MANIPULATION OF SOIL RESOURCE HETEROGENEITY IN A TALLGRASS PRAIRIE RESTORATION

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Abstract: Plant species diversity in native prairie ecosystems is influenced by heterogeneity of soil resources, which results from interactions among plant communities, soil properties, topography, and disturbance. Key factors which promote plant diversity in native prairie include soil moisture, rooting depth, and nutrient availability. Most prairie restorations in the Great Plains occur on former agricultural land and the soil template for these restorations has been physically homogenized through tillage practices. The reduction in soil resource heterogeneity in restored prairies may be causally related to low plant species diversity commonly encountered in these sites. To examine the role of soil heterogeneity in restoring prairie ecosystems, replicated blocks (n=4) of 4 plots consisting of different levels of soil heterogeneity were established in an agricultural field. The 4 plot types included: control (least heterogeneous with respect to soil resources), altered plant rooting depth, altered nutrient availability, and combined variation in plant rooting depth and nutrient availability (maximum heterogeneity). Plant rooting depth was varied by burying limestone barriers at 25 cm to create alternating strips of deep and shallow soil. Variation in soil nutrient (inorganic N) availability was established via increased N (+fertilizer), decreased N (+ recalcitrant C), and no change in N. All plots were seeded with the dominant native grasses and >30 forb species. Incorporation of recalcitrant C reduced total inorganic N availability 90% as a result of 98% reduction in available nitrate. Plots containing strips of low N availability exhibited significantly (p < 0.05) greater spatial variability than plots without this manipulation. Thus, the experimental design and methods implemented have increased heterogeneity of soil nutrients, and this will enable us to address the role of variation in soil resources on restoring tallgrass prairie.

Tallgrass prairie historically occupied approximately 60 million ha in the eastern third of the Great Plains region, and today only 4% of this ecosystem remains unplowed from agriculture (Samson and Knopf 1994). The majority of tallgrass prairie was lost to row crop systems because the most ideal conditions for soil aggregate formation, hence productive capability of soils, occur in grasslands (Allison 1968). Recently, increased interest in prairie restoration and incentives to reduce erosion have led to many grassland restorations on former cropland (Gebhart et al. 1994). The most commonly employed restoration approach is sowing the dominant, native, perennial grasses (Dunn et al. 1993), and establishment of these grasses is often successful (Sperry 1994, Wilson and Gerry 1995). However, less common grass and forb species, responsible for the high diversity of undisturbed tallgrass prairie, are inadequately repre-sented in many prairie restorations.

Diversity in tallgrass prairie ecosystems is maintained in part through plant-induced mechanisms, soil nutrient availability, topographic variation, and disturbance. For example, presence or absence of plants (Vinton and Burke 1995) and association of particular plant species (Wedin and Tilman 1990, Robles and Burke 1997) strongly influences variability in soil carbon (C) and nitrogen (N) pools. Lower species diversity observed in experimental grassland plots receiving long-term fertilizer additions (e.g. Collins and Steinauer 1998) provide indirect evidence that N-limitation and heterogeneity of soil N-pools promote diversity in prairie ecosystems (Inouye and Tilman 1995, Milchunas and Laurenroth 1995). Furthermore, topographic gradients include shallow upland soils with greater plant diversity than lowland sites, presumably due to reduced soil depth and water availability to plants (Gibson and Hulbert 1987, Schimel et al. 1991).

Our working hypothesis was that lower diversity in restored prairie on former cropland compared to native prairie likely results from differences in soil resource heterogeneity. Practices such as long-term conventional tillage, uniform application of fertilizer, monospecific crop production, and annual harvest of aboveground biomass impart greater homogeneity on soil resources in agroecosystems compared to native systems. Effects of long-term cultivation on soil properties and processes in former grassland soils are well documented. Conventionally tilled soils exhibit altered soil aggregate structure, higher decomposition rates, and lower soil organic matter as compared to grassland soils (Anderson and Coleman 1985, Elliot 1986, Burke et al. 1995). Thus, the soil template at the onset of restoration in former agricultural soil may differ greatly from unbroken prairie.

