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# EARLY SUCCESSION IN A TALLGRASS PRAIRIE RESTORATION AND THE EFFECTS OF NITROGEN, PHOSPHORUS, AND MICRONUTRIENT ENRICHMENTS

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**ABSTRACT.** The past decade has witnessed increased effort to restore prairie on former agricultural land in Indiana. We used the Upland Prairie Restoration to document community changes over a five year post-planting period and to examine the effects of acute fertilization with soil amendments. Growing seasons I and II were characterized by rapidly changing communities of annual weeds. Dominant species included *Hibiscus trionum*, *Cyperus esculentus*, *Setaria glauca* followed in Year II by *Setaria faberi* and *Ambrosia artemisiifolia*. Prairie grasses (*Andropogon gerardii* and *Sorghastrum nutans*) and forbs dominated by *Rudbeckia hirta* and *Ratibida pinnata* became evident during Years III–V. Prairie species density and cover, as well as their diversity, reached mature stage by Year V. The prairie restoration community showed no important responses to acute additions of phosphate, micronutrient mix, and a combination of phosphate and micronutrients. Nitrogen enrichment, however, promoted weed cover in early stages of community establishment. Weed dominance persisted throughout the five-year period of observation and strongly inhibited the establishment of native prairie species. Our results suggest that successful prairie restoration on former agricultural land should consider management practices that control nitrogen availability.

**Keywords:** Prairie restoration, succession, fertilizer, nitrogen, phosphorus, micronutrients

In pre-settlement Indiana, prairies made up about 15% of the area, primarily in the northwest and west-central portions of the state. Unfortunately, most of the original prairie has been lost to drainage, urbanization and agriculture (Samson & Knopf 1996). Only a few high quality remnant areas, such as Hoosier Prairie in Lake County, have been preserved; and fewer than a dozen small examples of diverse kinds of prairie are part of our state nature preserve system (Division of Nature Preserves 1999).

The growing public awareness of this loss of a fascinating part of our natural heritage is one reason that prairie and its restoration have become subjects of intense interest to many people in the American Midwest (Sayer 1999). Within the scientific community, the first attempts at habitat reconstruction involved the tallgrass prairie at the University of Wisconsin Arboretum between 1935–1941 (Bonta 1991). In Indiana over the past decade, prairie restoration has become a familiar tool for the Division of Nature Preserves (Rich Dunbar pers. comm.) and the Nature Conservancy (Nathan Simons pers. comm.). At least one commercial nursery (Spence Nursery, Muncie) has focused on developing a product line suitable for ecological restoration of prairie and wetland habitats.

In 1993, we initiated a tallgrass prairie restoration on a 25-acre site (10 ha) in Upland, Indiana. Previously, this site had a long agricultural history, first to raise row crops and more recently as pasture. The significant size of the Upland Prairie Restoration effort afforded opportunity to investigate questions relating to the successional changes associated with tallgrass prairie restoration on former agricultural land and the potential effects nutrient amendments might have on that early community development.

The earliest recorded tallgrass prairie restoration at University of Wisconsin attempted to establish a prairie community through the crude transplantation of blocks of sod (Bonta 1991). Since that pioneering effort, we have learned much about seed acquisition, site preparation, and planting (e.g., Schramm 1978, 1992). Likewise, the use of herbicides as a management tool has received significant attention (Packard & Mutel 1997) and a particularly rich literature regarding the use of fire has developed (e.g., Collins & Wallace 1990). Surprisingly, the role of soil amendments seems to have had scant attention as a factor for enhancing (or inhibiting) the establishment of a prairie restoration (Parkard & Mutel 1997). Some types of ecological restoration clearly benefit from fertilizer application. These include coal mine spoils (Singh et al. 1996), post limestone-quarry grasslands (Richardson & Evans 1986), grass swards and *Salix* scrub (Marrs et al. 1983), and montane forest (Tanner et al. 1990).

Soils in east-central Indiana frequently have concentrations of nitrogen, phosphorus, and micronutrients that may limit plant productivity. Studies of whether micronutrient amendments might enhance prairie or grassland communities appear lacking. A few relevant studies with phosphorus and especially nitrogen soil amendments are available. In some rangelands, low nitrogen levels can limit plant growth (Ownesby et al. 1970; Rains et al. 1975; Ownesby & Smith 1979; Hipp 1986; Brejda et al. 1995). Furthermore, individual species such as *Panicum virgatum* L. respond to nitrogen by increases in ramet size and flowering and seed production (Hartnett 1993). In other cases, nitrogen increases dry matter production (Stubbendieck & Nielsen 1989), especially in forbs (Seastedt et al. 1991). In some prairie communities, a high frequency of fire is one apparent cause of limited nitrogen. Burning depresses nitrogen availability through volatilization and immobilization of labile soil nitrogen (Seastedt et al. 1991; Benning & Seastedt 1995).

