 12 subplots within each WPHT (Inouye et al. 1987; Collins 1989). Percent dissimilarity (PD) was defined as 1-percent similarity,  $[PS = 1 - 0.5\sum |p_a - p_b|]$ , where  $p_a$  and  $p_b$  were the proportional cover of two species in a pair of subplots] (Whittaker 1975).

In year three, we delineated four plots in a periodically burned prairie that had never been cultivated on the same soil type as the restoration site (<1 km from the restoration site). The native prairie plots were the same dimensions as the restoration plots (6×8 m) and were partitioned into twelve 2×2-m subplots for sampling. The similarity of the restored prairie communities in each N treatment was compared to native prairie using PS. The proportional cover of each species was determined for each N treatment within a whole-plot in the restored prairie and was compared to the proportional cover of each species averaged among the four native prairie plots. The similarity of restored prairie communities in each WPHT was compared to native prairie using the average proportional cover of each species in each WPHT.

#### Statistical analyses

Our design included whole plots with strips of varying dimensions and replications assigned to the soil depth and N treatments, which

**Table 1** Relative cover of plant species in native prairie and the restored prairie soil N treatments in year three. Non-native species denoted by an asterisk (\*). Grass, sedge, forb, and woody growth forms indicated by *G*, *S*, *F*, and *W*, respectively. Soil N treatment

means were calculated from the average cover of each species in each N treatment in each whole plot (reduced-N and enriched-N,  $n=8$ ; ambient-N,  $n=16$ ). Nomenclature follows Great Plains Flora Association (1986)

	Growth form	Native Prairie	Restored Prairie N Treatment		
			Reduced	Ambient	Enriched
<b>Seeded dominant species (160 seeds/m<sup>2</sup>)</b>					
<i>Andropogon gerardii</i> Vitman	G	0.431	0.268	0.179	0.112
<i>Andropogon scoparius</i> Michx.	G	0.041	0.046	0.017	0.002
<i>Panicum virgatum</i> L.	G	0.227	0.435	0.576	0.742
<i>Sorghastrum nutans</i> (L.) Nash	G	0.058	0.135	0.062	0.055
<b>Seeded common species (16 seeds/m<sup>2</sup>)</b>					
<i>Aster ericoides</i> L.	F	-	-	-	-
<i>Artemisia ludoviciana</i> Nutt.	F	-	<0.001	<0.001	<0.001
<i>Bouteloua curtipendula</i> (Michx.) Torr.	G	<0.001	0.008	0.007	0.005
<i>Salvia azurea</i> Lam.	F	-	0.032	0.049	0.023
<i>Solidago canadensis</i> L.	F	0.002	-	-	-
<b>Seeded frequent species (10 seeds/m<sup>2</sup>)</b>					
<i>Amorpha canescens</i> Pursh	W	0.001	0.005	0.002	<0.001
<i>Asclepias verticillata</i> L.	F	0.004	0.003	0.004	0.003
<i>Aster oblongifolius</i> Nutt	F	-	-	-	-
<i>Ceanothus herbaceus</i> Raf.	W	-	-	-	-
<i>Dalea purpurea</i> Vent.	F	<0.001	0.003	0.005	0.001
<i>Kuhnia eupatorioides</i> L.	F	-	0.006	0.010	0.009
<i>Lespedeza capitata</i> Michx.	F	0.002	0.013	0.004	0.003
<i>Schrankia nuttallii</i> (DC.) Standl.	F	-	<0.001	<0.001	<0.001
<i>Solidago missouriensis</i> Nutt.	F	0.011	-	-	-
<i>Sporobolus asper</i> (Michx.) Kunth	G	-	0.001	0.001	0.001
<i>Sporobolus heterolepis</i> (A. Gray) A. Gray	G	0.016	-	-	-
<i>Vernonia fasciculata</i> Michx.	F	0.007	0.001	0.001	<0.001
<b>Seeded uncommon species (5 seeds/m<sup>2</sup>)</b>					
<i>Asclepias viridis</i> Walt.	F	-	0.001	<0.001	<0.001
<i>Aster sericeus</i> Vent.	F	-	-	-	-
<i>Baptisia australis</i> (L.) R. Br.	F	-	0.012	0.004	0.001
<i>Baptisia bracteata</i> Muhl. ex Ell.	F	-	0.001	0.001	<0.001
<i>Callirhoe involucrata</i> (T. & G.) A. Gray	F	-	<0.001	0.001	0.001
<i>Dalea candida</i> Michx. ex Willd.	F	-	0.002	0.002	<0.001
<i>Desmanthus illinoensis</i> (Michx.) MacM.	F	0.009	0.001	0.001	<0.001
<i>Echinacea angustifolia</i> DC.	F	-	-	-	-
<i>Koeleria pyramidata</i> (Lam.) Beauv.	G	-	-	-	-
<i>Liatrix punctata</i> Hook	F	-	-	-	-
<i>Lomatium foeniculaceum</i> (Nutt.) Coult. & Rose	F	-	-	-	-
<i>Oenothera macrocarpa</i> Nutt.	F	-	<0.001	<0.001	<0.001
<i>Penstemon cobaea</i> Nutt.	F	-	-	-	-
<i>Penstemon grandiflorus</i> Nutt.	F	-	-	-	-
<i>Psoralea tenuiflora</i> Pursh	F	-	0.002	0.001	<0.001
<i>Ratibida columnifera</i> (Nutt.) Wood & Standl.	F	-	0.003	0.004	<0.001
<i>Rosa arkansana</i> Porter	W	-	<0.001	<0.001	<0.001
<i>Ruellia humilis</i> Nutt.	F	-	0.005	0.005	0.006
<i>Senecio plattensis</i> Nutt.	F	-	-	-	-
<i>Sisyrinchium campestre</i> Bickn.	F	-	-	-	-
<i>Triodanis perfoliata</i> (L.) Nieuw.	F	-	-	-	-
<b>Volunteer species-restored prairie</b>					
<i>Abutilon theophrasti</i> Medic.*	F	-	0.003	0.002	0.001