The role of soil heterogeneity in prairie restoration has never been addressed experimentally, despite the recognition that variation in soil nutrient pools, plant rooting depth, and soil-water availability may promote floral diversity in native tallgrass ecosystems (Collins et al. 1998). Here we present a detailed description of the experimental design and methodology being used in a new tallgrass prairie restoration experiment to address the role of soil resource heterogeneity in restoring species diversity. Additionally, the effectiveness of manipulations on spatial heterogeneity of inorganic N and establishment of native grasses are evaluated.

METHODS
Study Site

Sixteen experimental plots were established in an 3.2 ha agricultural field at Konza Prairie Research Natural Area (KPRNA) located 9 km south of Manhattan, Kansas (Riley County). Soils in this field were mapped as a Reading silt loam with 0-1% slope (mesic Typic Arguidoll), and has been cropped continuously for about 50 years (Dodds et al. 1996). Unplowed deep lowland soils at KPRNA similar to this site are formed by colluvial and alluvial deposits and are typically dominated by warm-season (C_4) grasses such as big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Andropogon scoparius*), interspersed with a variety of other plant species. Floristic diversity at KPRNA is relatively high, with over 250 species occuring in native prairie habitats (Freeman 1998). Elevation is about 340 m above sea level, and average precipitation is 853 mm/yr (30-year average). Following harvest of the field in June 1997, residual crop litter and stubble were burned. Corners of all 16 plots and 3 random points within each plot were delineated and relative change in elevation measured with a level transit station.

Experimental Design

Replicated blocks (n = 4) consisting of 4 6–m x 8–m plots with different levels of soil resource heterogeneity were established (Fig. 1). Treatments were randomly assigned to plots within each block with a 6-m buffer strip between plots. The 4 treatments within each block included control, manipulation of available soil N, manipulation of plant rooting depth, and combined manipulation of both plant rooting depth and soil nutrient availability. Each plot was subdivided into 12 2-m x 2-m subplots for sampling (n = 192).

Manipulation of Soil Resources

Variation in plant rooting depth (and soil-water availability) was accomplished by burying native limestone slabs. Four 6-m x 62-m strips containing all experimental plots were excavated to a depth of 25 cm with a road grader and track loader. In plots designated for variation in plant rooting depth, rough cut limestone slabs 3-6 cm thick, ranging from 0.4 m to 0.7 m in width and length, were pieced together in 2 alternating 2-m x 6-m strips (Fig. 1). Crevices between limestone slabs were filled with limestone gravel. Following placement of limestone strips, soil was replaced in all plots with the same equipment used in excavation. Once the excavated soil settled, the area was leveled with a dual blade attachment towed from a tractor (commonly used to redistribute gravel roads). In Fall 1997, the soil was lightly cultivated (2-3 cm deep) to reduce establishment of weedy species.

