

## SOIL RESOURCES REGULATE PRODUCTIVITY AND DIVERSITY IN NEWLY ESTABLISHED TALLGRASS PRAIRIE

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**Abstract.** In native tallgrass prairie, soil depth and nitrogen (N) availability strongly influence aboveground net primary productivity (ANPP) and plant species composition. We manipulated these factors in a newly restored grassland to determine if these resources similarly constrain productivity and diversity during the initial three years of grassland establishment. Four types of experimental plots with six treatment combinations of deep and shallow soil at reduced-, ambient-, and enriched-N availability formed the basis of this study. The soil responses to the experimental treatments were examined over three years, and patterns in diversity and productivity were examined in year 3. The soil depth treatment did not significantly affect soil carbon (C) and N pools or ANPP and diversity. A pulse amendment of C added to the soil prior to planting increased soil microbial biomass and decreased potential net N mineralization rates to effectively reduce N availability throughout the study. Nitrogen availability declined over time in nonamended soils as a result of plant establishment, but adding fertilizer N alleviated the increasing immobilization potential of the soil. The level of ANPP was lowest and diversity highest in the reduced-N treatment, whereas the enriched-N treatment resulted in high productivity, but low diversity. As a result, diversity was inversely correlated with productivity in these newly established communities. The same mechanism invoked to explain decreased diversity under nutrient enrichment in old-field ecosystems and native grasslands (e.g., reduced light availability with increased production) was supported in the restored prairie by the positive relationship between ANPP and intercepted light, and a strong correlation between light availability and diversity. The effects of nutrient availability on plant community composition (diversity and richness) were due primarily to the responses of prairie species, as the productivity of early successional, nonprairie species was less than 1% of total ANPP after three years of establishment. These results show that the effects of resource availability on productivity and diversity are similar in young and mature grasslands, and that manipulation of a limiting nutrient during grassland establishment can influence floristic composition, with consequences for long-term patterns of diversity in restored ecosystems.

**Key words:** *aboveground net primary productivity (ANPP); diversity; grassland; Konza Prairie, Kansas (USA); nutrient enrichment; productivity; restoration; richness; tallgrass prairie.*

### INTRODUCTION

The interdependence of plant community diversity and productivity on patterns of resource availability has been demonstrated through experimental manipulation of limiting nutrients in a variety of ecosystems (Tilman 1987, 1993, Carson and Barrett 1988, Bakelaar and Odum 1978, Foster and Gross 1998, Bedford et al. 1999, Waide et al. 1999, Gough et al. 2000, Nilsson et al. 2002). Increased rates of local extinction (species loss) and decreased rates of local colonization (species gain) can contribute to reduced diversity when productivity is increased by nutrient enrichment (Tilman 1993), and this phenomenon is generally attributed to altered competitive relationships in response to reduced availability and/or heterogeneity of resources (Newman 1973, Grime 1979, Tilman 1982, Goldberg and

Miller 1990, Foster and Gross 1998, Gross et al. 2000, Stevens and Carson 2002). Understanding interactions among resource availability, productivity and diversity is relevant to the management, preservation, and restoration of native communities, especially in light of ongoing anthropogenic changes to the global nitrogen (N) cycle through increased fertilizer production, cultivation of N-fixing species, and nitrogen deposition (Vitousek 1994, Vitousek et al. 1997, Galloway 1998, Holland et al. 1999, Jenkinson 2001).

Tallgrass prairie is one of the most productive grasslands in North America (Lauenroth 1979, Knapp et al. 1998, Knapp and Smith 2001). Spatial and temporal patterns of annual aboveground net primary productivity (ANPP) in these grasslands are determined by a suite of factors, including regional climatic gradients (Sala et al. 1988), topographically associated soil properties (Briggs and Knapp 1995), activities of grazing animals (Vinton and Hartnett 1992, Knapp et al. 1999), and occurrence of periodic fires (Knapp and Seastedt 1986). In the absence of grazing, aboveground pro-

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ductivity in tallgrass prairie is mediated by fire, topography, and climate, which interact to affect the availability of three key resources: light, water, and N (Knapp and Seastedt 1986, Schimel et al. 1991, Knapp et al. 1993, Seastedt and Knapp 1993, Briggs and Knapp 1995, Blair 1997, Turner et al. 1997). Long-term studies at Konza Prairie Biological Station have shown that soil depth (associated with topographic position) and N availability (affected by fire and topography) can affect plant species diversity and productivity. For example, shallow upland prairie soils are less productive than deep lowland soils (Briggs and Knapp 1995) and support greater plant species diversity, presumably resulting from the competitive release of subdominant forbs from the dominant grasses (Towne and Owensby 1984, Abrams and Hulbert 1987, Gibson and Hulbert 1987, Collins 1992). Furthermore, long-term N additions have demonstrated that the dominance of grasses varies with N availability, and productivity of the dominant grasses is inversely related to community diversity (Collins et al. 1998). The relationship among nutrient availability, productivity, and species diversity may also have important consequences for grassland restoration, where the soil template is often relatively nutrient-rich and homogeneous, and the reestablishment of a diverse assemblage of native plants can be a difficult and slow process (Sperry 1983, Warkins and Howell 1983, Clarke and Bragg 1994, Howe 1994a, Kindscher and Tieszen 1998).

Understanding the factors that regulate productivity and diversity in restored grasslands is particularly relevant for tallgrass prairie, because less than five percent of the historic extent of this ecosystem remains undisturbed from agriculture (Samson and Knopf 1994). Although there is a long history of prairie restoration (Mlot 1990), and grassland restoration is used widely to conserve biodiversity, reduce soil erosion, and improve water quality (Jordan et al. 1988, Mlot 1990, Dunn et al. 1993), the linkage between structure and function in restored grasslands, and in restored ecosystems in general (Bradshaw 1987, Palmer et al. 1997), is unclear. Understanding the relationship among resource availability, plant productivity, and species diversity in newly established tallgrass prairie may be key for successfully restoring this species-rich ecosystem (Howe 1999).