Table 1 (continued)

	Growth form	Native Prairie	Restored Prairie N Treatment		
			Reduced	Ambient	Enriched
<i>Amaranthus retroflexus</i> L.	F	-	<0.001	<0.001	0.001
<i>Ambrosia psilostachya</i> DC.	F	0.009	0.001	0.001	0.001
<i>Asclepias syriaca</i> L.	F	0.088	0.004	0.001	0.003
<i>Bromus inermis</i> Leyss.*	F	-	0.004	0.039	0.037
<i>Chenopodium album</i> L.*	F	-	<0.001	0.001	0.001
<i>Conyza canadensis</i> (L.) Cronq.	F	-	0.003	0.008	0.004
<i>Cucurbita foetidissima</i> H.B.K.	F	-	<0.001	<0.001	<0.001
<i>Medicago sativa</i> L.*	F	-	<0.001	<0.001	<0.001
<i>Melilotus officinalis</i> (L.) Pall.*	F	0.002	0.001	0.001	<0.001
<i>Physalis virginiana</i> P. Mill.	F	<0.001	<0.001	0.002	0.001
<i>Phytolacca americana</i> L.	F	-	<0.001	0.006	<0.001
<i>Plantago</i> sp. L.	F	-	<0.001	<0.001	<0.001
<i>Rhus</i> sp. L.	W	-	<0.001	<0.001	<0.001
<i>Setaria glauca</i> (L.) Beauv.*	G	-	<0.001	<0.001	<0.001
<i>Symphoricarpos orbiculatus</i> Moench	W	<0.001	<0.001	0.001	0.001
<i>Taraxacum officinale</i> Weber*	F	-	<0.001	<0.001	<0.001
<i>Trifolium</i> sp.L.	F	-	<0.001	<0.001	<0.001
<i>Vicia sativa</i> L.*	F	-	0.002	<0.001	<0.001
<b>Native prairie species</b>					
<i>Rumex altissimus</i> L.	F	0.031	-	-	-
<i>Hedeoma hispidum</i> Pursh	F	0.021	-	-	-
<i>Carex</i> spp. L.	S	0.012	-	-	-
<i>Silphium integrifolium</i> Michx.	F	0.008	-	-	-
<i>Helianthus rigidus</i> (Cass.) Desf.	F	0.007	-	-	-
<i>Eleocharis</i> sp. R. Br.	G	0.003	-	-	-
<i>Helianthus annuus</i> L.	F	0.003	-	-	-
<i>Tridens flavus</i> (L.) Hitchc.	G	0.002	-	-	-
<i>Lepidium densiflorum</i> Schrad.	F	0.002	-	-	-
<i>Dichanthelium oligosanthes</i> (Schult) Gould	G	0.001	-	-	-
<i>Teucrium canadense</i> L.	F	0.001	-	-	-
<i>Poa pratensis</i> L.*	G	<0.001	-	-	-
<i>Asclepias incarnata</i> L.	F	<0.001	-	-	-
<i>Kochia scoparia</i> (L.) Schrad.*	F	<0.001	-	-	-
Unidentified species		0.015	0.004	0.002	0.005

resulted in different sample sizes (number of 2×2-m subplots) for the six treatment combinations. Furthermore, community responses were measured from the same experimental units for 3 years. Designs containing different sizes of experimental units (i.e., strips assigned to the soil treatments), unequal replication of treatments, and repeated measures result in different error structures associated with each treatment effect, interactions, and repeated measures (Milliken and Johnson 1992). Therefore, we used the mixed model procedure in SAS (SAS 1999) to analyze responses to the soil depth and N treatments so that we could specify random effects, use Satterthwaite's method to estimate denominator degrees of freedom associated with the different error structures, and choose the appropriate covariance structure for the repeated measures (Littell et al. 1996). Random effects assigned to the model included block, the interaction between block and the WPHT, N treatments randomized to horizontal strips, and depth treatments randomized to vertical strips. Fixed effects included the main effects and interactions of soil N, depth, and time. Responses to the WPHTs in year three were analyzed according to a randomized complete block design using the mixed model procedure in SAS (SAS 1999), with

block assigned as a random effect in the model. Inorganic N responses were log-transformed prior to statistical analyses to attain normality. All means comparisons were performed using the difference in least squares means procedure,  $\alpha=0.05$  (SAS 1999). Relationships among response variables were examined using Pearson's correlation coefficients (SAS 1999).

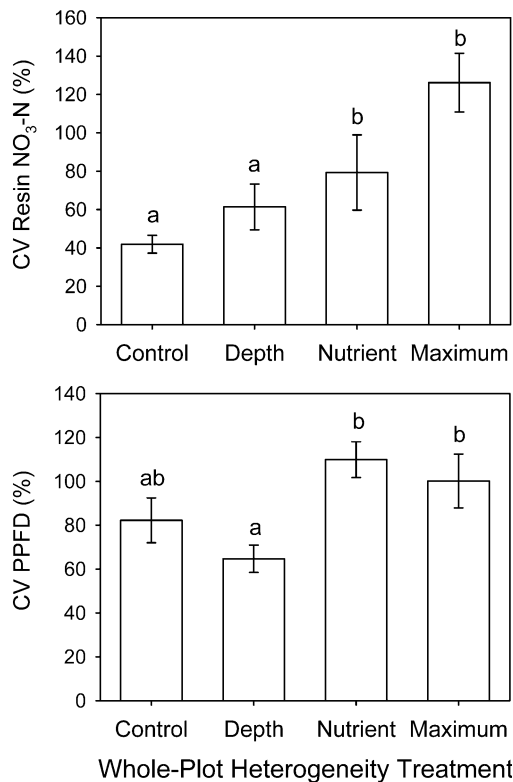
## Results

### Resource availability and heterogeneity

Native prairie contained lower levels and greater heterogeneity of  $\text{NO}_3\text{-N}$  than the restoration site in 1998. Average extractable  $\text{NO}_3\text{-N}$  in native prairie and the restoration site were 143.5 ( $\pm 24.5$ ) and 745.2 ( $\pm 45.8$ ) mg  $\text{N}/\text{m}^2$ , respectively. The variability (coefficient of varia-