Soil N heterogeneity was manipulated by altering N availability in 3 randomized 2-m x 8-m strips within experimental plots. Strips with reduced nitrogen availability were established in February 1998 by adding a recalcitrant form of C (sawdust) to immobilize nitrogen. Using a total soil C content (0-15 cm) and bulk density of 1.5% and 1.2 g/cm³, respectively, estimated total soil C of the field site was 2.7 kg/m². Sawdust was added to increase the C content to a level representative of prairie soils ($\approx$ 3% C or 2 times existing C content). Carpentry sawdust (49% C) was tilled into the top 15 cm of soil at a rate of 2.7 kg of C/m². All plots were tilled at this time to maintain similar conditions among plots for planting. Strips with increased nitrogen availability were fertilized by applying ammonium-nitrate (35%
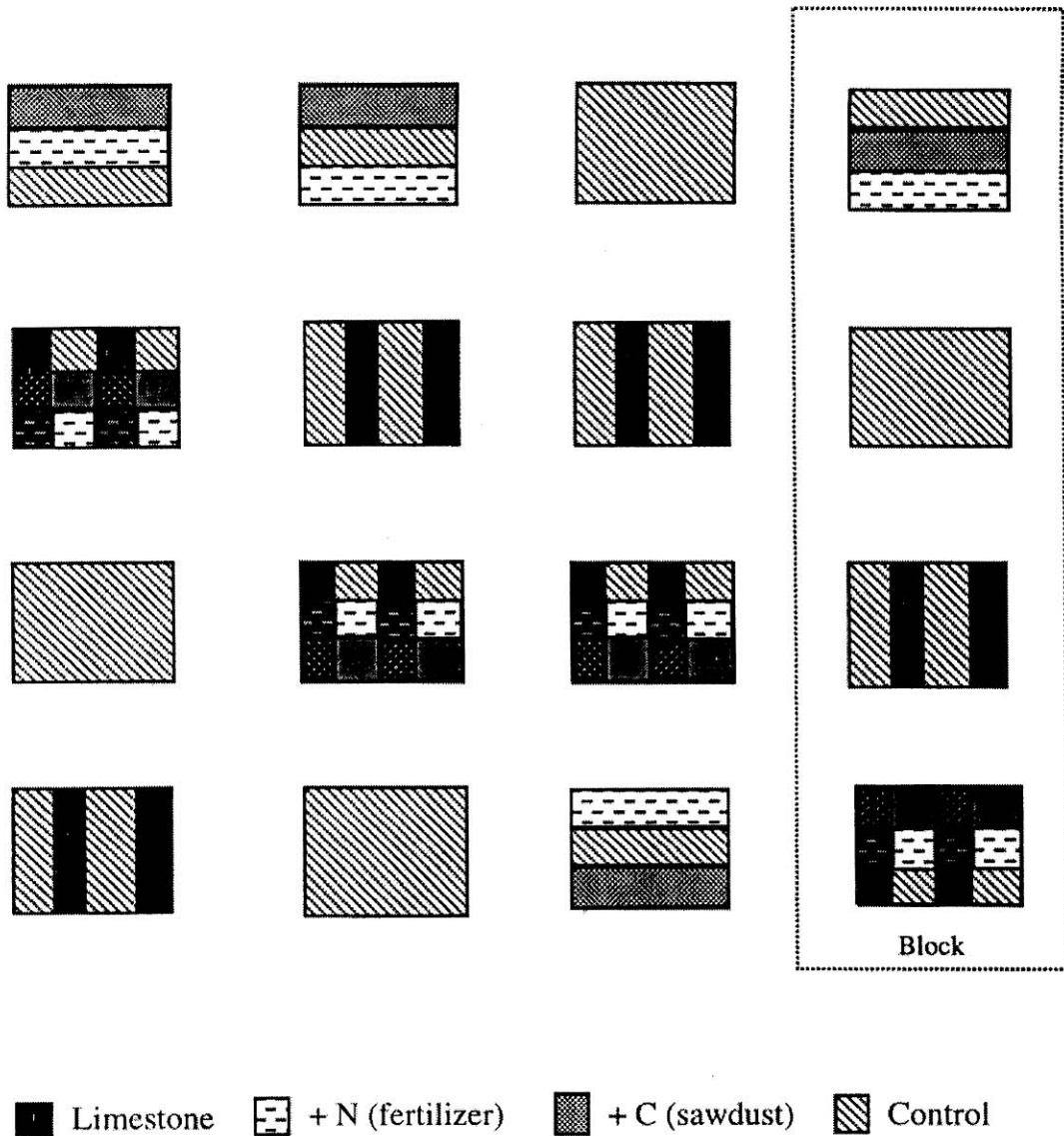
Fig. 1. Tallgrass prairie restoration experimental design. Four replicated blocks containing 4 6-m x 8-m treatment plots represented different levels of soil heterogeneity. Control plots received no manipulations and were least heterogeneous with respect to soil resources. Greater soil resource heterogeneity was achieved in plots receiving either alternating buried 2-m x 6-m strips of limestone or 3 randomized 2-m x 8-m strips of N availability. Maximum soil resource heterogeneity was represented in plots containing both limestone and N treatments.