We used an experimental approach to examine the relationship between productivity and diversity in newly established prairie in response to altered availability of soil resources known to influence productivity and community structure in mature tallgrass prairie. Two levels of soil depth and three levels of soil N availability were altered in a former agricultural field sown with native prairie species. Our objectives were to (1) evaluate the effectiveness of a pulse amendment of carbon to the soil in reducing N availability and the potential of added N to alleviate the increasing immobilization potential of the soil during the establish-

ment of this grassland; (2) quantify the effects of altered soil resource availability on aboveground plant productivity and diversity; and (3) assess the relationships between resource availability, productivity, and diversity. Specifically, we hypothesized that increasing C levels in the soil would promote microbial demand for N and reduce N availability to plants, and that fertilization would saturate microbial N requirements and provide excess N for plant uptake. Relationships between productivity and diversity in adjacent mature prairie, mediated by the dominance of  $C_4$  grasses as a function of N availability and soil depth, provided a theoretical framework to test whether diversity in newly established prairie was modulated by key soil resources through their effects on productivity. We predicted that varying levels of N availability (reduced-, ambient-, and enriched-N) and soil depth (deep and shallow) would impose a gradient of productivity in the restored prairie that would enable us to link community diversity to resource abundance through effects on productivity, as demonstrated in mature tallgrass prairie ecosystems (Wilson and Shay 1990, Collins and Wein 1998, Collins et al. 1998).

## METHODS

### *Study site*

Research plots were located in a former lowland agricultural field that had been cultivated for >50 yr at Konza Prairie Biological Station (KPBS), which is a long-term ecological research site located 9 km south of Manhattan, Kansas, USA (39°05' N, 96°35' W). Elevation at the site was ~340 m, and the 30-yr mean annual and growing season precipitation were 835 and 620 mm/yr, respectively. In the three years of study (1998, 1999, and 2000) total precipitation was 944, 825, and 628 mm, of which 593, 693, and 390 mm fell during the growing season (April through September) of each year, respectively. The soil was a gently sloping (0–1%) Reading silt loam (mesic Typic Argudoll) formed by colluvial and alluvial deposits. Prior to cultivation, the vegetation of the area would have been representative of lowland native tallgrass prairie at KPBS, dominated by the warm-season ( $C_4$ ) grasses *Andropogon gerardii* Vitman, *Andropogon scoparius* Michx., *Sorghastrum nutans* (L.), and *Panicum virgatum* L. (nomenclature follows Great Plains Flora Association [1986]), interspersed with a variety of less common grass and forb species (Abrams and Hulbert 1987).

### *Establishment of experimental plots*

In June 1997, sixteen 6 × 8 m plots (with 6-m buffer strips between all plots) were delineated in a previously cultivated field. Whole-plot treatments (WPTs) of control (I), altered soil depth (II), altered soil nutrient availability (III), and altered depth and nutrient availability (IV) were randomly assigned to four plots within

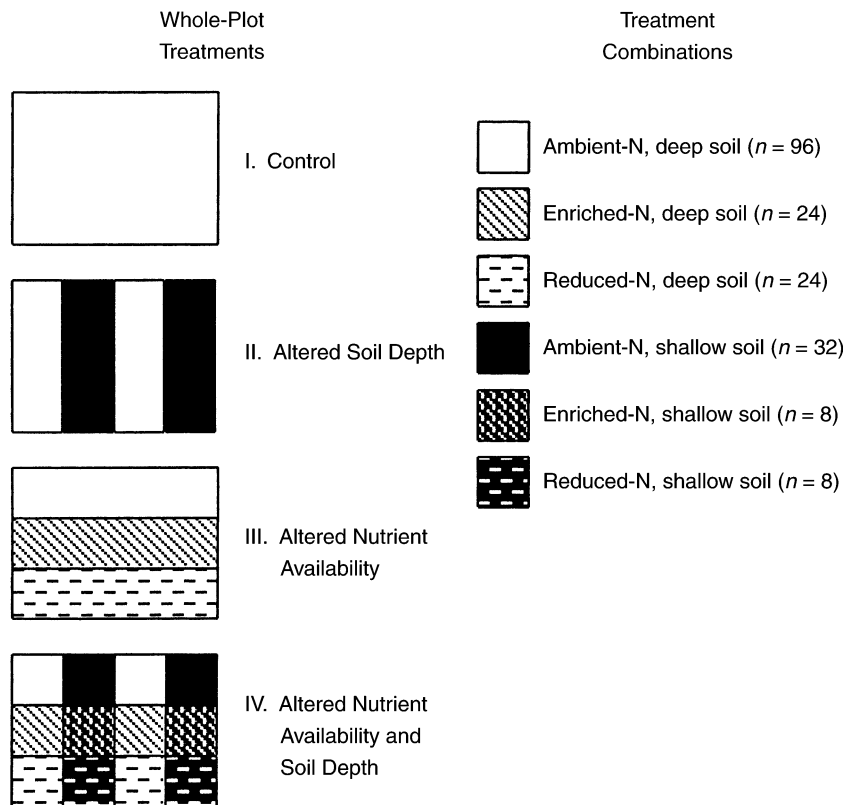


FIG. 1. Whole-plot treatment designs and resultant treatment combinations in the prairie restoration experiment. Whole-plots were separated by 6 m wide buffer strips seeded with native grasses. Four whole-plot treatments (WPTs) were randomly assigned to each block (no. blocks = 4;  $N = 16$ ). Each plot was divided into twelve  $2 \times 2$  m subplots ( $n = 192$ ). Deep and shallow soil treatments were randomly assigned to alternating  $2 \times 6$  m strips in WPTs II and IV. Soil nutrient treatments were randomly assigned to  $2 \times 8$  m strips in WPTs III and IV.

each of four blocks (Fig. 1). We excavated all of the plots to a depth of  $\sim 25$  cm and pieced together native limestone slabs in 2 m wide strips assigned to the shallow soil treatment in WPTs II and IV. The soil from all plots was then replaced, leveled, and disked (2–3 cm deep). Reduced-, ambient-, and enriched-N soil treatments were randomly assigned to each of three 2 m wide strips in WPTs III and IV. In February 1998, we reduced soil N by incorporating sawdust (49% C; C:N ratio = 122) into the soil. Sawdust was tilled into the soil to increase soil C to levels representative of native prairie soil ( $\sim 3\%$  C). Sawdust was applied at a rate of  $5.5$  kg dry mass/m<sup>2</sup> to double the existing C content, based on mean C content of 1.5% and bulk density of  $1.2$  g/cm<sup>3</sup> in the 0–15 cm depth. All plots were then tilled to ensure conditions were similar prior to planting. Strips assigned to the enriched-N treatment were fertilized with ammonium nitrate, applied at a rate of  $5$  g N/m<sup>2</sup> following germination of plants each year (July 1998, mid-June of 1999 and 2000). All plots were subdivided into twelve  $2 \times 2$  m subplots for sampling ( $n = 192$ ).