tion, CV) of  $\text{NO}_3\text{-N}$  in native prairie (66.1%) was nearly 3 times higher than the restoration site (23.7%).

The soil treatments were effective at altering resource availability and increasing soil heterogeneity. The addition of limestone limited plant rooting depth to an average depth of  $25 \pm 3$  cm (Baer et al. 1999). The pulse amendment of sawdust to the soil reduced the availability of  $\text{NO}_3\text{-N}$  for 3 years by increasing the microbial biomass and immobilization of N in the soil (Baer et al. 2003). Annual fertilization each year increased the availability of  $\text{NO}_3\text{-N}$  throughout the 3 years of restoration (Baer et al. 2003). As a result, WPHTs containing the soil N treatments (III and IV) had significantly greater heterogeneity (or CVs) of resin-collected  $\text{NO}_3\text{-N}$  than the control and soil depth heterogeneity WPHTs (denominator  $df=9$ ,  $F=6.08$ ,  $P=0.015$ ) (Fig. 2). Heterogeneity in light availability (PPFD) was also highest in the N and maximum heterogeneity WPHTs ( $ddf=9$ ,  $F=4.4$ ,  $P=0.0358$ ). Although resource heterogeneity varied among WPHTs, there were no differences in the mean availability of resin-collected  $\text{NO}_3\text{-N}$  ( $ddf=9$ ,  $F=1.9$ ,  $P=0.2055$ ) and PPFD ( $ddf=9$ ,  $F=1.0$ ,  $P=0.4327$ ) among the WPHTs.



**Fig. 2** Mean ( $\pm 1$  SE) coefficients of variation, CV, in resin-collected  $\text{NO}_3\text{-N}$  and light availability (PPFD) in the WPHTs following 3 years of restoration. Means accompanied by the same letter were not significantly different ( $\alpha=0.05$ )

## Community responses to soil depth and N availability over time

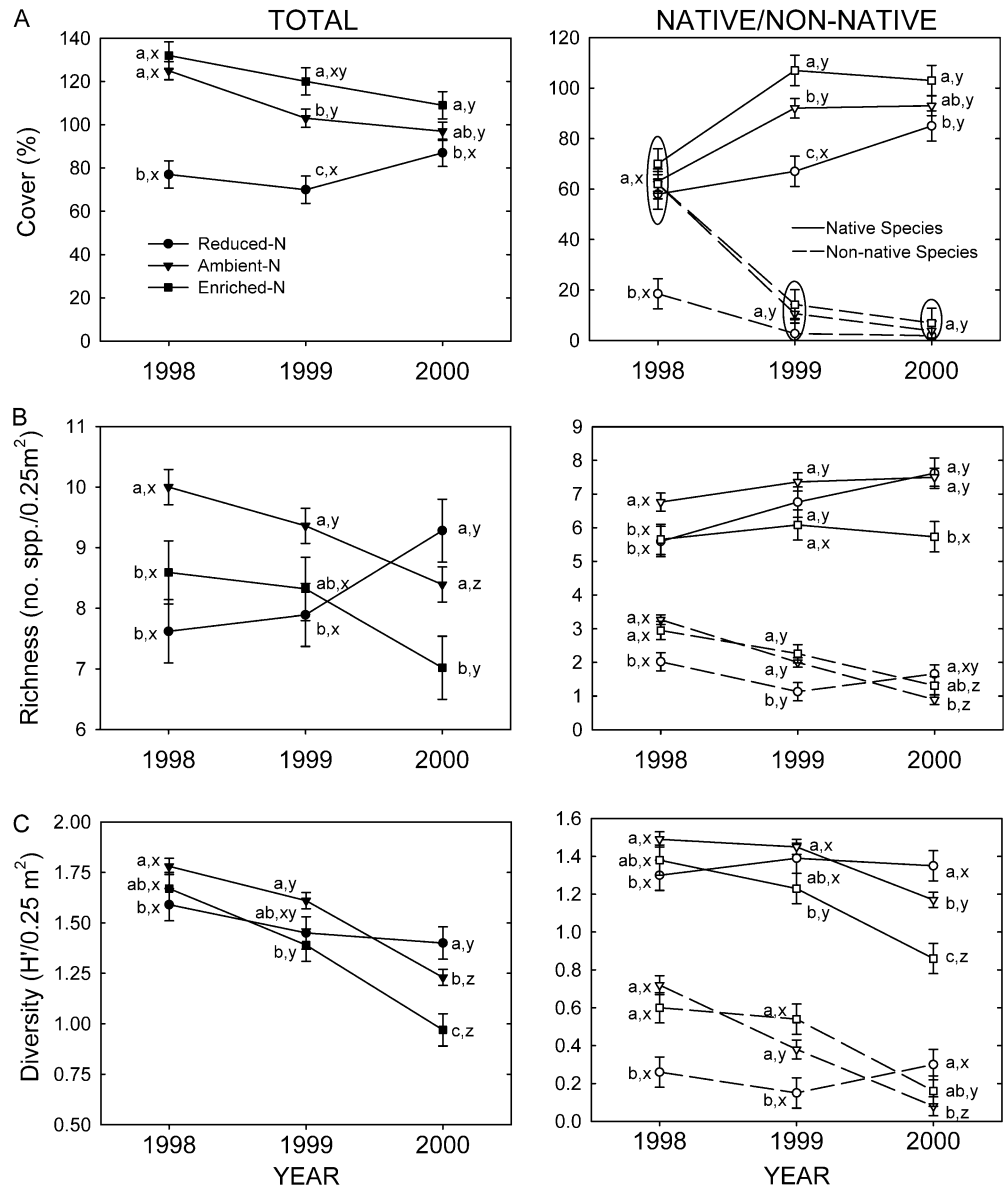
During the first 3 years of restoration, plant cover groups showed significant interactions between the N treatments and time, but were not affected by soil depth (Fig. 3A). Total cover was lowest in the reduced-N treatment and highest in the enriched-N treatment over all three years, but differences among the N treatments diminished with time ( $ddf=366$ ,  $F=5.9$ ,  $P<0.0001$ ). Less plant cover in the reduced-N soil in year one was due to lower cover of non-native species, and the cover of this group was negligible in all N treatments by year two ( $ddf=366$ ,  $F=7.3$ ,  $P<0.0001$ ). Native species cover was similar among the N treatments in year one, increased in the ambient-N and enriched-N treatments in year two, and was highest in the enriched-N soil and lowest in the reduced-N soil by year three ( $ddf=366$ ,  $F=4.5$ ,  $P<0.0001$ ).