N) at a rate of 5 g of N/m^2 (14.3 g of fertilizer/m^2) in July 1998. Fertilizer application was delayed until July, since initial N levels were relatively high at the onset of the experiment.

Maximum soil resource heterogeneity plots contained both the manipulations of plant rooting depth (alternating 2-m x 6-m strips of buried limestone) and altered nutrient availability (randomized 2-m x 8-m strips of variation in N). All plots (including controls) were initially excavated to a depth of 25 cm and were tilled or cultivated simultaneously to control for variation that may result from this disturbance.

Restoration Methods

All plots were sown to native prairie species in April 1998. The dominant grasses (big bluestem, Indiangrass, switchgrass and little bluestem) were

obtained from a local distributor in Kansas (Star Seed Inc., Beloit, KS) and less common grass and forb seed was either hand-collected locally or purchased from commercial sources (Appendix). All seeds were kept in cold dry storage until planting. Species and seeding rates selected were chosen to achieve a log–normal distribution of species representative of prairie habitats on Konza Prairie. Forty-two prairie species were assigned to 1 of 4 frequency categories and seeded at the following rates: dominant grasses (160 seeds/m^2), common (16 seeds/m^2), frequent (10 seeds/m^2), or uncommon species (5 seeds/m^2). With the exception of legumes, seeds were not treated to promote germination. Legume seeds were inoculated with species specific *Rhizobia* mixtures obtained from Prairie Moon Nursery (Winona, MN) just prior to planting. Average weight of 3 replicates of 100 seeds of each species was used to determine total weight of each species required per plot based on the frequency category assigned to each species.

Prior to planting, all plots were lightly raked. Less common grass and forb seeds were mixed with damp builders sand and hand broadcast evenly over plots. The dominant grass species were seeded with a grass drill (Truax Co., MN) designed to deliver fluffy grass seed at a uniform rate to a depth of 1.2-2.5 cm. Dominant grasses were seeded at the same rate (approximately 17 lbs/acre) within and between all plots to reduce potential edge effects. Following planting, prairie hay harvested the previous summer from KPRNA was spread on all plots to retain soil moisture, promote soil seed contact, and minimize loss of seeds by wind. Prairie hay was harvested before dominant grasses set seed, so the contribution of seeds to study plots from this source was considered minimal, and any seed within the prairie hay should further promote a log-normal distribution of species.

Plant Rooting Depth

In January 1998, plant rooting depth in limestone strips was assessed by measuring depth of soil to buried limestone with a graduated metal probe. Soil depth to limestone readings were taken in each subplot (3/strip or 6/plot) representing this treatment (n = 48).

Establishment of Native Grasses

In July 1998, establishment of native grasses planted was examined from 1-m transects delineated by a pin frame through the center of each subplot (n = 192). At 20-cm intervals, the dominant native grass closest to that pin was identified and measured

to assess the relative contribution of each species to dominant grasses established and examine effects of the different treatments on plant growth (height).

Inorganic N Availability

In June 1998, 2 soil samples (0-10 cm depth) were taken from each subplot with a 2-cm diameter core and composited. Sampling occured prior to N addition and approximately 4 months following incorporation of sawdust. Samples were passed through a 4-mm sieve to homogenize the soil and remove large pieces of plant debris. Inorganic nitrogen (NH_4-N and NO_3-N) content was determined by extracting 10-12 g of field moist soil with 50 mL of 2 M KCl on an orbital shaker for one hour, then filtering the suspension through a 0.4–mm polycarbonate membrane. Inorganic N concentrations were analyzed colorimetrically with an Alpkem Flow Solution autoanalyzer using the phenol blue method for NH_4-N and nitrate reduction to nitrite followed by diazotization for NO_3-N determinations. A subsample of approximately 50 g field moist soil was weighed, dried for 2 d at 60°C, and reweighed to determine gravimetric soil-water content.