#### *Plant community establishment*

In April 1998, all plots were sown with 42 native prairie species at rates selected to achieve a log-normal

distribution of species representative of native prairie (Howe 1994b). Each species was assigned to one of four sowing density categories: dominant grasses (160 seeds/m<sup>2</sup>), common (16 seeds/m<sup>2</sup>), frequent (10 seeds/m<sup>2</sup>), or uncommon (5 seeds/m<sup>2</sup>) species (Table 1). Seeds of the dominant C<sub>4</sub> grasses were obtained from a local distributor in Kansas (Star Seed, Beloit, Kansas, USA). All other grass and forb seeds were either hand collected locally or purchased. All seeds were kept in cold dry storage. Legume seeds were inoculated with species-specific rhizobia mixtures (Prairie Moon Nursery, Winona, Minnesota, USA). 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 Company, Minneapolis, Minnesota, USA) over the experimental plots and between the plots (at the same seeding rate) to reduce potential edge effects. All plots were then covered with native prairie hay. Baer et al. (1999) provide additional details regarding seed sources, storage, and treatment procedures. A fence was erected around the site to exclude deer. Management consisted of burning the entire site in early spring prior to the second growing season.

TABLE 1. Seeding categories and rates for each species used in a prairie restoration initiated in 1998.

Dominant grasses (160 seeds/m <sup>2</sup> )	Common species (16 seeds/m <sup>2</sup> )	Frequent species (10 seeds/m <sup>2</sup> )	Uncommon species (5 seeds/m <sup>2</sup> )
<i>Andropogon gerardii</i> (>99)	<i>Artemisia ludoviciana</i> (<1)	<i>Amorpha canescens</i> (9)	<i>Asclepias viridis</i> (2)
<i>Andropogon scoparius</i> (40)	<i>Aster ericoides</i> (0)	<i>Asclepias verticillata</i> (31)	<i>Aster sericeus</i> (<1)
<i>Panicum virgatum</i> (>99)	<i>Bouteloua curtipendula</i> (28)	<i>Aster oblongifolius</i> (0)	<i>Baptisia australis</i> (29)
<i>Sorghastrum nutans</i> (95)	<i>Salvia azurea</i> (76)	<i>Ceanothus herbaceus</i> (0)	<i>Baptisia bracteata</i> (4)
	<i>Solidago canadensis</i> (0)	<i>Dalea purpurea</i> (26)	<i>Callirhoe involucrata</i> (3)
		<i>Koeleria pyramidata</i> (0)	<i>Desmanthus illinoensis</i> (3)
		<i>Kuhnia eupatorioides</i> (16)	<i>Echinacea angustifolia</i> (0)
		<i>Lespedeza capitata</i> (27)	<i>Liatris punctata</i> (0)
		<i>Schrankia nuttallii</i> (<1)	<i>Lomatium foeniculaceum</i> (0)
		<i>Solidago missouriensis</i> (0)	<i>Oenothera macrocarpa</i> (2)
		<i>Sporobolus asper</i> (0)	<i>Penstemon cobaea</i> (0)
		<i>Sporobolus heterolepis</i> (6)	<i>Penstemon grandiflorus</i> (0)
		<i>Vernonia fasciculata</i> (2)	<i>Petalostemon candidus</i> (14)
			<i>Psoralea tenuiflora</i> (6)
			<i>Ratibida columnifera</i> (8)
			<i>Rosa arkansana</i> (1)
			<i>Ruellia humilis</i> (22)
			<i>Senecio plattensis</i> (0)
			<i>Sisyrinchium campestre</i> (0)
			<i>Triodanis perfoliata</i> (0)

Note: The percentage of subplots occupied by each species in year 3 is indicated in parentheses (192 subplots total).

#### Belowground methods

We sampled soil each year by removing and compositing two soil cores (10 cm deep  $\times$  2 cm diameter; one core from directly under plants and one from an unvegetated area between plants) from each 2  $\times$  2 m subplot that was sampled. All field moist soil samples for C and N analysis were crumbled by hand and passed through a 4-mm sieve in the laboratory and stored at 4°C. This mesh size was chosen to be consistent with methods used in long-term soil studies at KPBS (Blair 1997, Turner et al. 1997). Gravimetric soil water content was determined for all soil samples from approximately 20 g of soil (dried at 105°C).

Total soil carbon (TC) was measured from all the subplots in all WPTs prior to fertilization in June 1998 and after fertilization in July of 1999 and 2000 ( $n = 192$  annually). Percentage C was determined on a CN Analyzer (Carlo Erba, Milan, Italy) from a subsample of finely ground soil, dried at 60°C.

Microbial biomass carbon (MBC) and laboratory measures of nitrogen mineralization potentials (NMPs) were measured after fertilization each year from all subplots within WPTs I and IV ( $n = 96/\text{yr}$ ). MBC was determined using the fumigation-incubation procedure (Jenkinson and Powlson 1976) as modified by Voroney and Paul (1984). Based on preliminary trials, an inoculum of fresh C-amended soil (~10% of sample wet mass) was added to all C-amended soils after the fumigation to facilitate microbial utilization of labile C. Mineralized carbon (CO<sub>2</sub>) was analyzed on a gas chromatograph equipped with a thermal conductivity detector. Levels of NMPs were determined using short-term (10-d) aerobic incubations (Robertson et al. 1999).

Extractable inorganic N was determined from the same samples as MBC and NMPs in year one (after

fertilization in all subplots within WPTs I and IV,  $n = 96$ ) because fertilization was delayed until plants became established in the experimental plots. Extractable inorganic N was measured in all subplots of all WPTs in years two and three ( $n = 192$  annually). Approximately 20 g of field moist soil were extracted for inorganic N. Resin-collected inorganic N was measured in all subplots within all WPTs each year ( $n = 192$  annually). Resin bags were constructed of nylon, and contained 20 g of a 1:1 mixture of Dowex-50 strongly acidic cation exchangers and Dowex-1 strongly basic anion exchangers, preloaded with H<sup>+</sup> and Cl<sup>-</sup>, respectively (nos. I 8880 and IX8-50, respectively; Sigma, St. Louis, Missouri, USA). One resin bag was buried in the surface 10 cm of each subplot in July and retrieved in October each year. Inorganic N concentrations were determined for NMPs, direct soil extractions, and resin bags by agitating the samples at 200 revolutions per minute (rpm; rotational frequency 3.33 Hz) with 2 mol/L KCl for 1 h, then filtering the solutions through 0.4- $\mu\text{m}$  polycarbonate membranes. Ammonium and nitrate were determined colorimetrically on a Flow Solution autoanalyzer (Alpkem, Clackamas, Oregon, USA).