Species richness and diversity also varied among the N treatments over time, but were not affected by soil depth (Fig. 3B,C). Total richness declined over time in the ambient-N and enriched-N soil, but increased in the reduced-N soil from year two to year three ( $ddf=366$ ,  $F=7.6$ ,  $P<0.0001$ ). Native species richness increased each year in the reduced-N treatment, but remained unchanged in the ambient-N and enriched-N treatments ( $ddf=366$ ,  $F=2.9$ ,  $P=0.0217$ ). Total diversity also declined over time in the ambient-N and enriched-N treatments, but to a lesser extent in the reduced-N soil ( $ddf=366$ ,  $F=7.4$ ,  $P<0.0001$ ). Diversity of native species was similar across all years in reduced-N soil, but declined by year three in ambient-N and enriched-N soil ( $ddf=366$ ,  $F=9.6$ ,  $P<0.0001$ ). By year three, total and native species richness and diversity were highest in the reduced-N and lowest in the enriched-N soil. The interaction between time and the N treatments for non-native species was due to higher diversity ( $ddf=366$ ,  $F=10.0$ ,  $P<0.0001$ ) and richness ( $ddf=366$ ,  $F=7.7$ ,  $P<0.0001$ ) of this group in ambient-N and enriched-N than in the reduced-N soil in year one only.

By year three,  $C_4$  grasses dominated the restored prairie, but all grass species did not respond to the soil N and depth treatments in the same manner (Fig. 4A). *Panicum virgatum* was the most dominant species in the restoration as a whole, but the magnitude of its dominance varied among the soil N treatments, with lowest cover in the reduced-N soil and highest cover in the enriched-N soil ( $ddf=36$ ,  $F=12.3$ ,  $P<0.0001$ ). Cover of the second most abundant grass, *Andropogon gerardii*, showed an interaction between the soil N and depth treatments resulting from greater cover in deep, reduced-N soil relative to all other treatments ( $ddf=148$ ,  $F=4.8$ ,  $P=0.0099$ ) (Fig. 4A). *Sorghastrum nutans* and *Andropogon scoparius* were most abundant in the reduced-N soil (*S. nutans*:  $ddf=39$ ,  $F=12.3$ ,  $P<0.0001$ ; *A. scoparius*:  $ddf=39$ ,  $F=13.0$ ,  $P<0.0001$ ) (Fig. 4A).

In year three, community dominance in the N treatments reflected the pattern of *P. virgatum* cover ( $ddf=36$ ,  $F=8.0$ ,  $P=0.0013$ ) (Fig. 4B). Cover of *P. virgatum* was correlated with Simpson's index of dominance and negatively related

**Fig. 3** Temporal changes in mean ( $\pm 1$  SE) total, native, and non-native plant species **A** cover, **B** richness, and **C** diversity in the reduced-N, ambient-N and enriched-N treatments. A significant interaction between the nutrient treatments and time occurred for all variables. Differences among treatments within a year indicated by letters *a–c*; differences over time within a treatment indicated by letters *x–z*. Means accompanied by the same letter (*a–c* or *x–z*) were not significantly different ( $\alpha=0.05$ )