Analyses

Means and standard errors were calculated for height of dominant grass species and inorganic N concentrations (NO_3-N, NH_4-N, and total inorganic N) from subplots representing each treatment: control (n = 120); addition of recalcitrant C only, +C (n = 24); reduced rooting depth, + Limestone (n = 40); and combined treatments, Limestone + C (n = 8). Spatial variability of inorganic N availability following incorporation of recalcitrant C (prior to fertilization) was analyzed using a random-ized complete block design. Differences in variab-ility among treatments were examined with a one-way analysis of variance (ANOVA, $\alpha = 0.05$) on coefficients of variation (CV) for each of the 4 treatments determined from the 12 subplots within each treatment plot (SAS Institute 1989).

RESULTS AND DISCUSSION

Emergence of grass seedlings occurred approximately 6 weeks following planting and the height of dominant grasses by mid-summer ranged from 8 to 106 cm. Percent contribution of big bluestem, Indiangrass, switchgrass and little bluestem to the total grasses examined (n = 960) were 34%, 28%, 21%, and 15%, respectively. Big bluestem and Indiangrass were the most frequently encountered native grass species in most treatments. All domin-

Table 1.   Mid-summer (July 1998) average height (standard error) of dominant native grass species seeded in April 1998.   Averages for each treatment combination were determined from 5 grasses in each of 192 subplots (number of grasses examined, n = 960).   Treatments included: control (n = 600, 120 subplots); Limestone (n = 200, 40 subplots), +C (n = 120, 24 subplots), and Limestone + C (n = 40, 8 subplots).

		Control	Limestone	+C	Limestone + C
Andropogon gerardii	avg	41.2 (1.1)	38.1 (1.6)	26.1 (1.9)	22.9 (2.7)
	n	190	78	50	15
Andropogon scoparius	avg	26.1 (1.1)	27.0 (1.5)	18.1 (2.6)	15.3 (4.8)
	n	94	33	18	7
Panicum virgatum	avg	47.6 (1.2)	48.5 (2.2)	33.3 (4.1)	23.3 (3.2)
	n	136	45	17	7
Sorghastrum nutans	avg	36.2 (1.0)	37.3 (1.8)	27.5 (1.7)	20.2 (2.9)
	n	180	44	35	11

ant grass species we planted responded similarly to the treatments in place at the time of this investigation (Table 1). Average plant height was 23-37% lower in the sawdust treatment as compared to control subplots. Growth of the dominant grasses was further inhibited in combined sawdust and limestone treatments (e.g., average height was 44-51% lower than unmanipulated subplots). Responses of dominant native grasses to the treatments were likely related to differences in soil resources, particularly inorganic N availability.

The treatments appear to have promoted the desired heterogeneity in soil resources. In plots containing buried strips of limestone, plant rooting depth has been reduced to an average 24.7 ± 3.1 cm, ranging from 9 to 30 cm. Incorporation of recalcitrant C (sawdust) was effective in reducing inorganic N availability (Fig. 2). Average total inorganic N was > 90% lower in C addition and combined limestone and C treatments compared to control subplots. Substantial reductions in total inorganic N resulted primarily from reduced production or enhanced consumption of NO_3-N. The average NO_3-N concentrations in C addition subplots were only 2% of NO_3-N concentrations in control plots. Coefficients of variation of total inorganic N and NO_3-N from the treatment plots receiving additional C were significantly greater than plots which did not receive sawdust (Table 2). Thus, recalcitrant C addition in randomized strips successfully enhanced spatial heterogeneity of inorganic N, particularly NO_3-N, in plots receiving this treatment.