Bulk density in the surface 10 cm was determined from 5.3 cm diameter soil cores (dried at 105°C) removed from four randomly selected subplots from each of the six treatment combinations. A bulk density of 1 g/cm<sup>3</sup> was used for native prairie soil (Turner et al. 1997). All dry-mass-based concentrations of C and N were converted to a volumetric basis prior to statistical analyses, using bulk densities of each treatment combination.

#### Aboveground methods

At the midpoint of the third growing season (2000), light availability was measured in two permanently lo-

cated 50 × 50 cm quadrats in each subplot of all WPTs. 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, Washington, USA). 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 in each subplot. Available and intercepted PPFD, expressed as a percentage of maximum PPFD, were calculated for each subplot ( $n = 192$ ).

In year three, percent cover of each plant species was determined in spring (June) and summer (August) for all plants rooted within two permanently located 50 × 50 cm quadrats in every subplot of all WPTs. The maximum cover value of each species from these seasonal surveys was used to calculate diversity. Cover values were averaged from the replicate 0.25-m<sup>2</sup> quadrats in each subplot prior to determining diversity and richness ( $n = 192$ ). Diversity was calculated for each subplot using Shannon's diversity index, where  $H' = -\sum p_i \ln p_i$  and  $p_i$  represents the proportion of total cover contributed by each species.

At the end of the third growing season, we harvested all aboveground vegetation in a 0.10-m<sup>2</sup> area outside of the permanent species composition sampling quadrats in each subplot ( $n = 192$ ). Current year's biomass was separated from the previous year's biomass, and biomass produced in 2000 was further separated into sown and volunteer categories. All plant material was dried at 60°C and weighed to estimate aboveground net primary productivity (ANPP; Briggs and Knapp 1991).

#### Statistical analyses

Our experimental design was unique in that each block consisted of four different whole-plot treatments containing varying dimensions and replications of experimental units (strips) assigned to the six possible treatment combinations (Fig. 1). Designs containing different sizes of experimental units and unequal replication of treatments result in different error structures associated with each treatment (Milliken and Johnson 1992). Consequently, we used the mixed-model procedure in SAS (SAS 1999) to analyze our results so that we could (1) specify random effects of blocks, interaction between blocks, and the soil depth and nutrient treatments, and interaction between the whole-plot treatments with the soil depth and nutrient treatment combinations, (2) calculate type III  $F$  tests for fixed effects of the soil nutrient, soil depth, and interactions of these treatments, and (3) use Satterthwaite's method to estimate denominator degrees of freedom associated with the different error structures inherent to our experimental design (Milliken and Johnson 1992, Littell et al. 1996). Repeated measures were included in the analyses for TC, MBC, and NMPs to test for significant changes in these variables over time and

interactions between time and soil treatments. The mixed procedure enabled us to select the most appropriate covariance structures, which minimized Akaike's Information Criterion and Schwartz's Bayesian Criterion, for repeated-measures analyses (Littell et al. 1996). Extractable and resin-collected inorganic N were measured each year, but were not analyzed using repeated measures, because N availability at one time may not influence N availability in following years due to variability in timing and amount of rainfall each year. Resin-collected nitrate was log-transformed to attain normality prior to statistical analyses. If no interaction occurred between the soil treatments (or soil treatments with time for TC, MBC, and NMPs), then the main effects of the soil nutrient and/or soil depth treatments were compared over both levels of soil depth or all levels of nutrient availability, respectively. All means comparisons were performed using the difference in least-squares means procedure, with  $\alpha = 0.05$  (SAS 1999).

Relationships between diversity, richness, productivity, soil N, and light availability were examined in year three. Due to a significant main effect of the nutrient treatments for all variables, Pearson's correlation coefficients were determined from the mean response of each variable to each nutrient treatment from the independent whole-plot treatments,  $n = 32$  (SAS 1999).

## RESULTS

### Soil C and N pools

The soil nutrient treatments affected several belowground properties and processes relevant to plant productivity (Table 2), whereas the soil depth treatment had no significant effect on any of the soil responses measured. An interaction between time and the nutrient treatments occurred for total carbon (TC) resulting from a consistent decrease in TC over time in the C-amended (reduced-N) treatment that did not occur in ambient or enriched-N treatments ( $F = 3.98$ ,  $df = 378$ ,  $P = 0.008$ ; see Fig. 1 for no. observations in this and subsequently reported experiments). Although bulk density in C-amended (reduced-N) soil was 13% lower ( $1.20 \pm 0.02$  g/cm<sup>3</sup>) than the nonamended treatments ( $1.37 \pm 0.01$ ), TC on an areal basis (0–10 cm depth) in the amended soil was significantly higher than in the ambient-N and enriched-N treatments in the first year of study, and was comparable to that measured in nearby undisturbed prairie (Rice and Garcia 1994). Despite the decline in TC in the amended soil over time, TC remained significantly higher than in the ambient-N and enriched-N soil through year three (Table 2).

The "pulse" amendment of C resulted in a significant main effect of the soil nutrient treatments on microbial biomass C (MBC) over all three years of the study, despite a strong main effect of time across all levels of the soil nutrient and depth treatments. The level of MBC exhibited a more than fourfold increase

TABLE 2. Mean ( $\pm 1$  SE) total carbon (TC), microbial biomass carbon (MBC), nitrogen mineralization potential (NMP), extractable  $\text{NO}_3\text{-N}$ , and resin-collected  $\text{NO}_3\text{-N}$  each year in the surface 10 cm of soil in the nutrient treatments over both levels of soil depth.