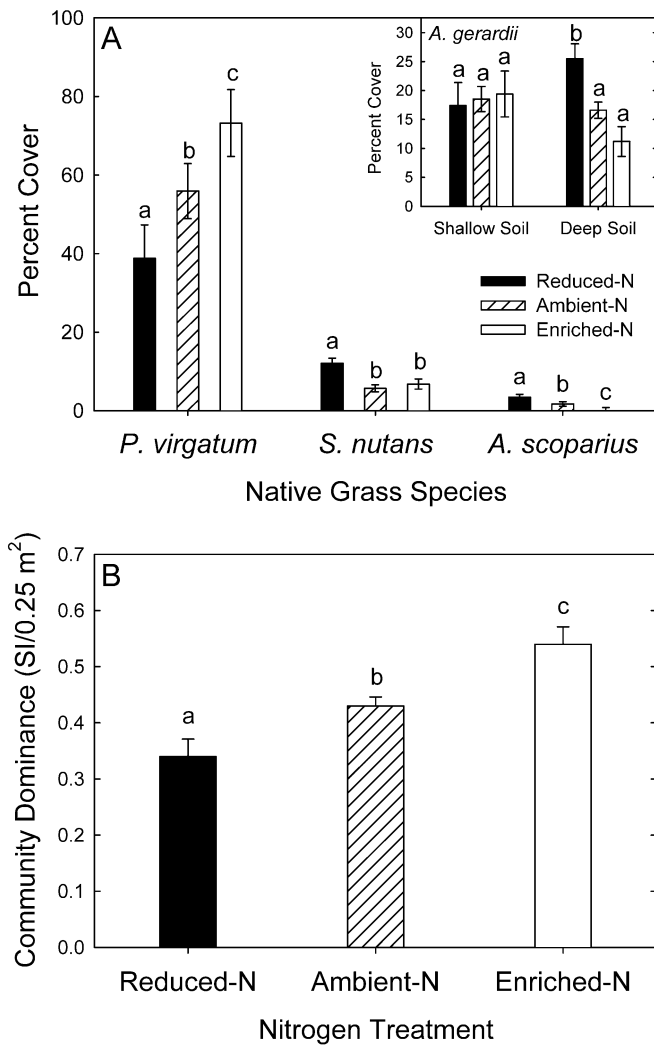
to community diversity (Fig. 5). The relative cover of all other  $C_4$  grasses, however, was inversely related to dominance (*A. gerardii*:  $r=-0.72$ ,  $P<0.001$ ; *S. nutans*:  $r=-0.73$ ,  $P<0.001$ ; and *A. scoparius*:  $r=-0.69$ ,  $P<0.001$ ).

We also compared community structure of restored prairie in the soil N treatments to that of native prairie in year three (Table 1). The restored prairie community resembled native prairie in that prairie species comprised >90% of total cover and warm-season grasses dominated cover. The occurrence of non-native species was negligible in both native and restored prairie (<2 spp./0.25 m<sup>2</sup>). The composition of native and restored communities differed in that *A. gerardii* was the dominant species in native prairie, there was little overlap in forb species, and the average cover of forb species in native prairie was twice that of the restored prairie. Diversity in the reduced-N soil was most similar to native prairie ( $H^{\prime}=1.48\pm 0.12$ ). The PS of the restored prairie community to native prairie

was highest in the reduced-N soil and lowest in the enriched-N soil ( $ddf=39$ ,  $F=10.9$ ,  $P=0.0002$ ) (Fig. 6).

#### Community responses to heterogeneity

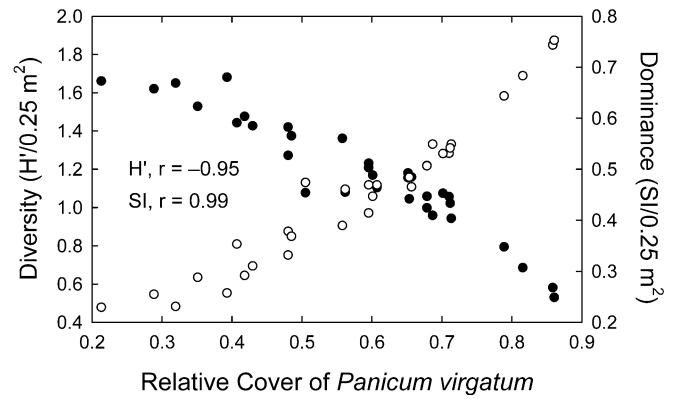
Plant community responses to the WPHTs were examined in year three, when the restored prairie was predominantly comprised of prairie species. Total species richness was one of the few community measures to show a response to the WPHTs, with lowest richness occurring in the nutrient WPHT ( $ddf=9$ ,  $F=4.37$ ,  $P=0.037$ ) (Table 2). Diversity, dominance, relative cover of *P. virgatum*, and community similarity to native prairie were not different among the WPHTs. Two measures of community heterogeneity varied among the WPHTs (Table 2). The CV in dominance ( $ddf=9$ ,  $F=10.48$ ,  $P=0.003$ ) and CV in relative cover of the dominant species, *P. virgatum* ( $ddf=9$ ,  $F=6.78$ ,  $P=0.011$ ) were lowest in the control WPHT (Table 2). The



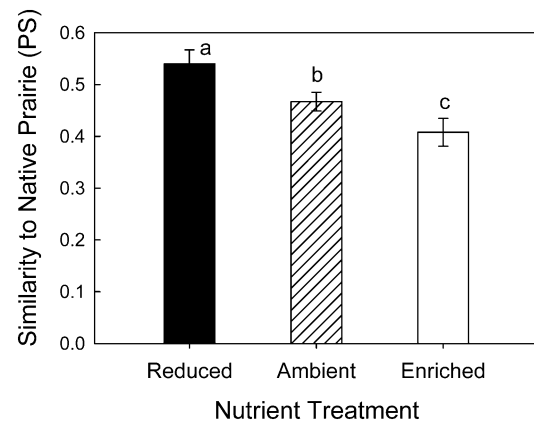
**Fig. 4A, B** Native grass cover and dominance in year three. **A** Percent cover of the four prairie grasses that were seeded at rate of 160 seeds/m<sup>2</sup>. A significant main effect of the soil N treatment occurred for *Panicum virgatum*, *Sorghastrum nutans*, and *Andropogon scoparius*; a significant interaction occurred between the soil N and soil depth treatments for *Andropogon gerardii*. For each species, means with the same letter were not significantly different ( $\alpha=0.05$ ). **B** Simpson's Dominance Index, *SI*, in year three; means accompanied by the same letter were not significantly different ( $\alpha=0.05$ )

variability in dominance was also higher in the nutrient WPHT than all other WPHTs.