As expected, inorganic N concentrations at the onset of restoration were high relative to undisturbed prairie soils. Potential fates of NO_3-N in soil (whether derived from fertilizer or mineralized from soil organic matter) include plant uptake, leaching, or microbially-mediated transformations (Paul and Clark 1996). At the time of our initial sampling, plants in restoration plots were just beginning to establish, so plant uptake of NO_3-N was considered negligible. Thus, microbial processes were likely responsible for changes in inorganic N availability.

Several mechanisms are potentially responsible for the reduction in inorganic N in the C addition treatments. Cropland soils generally exhibit lower CO_2 evolution, lower N-immobilization, and greater net N-mineralization rates than grassland soils, suggesting that the microflora of tilled agricultural soils are C-limited whereas grassland soils are N-limited (Schimel 1986). Addition of recalcitrant C to cropland soil likely alleviated C limitation, stimulated microbial activity, and increased immobilization of inorganic N in the microbial biomass. Second, microbes generally prefer to assimilate NH_4-H (Jones and Richards 1977), but microbial assimilation of NO_3-N at soil microsites where NH_4-N is not available may partially account for immobilization of inorganic N through dissimilatory reduction of nitrate to ammonium (Davidson et al. 1990). Third, enhanced immobilization, or a reduction in net N mineralization may have resulted in lower rates of nitrification by reducing availability of ammonium. Finally, conversion of nitrate to dinitrogen gas (denitrification) demands high levels of
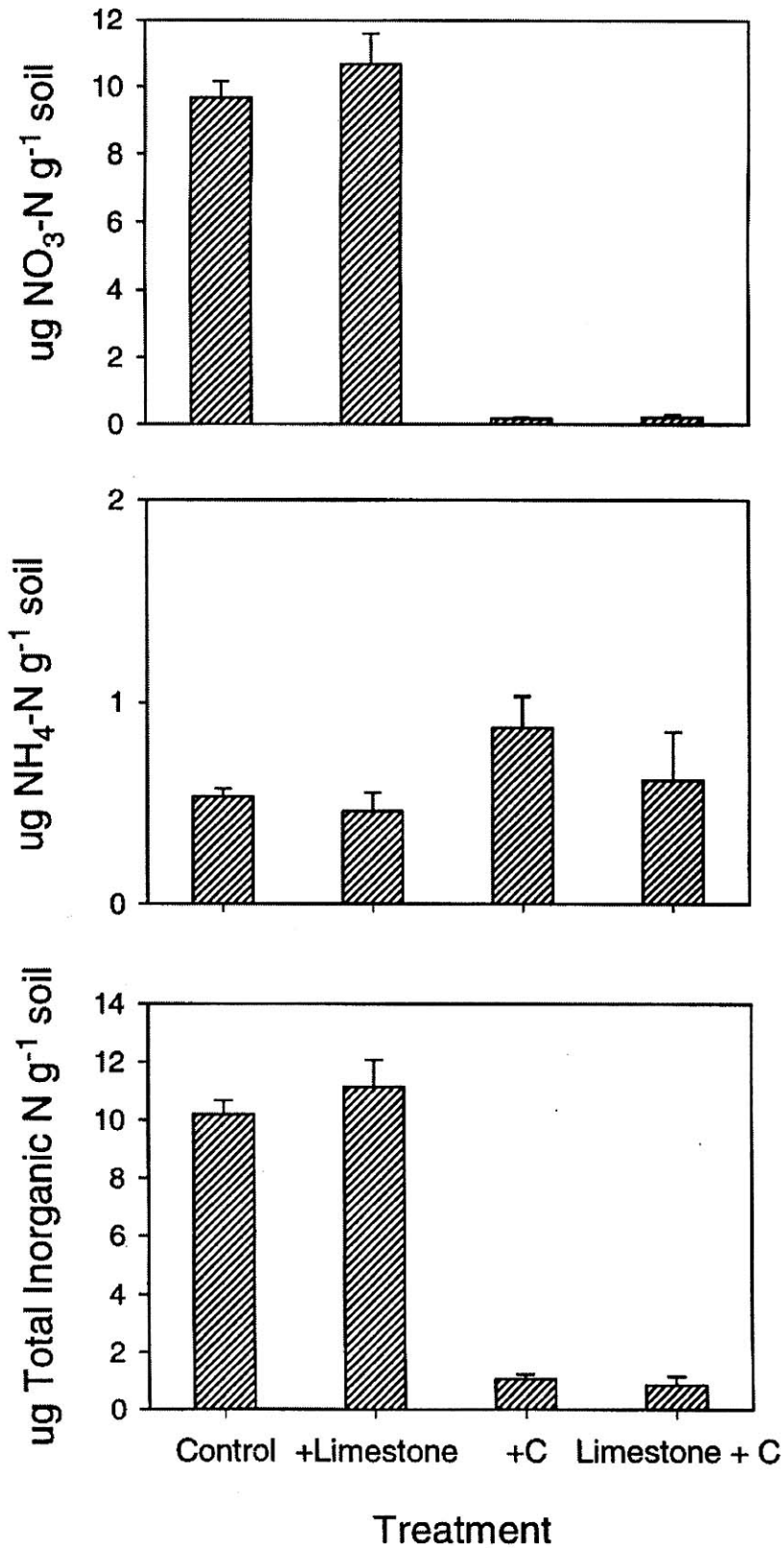
Fig. 2. Average (± standard error) NO_3-N, NH_4-N, and total inorganic N concentrations from subplots representing 4 treatments: control, carbon addition (+C), buried limestone (+Limestone), and combined carbon addition and buried limestone (Limestone + C).