Year	Reduced-N	Ambient-N	Enriched-N	Time ME
TC ( $\text{g}/\text{m}^2$ ) <sup>†</sup>				
1	2961 (158) <sup>a,x</sup>	2412 (21) <sup>a,y</sup>	2448 (40) <sup>a,y</sup>	
2	2738 (78) <sup>ab,y</sup>	2533 (34) <sup>b,x</sup>	2622 (48) <sup>a,x,y</sup>	
3	2615 (80) <sup>b,x</sup>	495 (25) <sup>b,x</sup>	2486 (23) <sup>a,x</sup>	
MBC ( $\text{g}/\text{m}^2$ )				
1	66 (7)	35 (4)	33 (4)	39 (4) <sup>a</sup>
2	265 (34)	162 (16)	204 (20)	184 (16) <sup>b</sup>
3	258 (27)	169 (13)	208 (25)	192 (15) <sup>b</sup>
Trt ME	187 (15) <sup>x</sup>	122 (8) <sup>y</sup>	146 (11) <sup>y</sup>	
NMP ( $\text{mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ )				
1	-11.7 (5.1) <sup>ax</sup>	50.1 (4.5) <sup>ay</sup>	47.9 (6.4) <sup>ay</sup>	
2	-2.9 (0.6) <sup>ax</sup>	16.4 (3.7) <sup>by</sup>	41.9 (14.2) <sup>az</sup>	
3	1.7 (1.4) <sup>ax</sup>	20.3 (6.1) <sup>by</sup>	35.0 (5.6) <sup>az</sup>	
Extractable $\text{NO}_3\text{-N}$ ( $\text{mg}/\text{m}^2$ )				
1	42 (17) <sup>x</sup>	309 (35) <sup>y</sup>	331 (61) <sup>y</sup>	
2	25 (4) <sup>x</sup>	78 (7) <sup>y</sup>	149 (18) <sup>z</sup>	
3	29 (6) <sup>x</sup>	95 (9) <sup>y</sup>	217 (33) <sup>z</sup>	
Resin-collected $\text{NO}_3\text{-N}$ ( $\mu\text{g}/\text{bag}$ )				
1	170 (33) <sup>x</sup>	660 (105) <sup>y</sup>	2945 (612) <sup>z</sup>	
2	190 (24) <sup>x</sup>	326 (39) <sup>x</sup>	2170 (553) <sup>y</sup>	
3	252 (79) <sup>x</sup>	222 (20) <sup>x</sup>	712 (199) <sup>y</sup>	

Notes: A significant interaction occurred between time and the nutrient treatments for TC and NMPs; differences among years within a treatment indicated by letters (a-c) within a column and differences among treatments within a year indicated by letters (x-z) within a row. Significant main effects of the nutrient treatments (Trt ME) and time (Time ME) occurred for MBC, indicated by different letters in the last row and column, respectively. Extractable and resin-collected  $\text{NO}_3\text{-N}$  were analyzed separately by year; means accompanied by the same letter within a row (year) were not significantly different ( $\alpha = 0.05$ ).

<sup>†</sup> Comparison between reduced-N and enriched-N treatments for TC was significant at  $P = 0.061$ .

from year one to years two and three ( $F = 71.46$ ,  $df = 172$ ,  $P < 0.001$ ). The carbon amendment maintained significantly higher MBC in the reduced-N treatment over all three years ( $F = 17.29$ ,  $df = 6$ ,  $P = 0.003$ ). In year three, MBC was 52% and 24% greater in this treatment relative to ambient-N and enriched-N soil, respectively (Table 2).

Nitrogen mineralization potentials (NMPs) showed a significant interaction between time and the nutrient treatments (Table 2). In all years, NMPs were lowest in the reduced-N treatment, with net immobilization of N occurring in the first two years. Ambient-N and enriched-N soils exhibited net N-mineralization in all years. The interaction resulted from the increasing immobilization potential in the soil in the absence of any nutrient treatments, as indicated by a >50% reduction in NMPs in the ambient-N treatment from year one to year two, while the C addition and N enrichment treatments imposed significantly lower and higher NMPs, respectively, relative to the ambient-N soil in all three years ( $F = 4.37$ ,  $df = 177$ ,  $P = 0.002$ ).

The effects of the nutrient treatments on NMPs created a gradient of inorganic N availability at both soil depths. In all years, extractable  $\text{NO}_3\text{-N}$  was lowest in the C-amended soil (Table 2). In year one, extractable  $\text{NO}_3\text{-N}$  was significantly lower in the reduced-N treat-

ment relative to the ambient-N and enriched-N treatments (192,  $F = 33.90$ ,  $df = 34$ ,  $P < 0.001$ ), but extractable  $\text{NO}_3\text{-N}$  in the ambient-N and enriched-N soil was similar due to either high residual N, little uptake of N, or a combination of these factors in the initial year of plant establishment. Extractable  $\text{NO}_3\text{-N}$  was significantly higher in the enriched-N treatment than in the reduced-N treatment in years two ( $F = 25.18$ ,  $df = 27$ ,  $P < 0.001$ ) and three ( $F = 23.47$ ,  $df = 25$ ,  $P < 0.001$ ).

Resin bags were collected in October each year to provide a relative index of in situ N availability across a growing season (Table 2). In year one, resin-collected  $\text{NO}_3\text{-N}$  differed among all nutrient treatments, increasing from reduced-N to enriched-N treatments ( $F = 45.69$ ,  $df = 31$ ,  $P < 0.001$ ). Resin-collected  $\text{NO}_3\text{-N}$  was significantly higher in the enriched-N treatment than in unfertilized soil in years two ( $F = 19.57$ ,  $df = 13$ ,  $P < 0.001$ ) and three ( $F = 7.96$ ,  $df = 7$ ,  $P = 0.016$ ).

#### Plant production responses

In year three, sown prairie species accounted for >99% of total aboveground net primary productivity (ANPP), and total ANPP differed among the soil nutrient treatments, but was unaffected by soil depth (Fig.