The four WPHTs exhibited the same degree of similarity to the native prairie community (Table 2). At this scale, the restored prairie communities were generally less diverse than native prairie, despite the presence of a few more species. Community dominance was similar between the native and restored prairie, however, the relative cover of *P. virgatum* in the restored prairie was 2–3 times that of native prairie. All measures of community heterogeneity in the restored prairie were comparable to those of native prairie, with the exception of the variability in relative cover of *P. virgatum*, which was higher in native prairie because it was less dominant.



**Fig. 5** Relationships between diversity, dominance and the relative cover of *P. virgatum* in year three ( $r$  Pearson's correlation coefficient); correlations were performed on the average relative cover, diversity and dominance in each of the soil N treatments from the independent whole plot ( $n=32$ )



**Fig. 6** Similarity of restored prairie communities to native prairie and relationship between similarity and N availability in year three. Mean ( $\pm 1$  SE) proportional similarity (*PS*) of restored prairie communities N-availability treatments to native prairie were calculated from the average *PS* of restored prairie to native prairie in each N treatment from independent whole-plots (reduced-N,  $n=8$ ; ambient-N,  $n=16$ ; enriched-N,  $n=8$ ). Means accompanied by different letters were significantly different ( $\alpha=0.05$ )

At the whole plot scale, diversity and community heterogeneity (mean PD) were not directly related to heterogeneity in soil N availability. Instead, diversity and community heterogeneity were strongly correlated with light availability ( $P<0.0001$ ) and inversely related to the relative cover of *P. virgatum* ( $P<0.0002$ ), due to this species' high biomass and cover, which had a negative effect on light availability below the canopy ( $P=0.0002$ ) (Fig. 7).

## Discussion

### Resource availability and plant community structure

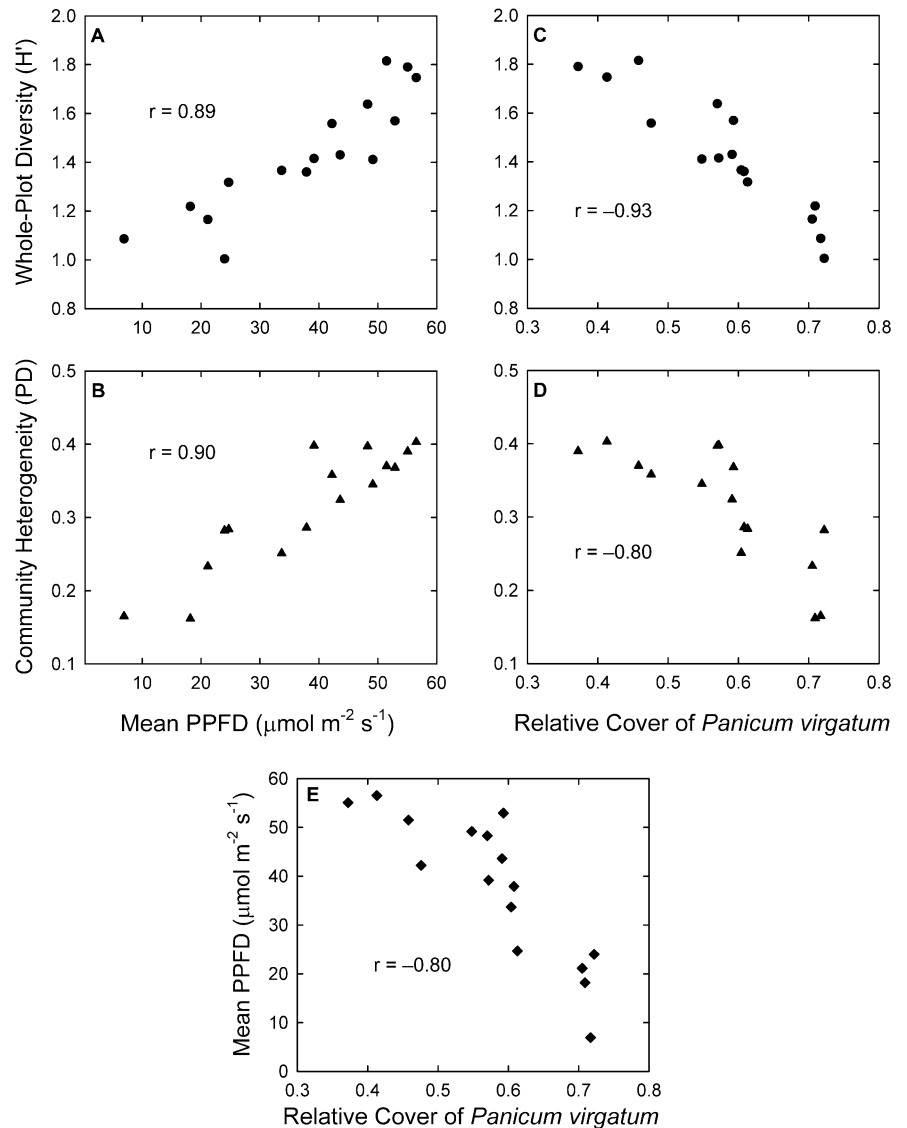
At the onset of our restoration, N availability (extractable NO<sub>3</sub>-N) was spatially less variable in the restoration site than in native prairie, due to long-term agricultural



**Table 2** Average ( $\pm 1$  SE) community structure and heterogeneity characteristics in the restored prairie heterogeneity treatments and native prairie in year 2000. Means accompanied by the same letter were not significantly different