Table 2.   Mean and coefficients of variation (CV) for inorganic N (µg/g soil) in restoration plots representing 4 treatments: control, manipulation of rooting depth (+Limestone), manipulation of inorganic N availability (+Carbon), and combined manipulation of rooting depth and N (Limestone + Carbon = maximum heterogeneity).   Significant differences in average CV (n = 4) between treatments indicated by different letter superscript (p < 0.05, 1-way ANOVA).

Treatment		NO_3-N	NH_4-N	Total Inorganic N
Control	Mean	6.98	0.45	7.43
	CV (%)	44.83[a]	52.42	39.73[a]
+ Limestone	Mean	12.32	0.47	12.79
	CV (%)	28.34[a]	105.47	27.85[a]
+ Carbon	Mean	6.09	0.68	6.76
	CV (%)	84.98[b]	66.14	75.28[b]
Limestone + Carbon	Mean	6.05	0.55	6.6
	CV (%)	101.62[b]	72.04	90.95[b]
	F	17.78	0.89	16.82
	Pr > F	0.0002	> 0.05	0.0002

nitrate, C, and anaerobic soil microsites (Tiedje 1988). Sawdust addition may have provided conditions for enhanced denitrification. However, this seems unlikely because a previous study of denitrification in this agricultural field revealed low denitrification potential (N + C ammended soil) in the surface interval of the soil profile (Sotomayer and Rice 1996).

Increased spatial heterogeneity of soil inorganic N as a result of C addition was evident, and we predict that variation in N resulting from this manipulation will influence restoration of species diversity. Nitrogen availability strongly influences diversity and productivity in tallgrass prairie ecosystems (Seastedt and Knapp 1993, Blair 1997). Experimental plots annually burned and fertilized (+ 10 g of N/m^2) from 1989 to 1994 at KPRNA exhibited a 10-fold increase in soil inorganic N, greater aboveground biomass, and lower species richness of C$_3$ grasses, forbs and woody plants compared to control plots (Collins et al. 1998). Lower diversity in these plots may be influenced by greater homogeneity in soil N availability and relief of N limitations characteristic of tallgrass prairie soils.