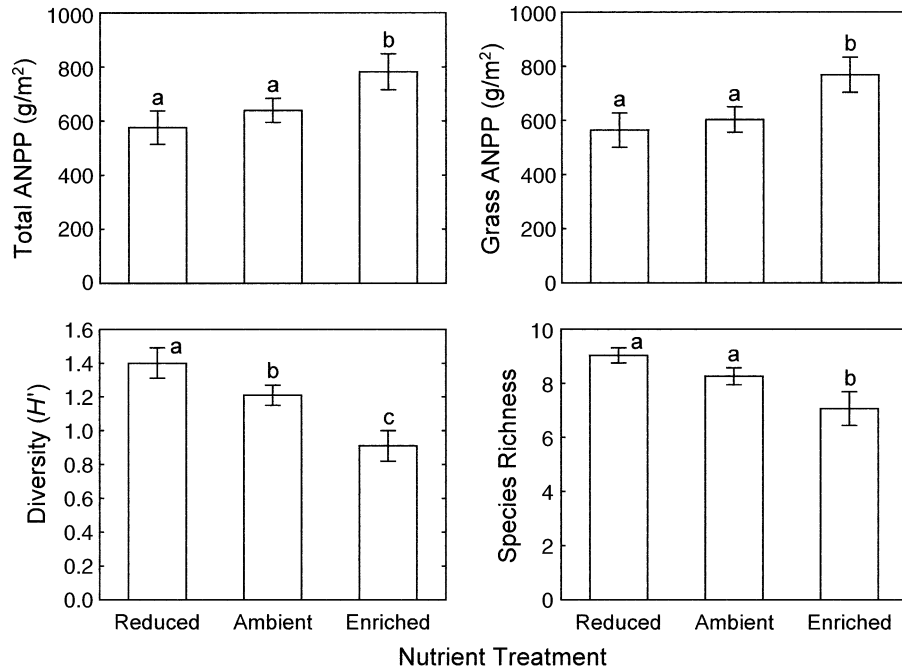


FIG. 2. Mean ( $\pm 1$  SE) total aboveground net primary productivity (ANPP), ANPP of the dominant  $C_4$  grasses, plant diversity (Shannon's index,  $H'$ ), and plant species richness (no. species/0.25 m<sup>2</sup>) in response to the nutrient treatments, averaged over both levels of soil depth in year three. Means accompanied by the same letter were not significantly different ( $\alpha = 0.05$ ).

2). The enriched-N treatment exhibited 22% and 36% higher ANPP than the ambient-N and reduced-N treatments, respectively ( $F = 4.6$ ,  $df = 171$ ,  $P = 0.011$ ). The dominant grasses accounted for >90% of total ANPP in all treatments, and productivity of this group drove the response of total ANPP to the nutrient treatments ( $F = 4.7$ ,  $df = 171$ ,  $P = 0.011$ ; Fig. 2). Forbs accounted for <10% of total ANPP, and there were no differences in productivity of forbs among the soil treatments, due to the high variability in the occurrence of forbs among treatments (data not shown).

The accumulation of previous year's biomass in 2000 reflected productivity patterns from 1999, and main effects of soil nutrient levels and soil depth were present. Litter accumulations were significantly lower in the reduced-N treatment ( $586 \pm 57$  g/m<sup>2</sup>) than in the ambient-N ( $697 \pm 44$  g/m<sup>2</sup>) or enriched-N ( $876 \pm 56$  g/m<sup>2</sup>) treatments over both levels of soil depth ( $F = 6.31$ ,  $df = 48$ ,  $P = 0.004$ ). Despite the lack of soil depth effects on ANPP in year three, litter accumulations indicated an effect of soil depth in the previous year. Litter mass in the shallow soil ( $591 \pm 38$  g/m<sup>2</sup>) was significantly lower than in deep soil ( $725 \pm 32$  g/m<sup>2</sup>) across all nutrient treatments ( $F = 4.58$ ,  $df = 169$ ,  $P = 0.034$ ).

Total ANPP was not directly correlated with N availability ( $r = 0.24$ ,  $P = 0.188$ ), largely as a result of similar productivity in the reduced-N and ambient-N soil (Fig. 2). However, there was enough variation in total ANPP and litter accumulations to result in sig-

nificant positive correlations with percentage of intercepted photosynthetic photon flux density (PPFD; Fig. 3).

#### Plant community responses

More than 70 plant species were recorded during the first three years of grassland establishment (Baer 2001). Patterns in plant species diversity and richness in year three were largely attributed to responses of sown species, which comprised >70% of total cover across all nutrient treatments (Baer 2001). Diversity and richness were affected by the nutrient treatments only (Fig. 2). Diversity was highest in the reduced-N treatment and lowest in the enriched-N treatment ( $F = 8.6$ ,  $df = 21$ ,  $P = 0.002$ ). Total plant diversity was inversely related to both N availability and productivity in year three (Fig. 4). The strong negative relationship between diversity and total biomass suggested that differences in diversity among nutrient treatments resulted from treatment-induced differences in ANPP rather than the direct effects of soil nutrient availability per se. This contention was supported by the strong negative correlation between light availability (PPFD) at the soil surface and plant diversity (Fig. 4).

In most cases, patterns in plant species richness (number of species per 0.25 m<sup>2</sup>) were similar to those of diversity. However, unlike diversity, richness was similar in the reduced- and ambient-N treatments (Fig. 2) and, therefore, was unrelated to N availability.

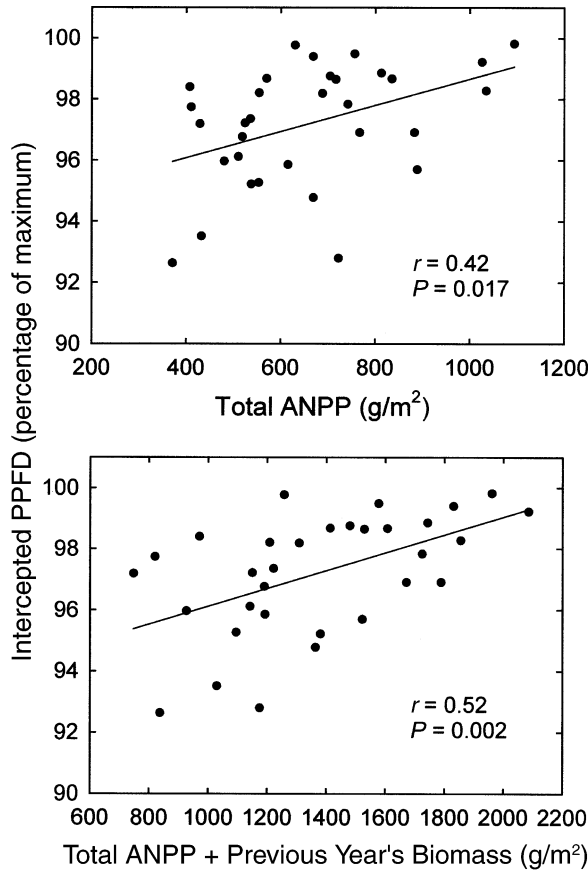


FIG. 3. Relationships between light interception (percentage of photosynthetic photon flux density [PPFD] intercepted by the canopy and litter, measured at the soil surface) and (top) ANPP and (bottom) previous year's dead biomass. Analyses were based on mean values by nutrient treatments in each whole plot ( $n = 32$ ). Significant relationships were determined from Pearson's correlation coefficients derived using SAS (SAS 1999).