	Whole-plot heterogeneity treatment				Native prairie
	Control	Depth	Nutrient	Maximum	
<b>Community structure</b>					
Richness (no. spp.)	23.75 (1.18) b	24.75(1.89) b	21.00 (1.08) a	26.00 (0.41) b	19.50 (1.37)
Diversity ( $H'$ )	1.58 (1.13)	1.33 (0.10)	1.30 (0.10)	1.51 (0.14)	1.83 (0.14)
Dominance (SI)	0.33 (0.07)	0.44 (0.04)	0.42 (0.04)	0.38 (0.05)	0.32 (0.03)
Relative cover of <i>P. virgatum</i> (0.25 m <sup>2</sup> )	0.49 (0.08)	0.63 (0.03)	0.61 (0.04)	0.58 (0.05)	0.22 (0.03)
Similarity to native prairie	0.51 (0.06)	0.47 (0.03)	0.52 (0.03)	0.47 (0.04)	–
<b>Community heterogeneity</b>					
Richness (CV, %)	27.22 (1.80)	31.39 (5.33)	30.83 (6.22)	26.72 (2.83)	25.06 (4.64)
Diversity (CV, %)	25.63 (2.40)	29.38 (7.36)	36.22 (6.00)	29.68 (3.33)	23.93 (4.07)
Dominance (CV, %)	25.11 (4.68) a	42.40 (2.38) b	57.72 (4.51) c	40.11 (5.16) b	41.78 (6.90)
Relative cover of <i>P. virgatum</i> (CV, %)	17.34 (3.67) a	42.44 (5.74) b	42.92 (3.71) b	37.26 (5.95) b	56.18 (10.15)
Within plot dissimilarity (mean PD)	0.33 (0.06)	0.28 (0.04)	0.32 (0.04)	0.33 (0.04)	0.40 (0.03)

**Fig. 7** Relationships between diversity, community heterogeneity, light availability, and the relative cover of *P. virgatum* in the WHPTs in year three ( $r$  Pearson's correlation coefficient)



practices (i.e., conventional tillage) that homogenize soil conditions. Although the initial assessment of heterogeneity was conducted at the field scale (ha), it is reasonable to assume that these patterns in heterogeneity between the restored and native prairie sites persisted at the spatial scale of the experimental treatments applied within in the restored prairie plots (2 m<sup>2</sup>).

Plant community structure and diversity in native grassland at the Konza Prairie LTER site was considered the target community for evaluating the role of resource availability on community recovery through restoration. The two factors we investigated, soil depth and N availability, did not influence diversity in newly restored prairie in a manner consistent with their effects in native grasslands at KPBS and elsewhere. Van Auken et al. (1994) demonstrated that growth of C<sub>4</sub> grasses increased with soil depth, which promoted the coexistence of grassland species. At KPBS, plant diversity varies with topography (or soil depth), with higher diversity occurring in shallow soil uplands than in deeper soil lowland areas (Towne and Owensby 1984; Gibson and Hulbert 1987; Collins 1992). Contrary to our expectations, soil depth had little effect on community structure during the early stages of restoration. This likely resulted from ineffectiveness of the thin soil treatment in reducing soil moisture (S. Baer, unpublished data), as occurs in the shallow upland soils of native prairie and influences landscape differences in gas exchange rates of the dominant prairie grasses, patterns of productivity, and diversity (Gibson and Hulbert 1987; Knapp et al. 1993). In our restoration, diversity was similar in deep and shallow soils due to the successful establishment and dominance of *P. virgatum* in both soil depths.

Variability in mean levels and heterogeneity of soil resources has important implications for community development and maintenance of diversity (McLendon and Redente 1992; Marrs 1993; Pywell et al. 1994; Janssens et al. 1998). Temporal changes in diversity in our restoration were strongly influenced by soil N availability (Fig. 3) and its role in mediating the dominance of one species (Fig. 4). In systems recovering naturally from disturbance, soil fertility influences the successional trajectory of plant communities if nutrient availability favors early or late successional species (Carson and Barrett 1988; Redente et al. 1992; Collins and Wein 1998; Marrs 1993; Janssens et al. 1998; Paschke et al. 2000). Reducing soil fertility by adding C has been suggested as a method to reduce the occurrence of early successional, weedy species with high nutrient requirements (Morgan 1994; Blumenthal et al. 2003). Similarly, high levels of soil nutrients may facilitate the establishment and/or persistence of early successional species (Pashke et al. 2000; Blumenthal et al. 2003). In the initial year of our experiment, differences in the successional composition (i.e., native and non-native species) of communities developing under different levels of N availability were evident (Fig. 3). Carbon addition significantly reduced the cover of non-native species, but not native species, in year one. Although non-native species were negligible in all

soil N treatments by the second year, diversity and richness of native species were highest in the reduced-N soil, where non-natives were initially least abundant, by the third year of restoration. Thus, the dynamics of developing communities in restored ecosystems are influenced by soil fertility. However, restored prairie communities may differ from communities undergoing natural succession in that nutrient availability appears to have a greater effect on the diversity of reintroduced prairie species in subsequent years, rather than the successional trajectory of the plant community.

Measures of restoration success range from the re-establishment of particular species, to the resemblance of a community to a pre-defined target community, to recovery and/or maintenance of whole ecosystem structure and function (Ewel 1987; Pywell and Putwain 1996; Bakker et al. 2000). After 3 years, our restored prairie was broadly similar to native prairie in that native C<sub>4</sub> grasses dominated cover and numerous less abundant grass and forb species contributed the most to species richness (Table 1). The restored prairie, however, was distinctly different from native prairie with respect to the identity of the dominant species, composition of forb species, and an overall lower representation of forbs in the restored prairie (Table 1). Highest community similarity to native prairie occurred in the reduced-N treatment, underscoring the potential importance of resource availability on restoration success, particularly for resources that are limiting in the native community, i.e. N in tallgrass prairie (Blair et al. 1998).