Thus far, the treatments imposed have successfully promoted heterogeneity in the soil environment with respect to N availability and plant rooting depth. Response of dominant native grasses to treatments, specifically reduced growth in plots receiving additional C, may further promote resource heterogeneity in plots by altering light availability, aboveground organic matter inputs, and belowground root distribution and production. Although effects of manipulated plant rooting depth (buried limestone) could not be evaluated yet, this manipulation should also promote restoration of diversity by providing variability in soil-water availability to plants. Variation in topographic position results in areas with shallow soils and limited water availability to plants. Shallow upland sites at KPRNA exhibit lower aboveground net primary production but greater species diversity compared to lowland areas (Briggs and Knapp 1995).

The experimental design and manipulations described here are not intended to be used as a restoration approach. Rather, the goal of this investigation was to evaluate the role of soil heterogeneity in restoring the function and diversity of tallgrass prairie. If successful, other means of manipulating soil resource heterogeneity may be designed and implemented for specific types of restoration projects. Alternatively, site-specific soil heterogeneity may become a criteria in choosing critical areas for restoration efforts.

ACKNOWLEDGMENTS

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Appendix. Restoration species, planting rate (seeds/m²), and seed sources. Seed source abbreviations: a = Star Seed Inc., Beloit, KS; b = Ion Exchange, Harper's Ferry, IA; c = Iowa Prairie Seed Co., Sheffield, IA; d = Hamilton, Elk Creek, MO; e = Prairie Moon Nursery, Winona, MN; f = hand-collected from Flint Hills region, Riley Co., KS.

Common Name	Species	Seeding Rate	Seed Source
big bluestem	Andropogon gerardii	160	a
Indian grass	Sorghastrum nutans	160	a
little bluestem	Andropogon scoparius	160	a
switchgrass	Panicum virgatum	160	a
blue sage	Salvia azurea	16	d
Canada goldenrod	Solidago canadensis	16	b
heath aster	Aster ericoides	16	b
prairie sage	Artemisia ludoviciana	16	c
sideoats grama	Bouteloua curtipendula	16	b
aromatic aster	Aster oblongifolius	10	b
false boneset	Kuhnia eupatorioides	10	f
inronweed	Vernonia fasciculata	10	f
junegrass	Koeleria pyramidata	10	b
leadplant	Amorpha canescens	10	f
low goldenrod	Solidago missouriensis	10	f
New Jersey Tea	Ceanothus herbaceous	10	f
prairie dropseed	Sporobolus heterolepis	10	b
purple prairie clover	Dalea purpurea	10	b
roundhead lespedeza	Lespedeza capitata	10	b
sensitive briar	Schrankia nuttallii	10	d
tall dropseed	Sporobolus asper	10	b
whorled milkweed	Asclepias verticillata	10	b
blue-eyed grass	Sisyrinchium campestre	5	b
dotted blazing star	Liatris punctata	5	f
false blue indigo	Baptisia australis	5	f
fringed-leaf ruellia	Ruellia humilis	5	b
Illinois bundleflower	Desmanthus illinoensis	5	f
large flowered beard tongue	Penstemon grandiflorus	5	b
Missouri evening primrose	Oenothera macrocarpa	5	f
peppergrass	Lepidium densiflorum	5	f
prairie coneflower	Ratibida columnifera	5	b
prairie ragwort	Senecio plattensis	5	e
prairie rose	Rosa arkansana	5	b
purple beard tongue	Penstemon cobaea	5	f
purple cone flower	Echinacea angustifolia	5	b
purple poppy mallow	Callirhoe involucrata	5	d
silky aster	Aster sericeus	5	b
spider milkweed	Asclepias viridis	5	f
Venus looking glass	Triodanis perfoliata	5	e
white prairieclover	Petalostemum candidum	5	b
wild alfalfa	Psoralea tenuiflora	5	f
wild blue indigo	Baptisia bracteata	5	b