DISCUSSION

*Soil treatment effects and N availability*

Patterns in N availability in the restored prairie were influenced by the nutrient manipulations, but also were clearly influenced by the establishment of perennial vegetation. The "pulse" amendment of C promoted a sufficient increase in microbial biomass and immobilization potential of the soil to reduce nitrogen mineralization potentials (NMPs) and extractable NO<sub>3</sub>-N for the first three years of grassland establishment (Table 2). Temporal changes in NMPs and inorganic N levels in the ambient-N soil demonstrated the effect of vegetation establishment on N supply rates and available soil N pools in the absence of any manipulations. The decline in NMPs and extractable NO<sub>3</sub>-N over time in the ambient-N soil was most likely influenced by increasing plant uptake and microbial immobilization associated with C inputs from developing root systems (Burke et al. 1995, Hu et al. 1995, Staben et al. 1997,

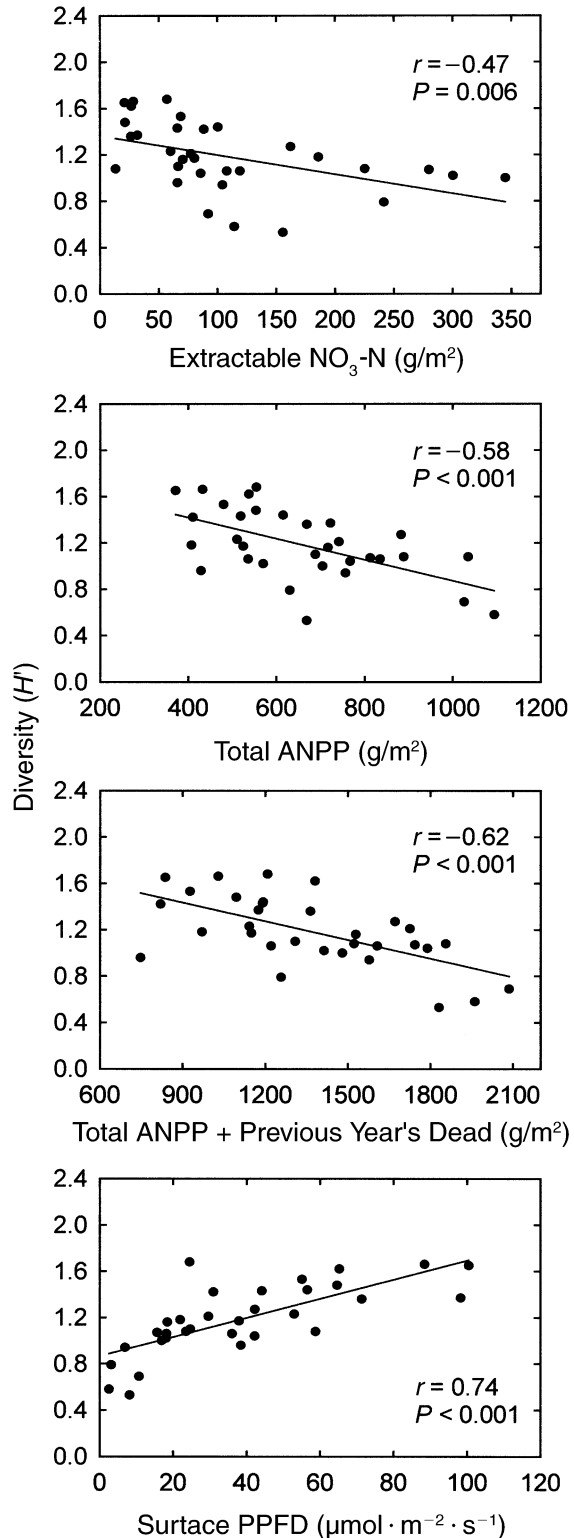


FIG. 4. Relationships between diversity and N, biomass, and light availability. Correlations were performed on the mean of extractable NO<sub>3</sub>-N, total ANPP, and standardized photosynthetic photon flux density (percentage of maximum PPFD  $\times$  mean maximum of 1365  $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ) by nutrient treatment in each whole plot ( $n = 32$ ). Significant relationships were determined from Pearson's correlation coefficients derived using SAS (SAS 1999).



Baer et al. 2000, Baer et al. 2002). Annual fertilization in the enriched-N treatment effectively offset the increasing immobilization potential of the soil (Table 2), maintaining higher N availability throughout the study.

Inorganic N collected on ion exchange resins provided a relative index of in situ N availability over each growing season (Table 2). Due to potential differences in water availability among the soil treatments, we considered resin-collected nitrate to be a better indicator of N availability than ammonium or nitrate plus ammonium (Binkley 1984). Reduced  $\text{NO}_3^-$ -N accumulation on ion exchange resins in C-amended soil in year one was likely the result of increased microbial biomass and competition between soil microbes and plants for N (Binkley 1984). Temporal changes in resin-collected  $\text{NO}_3^-$ -N demonstrated that the soil nutrient treatments had the strongest effect on N availability in year one, and that the relative difference in N availability between reduced-N and ambient-N treatments diminished over time (Table 2). As with extractable N, increasing plant uptake and microbial immobilization in the ambient-N treatment were probably responsible for the decreasing disparity in N availability between reduced and ambient-N soil. Potential differences in soil water content associated with less transpiring surface area or increased water holding capacity in the C-amended soil also may have contributed to increasing similarity in resin-collected  $\text{NO}_3^-$ -N between the ambient-N and reduced-N soil treatments over time.

#### *Patterns and controls of aboveground productivity during grassland establishment*

By the third year of establishment, sown prairie species comprised >99% of total aboveground net primary productivity (ANPP), and the productivity across all treatments ( $660 \pm 38 \text{ g/m}^2$ ) in the newly seeded prairie exceeded the 30-yr average ANPP ( $527.5 \pm 26.9 \text{ g/m}^2$ ) in the most productive areas of nearby native prairie, annually burned lowlands at Konza Prairie Biological Station (KPBS; Knapp et al. 1998). Similar to annually burned lowlands at KPBS (Towne and Owensby 1984), total productivity in the three-year-old grassland was dominated by  $C_4$  grasses (Fig. 2).