The low abundance of forbs (Warkins and Howell 1983; Howe 1994a, 1994b, 1999; Brown and Bugg 2001) and dominance of *P. virgatum* (Schramm 1990; Corbett et al. 1996; Baer et al. 2002) was not unique to our experiment. Many studies have noted the difficulty in establishing subdominant forb species in grassland restorations (Warkins and Howell 1983; Zajicek et al. 1986; Howe 1999; Jackson 1999). The tendency of *P. virgatum* to dominate tallgrass prairie restorations may be related to high residual soil N levels prior to restoration (Baer et al. 2000, 2002), also evidenced by higher NO<sub>3</sub>-N availability in our restoration site relative to native prairie in 1998. Positive responses of *P. virgatum* to N enrichment in native prairie (unpublished LTER data) are also consistent with our observations in restored prairie. Manipulating soil fertility directly (e.g., C amendments) to steer the recovery of plant diversity may be feasible for small-scale prairie restorations, but expansive restorations may need to rely on other management approaches to reduce soil fertility. Burning may be an important management option for increasing productivity and reducing N availability early in the restoration process (Baer et al. 2003), but early spring fires, as we conducted in year two, can further favor the dominance of warm-season grasses in prairie restorations (Howe 1994b, 1995; Copeland et al. 2002). The strong inverse relationship between the relative cover of *P. virgatum* and diversity in our experiment (Fig. 6) suggests that restoration of agricultural lands would benefit from reduced seeding rates of species that respond strongly to

enhanced resource availability, and are prone to dominate restored communities. Variable fire regimes, grazing, and/or mowing may also be required to reduce the dominance of native grasses and maintain diversity in restored grassland communities (Howe 1994a, 1995, 1999).

#### Resource heterogeneity and plant community structure

Heterogeneity in the landscape results from the interaction between biological and physical patchiness (Wu and Loucks 1995). The “environmental heterogeneity hypothesis” has been invoked as a potential mechanism for the maintenance of diversity (Levin 1974) if spatial variability in resources promotes species coexistence (Grime 1979; Huston 1979; Tilman and Pacala 1993; Caldwell and Pearcy 1994). Native tallgrass prairie communities are generally dominated by a few species of perennial grasses, but also contain a large number of satellite species at low abundances (Collins and Barber 1985; Collins and Glenn 1990). Satellite species, which contribute the most to the diversity of tallgrass prairie, are maintained in part by the high degree of heterogeneity in soil properties and vegetation pattern resulting from both abiotic (i.e., topography, soil texture, fire) and biotic (i.e., grazing, plant species, animal disturbances) factors (Vinton and Burke 1995; Burke et al. 1999; Knapp et al. 1999; Hook and Burke 2000).

Our study tested whether environmental (soil) heterogeneity facilitated the recovery of diversity and community heterogeneity during the initial stages of grassland restoration, where long-term conventional agricultural practices homogenize the spatial variability of soil resources (Rover and Kaiser 1997). Although the soil treatments successfully increased the spatial heterogeneity of resources (Fig. 2), there was little evidence that restored prairie community structure tracked resource heterogeneity at the imposed spatial scale (Table 1). Species richness was the only community measure that responded to the whole-plot heterogeneity treatments, but not according to our expectations (i.e., highest in maximum heterogeneity treatment and lowest in the most homogeneous treatment). The fewest number of species occurred in the nutrient heterogeneity treatment, which contained the largest patch-size of high N availability favorable to the growth of the dominant species (*P. virgatum*). Higher, and similar, species richness among all other heterogeneity treatments suggests that either reducing the size of high resource patches (i.e., maximum heterogeneity plots) or minimizing overall conditions conducive to a positive growth response of a dominant species (i.e., no N enrichment in the control and depth heterogeneity plots) may facilitate the re-establishment of more prairie species. Diversity was similar among the heterogeneity treatments (Table 2), which may relate to the successful establishment and dominance of *P. virgatum* across all levels of resource availability, and similar average plot-level cover of *P. virgatum* (Table 2), despite differential growth responses to the N treatments (Fig. 4). Collins and Wein (1998) also

found no evidence that vegetation composition tracked heterogeneity in soil nutrient enrichment due to the increased abundance of a dominant species over all levels of nutrient heterogeneity. The differential response of *P. virgatum* to N availability (Fig. 4) was also largely responsible for the differences observed in community heterogeneity, specifically the least variability in dominance occurring in the most homogeneous treatment, i.e. control plots (Table 2). Diversity and community heterogeneity depended more on the relative cover of the dominant species and its affect on light availability, rather than soil N heterogeneity per se (Fig. 7). Silvertown et al. (1994) observed a similar phenomenon in that plant composition responded more to the heterogeneity in biomass production (and competition for light) rather than to experimentally altered heterogeneity in rainfall.

#### Conclusions

Restoration generally aims to accelerate natural successional processes (Jordan et al. 1988). Our experimental design enabled us to test the applicability of generalities regarding community responses to soil fertility that have been well established in old-field systems and native grasslands. We documented that soil fertility can regulate diversity in the early stages of ecological restoration, through its influence on a dominant species. Unlike many herbaceous communities recovering naturally from disturbance, soil fertility had more influence on the diversity of the restored (target) species than the successional trajectory of the community. Mean levels of soil N availability in the restored prairie were a more important determinant of the degree of community similarity to native prairie than the heterogeneity of this resource at the spatial scale we examined. Our results indicate that spatial heterogeneity of soil resources imposed on a 2-m<sup>2</sup> scale may not be sufficient to restore a diverse prairie community where a dominant species is a successful competitor across the range of resource (N) availability. Soil fertility should be considered when selecting grassland species to reintroduce into formerly cultivated systems because a strong positive response of a single species to high nutrient conditions can limit the recovery of floristic diversity, and ultimately, restoration success.

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