Productivity was most affected by treatment-induced differences in soil N availability, exhibiting a strong positive response to the addition of a limiting nutrient (Fig. 2). The similarity in productivity among the ambient-N and reduced-N treatments likely resulted from the low N requirements and high N use efficiency of the  $C_4$  grasses (Tilman and Wedin 1991, Ojima et al. 1994). In native prairie, shallow-soil uplands are generally less productive than deep-soil lowlands (Knapp et al. 1993, 1998). Lower productivity occurred in shallow soil relative to deep soil in year two, as evidenced by greater litter accumulations in the deep soil treatment, but this pattern was not maintained into year three of this study. The similarity in productivity across

both soil depths when the site was not burned prior to the third growing season was consistent with landscape patterns of ANPP in unburned native tallgrass prairie, where differences in ANPP between uplands and lowlands in unburned watersheds are markedly less than the difference in annually burned watersheds (Knapp et al. 1993). The absence of burning prior to year three resulted in large quantities of detritus among all treatments, which can substantially reduce light availability and ameliorate differences in soil moisture and ANPP between upland and lowland prairie (Knapp 1984, Knapp and Seastedt 1986, Knapp et al. 1993).

In contrast to our expectations based on patterns in native prairie, forb productivity as measured in the third growing season did not respond to the soil depth treatment. Inadequate competitive release from the native grasses and/or reduced growth due to the presence of large quantities of the previous year's dead biomass may have contributed to the overall low productivity and highly variable biomass of forbs among the treatments. Higher biomass of forbs in shallow upland prairie relative to deep soil lowlands at KPBS (Briggs and Knapp 1995) occurred in the presence of overall lower total productivity and less litter accumulation than were present in the three-year established grassland.

#### *Linking resource availability to productivity and diversity*

In native prairie at KPBS, plant species diversity is highest on shallow, upland soils, and is lowest in more productive lowland sites, or those enriched with supplemental N (Gibson and Hulbert 1987, Gibson 1988, Collins 1992, Collins et al. 1998). However, as with productivity in year three, diversity in our experimental plots did not differ between soil depth treatments. The shallow-soil treatment likely did not constrain grass productivity sufficiently to allow competitive release of the forbs, as ANPP in the shallow soil subplots was still higher than the long-term average of ANPP in the most productive areas at KPBS.

Plant species diversity and richness in the restored prairie were most strongly influenced by the nutrient treatments (Fig. 2). The decline in diversity in fertilized soil over time was consistent with the effects of nutrient enrichment on plant species diversity in old-field systems (Tilman 1987, Carson and Barrett 1988, Foster and Gross 1998) and mature grasslands (Wilson and Shay 1990, Collins and Wein 1998, Collins et al. 1998). This response has been attributed to increased shading and competition for light associated with increased biomass production (Tilman and Pacala 1993, Huston and De Angelis 1994, Abrams 1995, Collins et al. 1998) and accumulation of detritus (Tilman 1993, Foster and Gross 1998, Gough et al. 2000) under nutrient enrichment. These mechanisms also appear to be important in our newly established plant communities, where current and previous years' productivity were elevated in response to supplemental N (Fig. 2), positive relation-

ships occurred between biomass and intercepted light (Fig. 3), and light availability was strongly correlated with diversity (Fig. 4).

Across numerous community types and trophic levels, the relationship between diversity (and richness) and productivity in native systems is generally hump-shaped, whereas experimental manipulations of productivity with nutrient additions commonly result in an inverse and linear relationship between diversity and productivity in herbaceous communities (review by Mittelbach et al. [2001]). Although Mittelbach et al. (2001) suggested the short-term nature and small spatial scale of these studies is problematic to their interpretation and relevance to natural systems, this pattern may be important in the context of restoration. The primary goal of restoration is to expedite the successional process by promoting establishment of species characteristic of native (mature) communities that reflect long-term evolutionary interactions. Soil nutrient availability has been shown to influence the successional trajectory of newly established communities if fertility favors early or late seral species (Redente et al. 1992, Collins and Wein 1998). Inhibited establishment of nonnative species or early successional species has been demonstrated in young restored grasslands with experimentally reduced levels of N availability (Wilson and Gerry 1995, Morghan and Seastedt 1999, Blumenthal 2001). In our study, diversity and productivity of nonnative and early successional annual grasses and forbs were negligible by the third year of establishment (<1% of total ANPP), despite a strong effect of soil nutrient availability on this group in the initial year of study (Baer 2001), indicating that nutrient availability can have a substantial impact on initial floristic composition. Although the inverse relationship between diversity and productivity in our study could be related to the immature state of this community (Mittelbach et al. 2001) and a strong response of a few species (i.e.,  $C_4$  grasses) to an increase in a limiting nutrient (Tilman 1987), this relationship still provides insight into the mechanisms underlying long-term restoration success. This is particularly the case if early floristic composition, influenced by site fertility, is a determinant of longer-term patterns of diversity.

#### CONCLUSIONS

This experiment has demonstrated that initial soil nutrient conditions can modulate floristic diversity in newly established prairie through the influence of N on aboveground productivity, as has been shown in successional old-field systems and undisturbed native prairie. The response of the dominant  $C_4$  grasses to nutrient availability in these young plant communities was an important determinant of light availability and, subsequently, diversity. Diversity was maximized in soils that were manipulated to more closely resemble native prairie soil with respect to total carbon levels and N

availability. Nitrogen availability early in the establishment phase had greater consequence for diversity than did soil depth. The discrepancy between the effects of soil depth on diversity in the young and mature prairie was attributed to inadequate competitive release of forbs in shallow soils in the presence of high aboveground net primary productivity (ANPP).

Studies such as this demonstrate that experimental restorations can be used to test ecological theory (Bradshaw 1987, Palmer et al. 1997). Overall, the patterns in productivity and diversity that we observed during the early stages of restoration largely conformed to patterns and mechanisms that control community structure in successional and mature plant communities. Moreover, our results are relevant to questions regarding the rate at which community structure develops relative to the rate at which ecosystem processes recover during restoration (e.g., Zedler and Callaway 1999). We documented a clear linkage between community structure (diversity) and ecosystem processes (productivity) during the earliest stages of ecological restoration. Thus, ecological theory, along with a basic understanding of community structure and function, can be used to guide community and ecosystem restoration.

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