While some studies of prairie communities support a positive role for nitrogen amendments, others issue caution. Excess nitrogen can enhance the growth of annual weeds and exotics (Berg 1995; Milchumas & Lauenroth 1995; Paschke et al. 2000). This weedy growth could have particularly adverse effects during the critical stage of establishing seedlings of native prairie species. Because of increased weed content, the tempo of ecological succession in which native perennials, particularly grasses, displace annual weeds may be slowed (Wedin & Tilman 1990). In addition to enhancing weed content, nitrogen enrichment may lead to a reduction in species richness, as reported for native grasslands (Collins et al. 1998) as well as in *Andropogon gerardii* Vit. plantings (Foster & Gross 1998). Forb species, more than grass species, appear sensitive to adverse effects of nitrogen enrichment (Gibson et al. 1993).

A few studies have looked at the effects of phosphorus amendments in prairie communities. On mature Konza Prairie, Gibson et al. (1993) saw no effect on herbaceous cover following three years of phosphate enrichment. Most studies of phosphorus enrichment have focused on their interaction with mycorrhizal fungal. Eom et al. (1999) observed decreases in extraradical mycorrhizal hyphae under conditions of phosphate enrichment. Hetrick et al. (1989) found that the biomass of big bluestem seedlings was unresponsive to phosphorus fertilizer. However, their greenhouse studies indicated that warm-season grasses, when wanting in mycorrhizal fungi, responded positively to phosphorus fertilizer (Hetrick et al. 1990).

At the time of initiating the Upland Prairie Restoration, we had reasons to expect that the site had a compromised mycorrhizal community (McGonigle & Miller 1993). The site had no recent history of supporting prairie species. Instead, it had experienced poor soil management under a regime of row crop production and pasture, conditions poorly suited for maintaining diverse and abundant mycorrhizae. Consequently, we were interested in whether phosphorus fertilizer might supplement or replace the nutrients normally garnered by mycorrhizal fungi.

In summary, our objectives in this multiple season study were: 1) to describe the pattern of community succession on a tallgrass restoration initiated on agricultural soils, and 2) to examine the effects of phosphate, micronutrient, micronutrients plus phosphate, and nitrogen enrichment on the development and structure of this community.

## METHODS

The Upland Prairie Restoration consists of a 25-acre (10 ha) site owned by Avis Industrial Corp., Upland, Indiana (N40°27.2′, W85°0′). Before the onset of restoration, the rolling field produced row crops (corn and soybeans) and pasture of Kentucky blue-grass (*Poa pratensis* L.), fescues (*Festuca* spp.), and various weedy and oldfield forbs. Routine analysis (by Central Laboratory, Indianapolis, and A & L Great Lakes Laboratories, Fort Wayne, Indiana) indicated that fertility of the site varied. The eastern half overall had higher levels of soil nutrients. The western half was especially deemed low or very low in phosphorus (Bray P1 of 4–10 ppm) and the micronutrients boron and zinc, while the eastern half had medium phosphorus levels (8–26 ppm) and mostly adequate micronutrient concentrations. Across the study area, total Kjeldahl nitrogen ranged from 0.13–0.28%.

In April 1993, the vegetation was treated with Round-up® herbicide (glyphosate - a product of Monsanto Agricultural Chemicals) at recommended rates. In early June, after plant die-back, the ground was tilled, disked, and planted with cold-treated, hand-collected prairie seed mixes. The seed mixes were presumed to contained regional genotypes since they were gathered from prairie fragments in eastern Illinois and western Indiana. Across most of the area, big blue-stem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans* (L.) Nash) predominated in the seed mix. Although these grasses formed the bulk of the seed mix, it contained a diversity of other grasses and forbs with a total count of approximately 50 species.

Before seed germination, we laid out six treatment blocks in a randomized complete block experimental design. One pair of blocks (A1 and A2) occupied flat topography in the northeast corner of the field (Fig. 1). The particular seed mix for this area contained an abundance of forbs and little blue-stem (*Schizachyrium scoparium* (Michx.) Nash) but had minimal seed from tallgrass species. A second pair of blocks (B1 and B2) was placed in the center of the 25-acre (10 ha) site, a flat area near the base of an east-facing slope. This seed mix was rich in several tallgrass species (<10% forb content). The final pair of treatment blocks (C1 and C2) was sited on a well-drained, east-facing slope near the west margin of the field where the seed mix was enriched with forbs (approximately 20% of seed content).

Each of the 36 × 17 m blocks contained five randomly assigned treatment strips: control, micronutrients, nitrogen, phosphate, and phosphate + micronutrients. The treatment strips, separated from each other by 2 m wide buffer zones, were 17 × 5 m. This provided sufficient area for two sampling zones 15 m in length for a total of 30 potential sample areas per treatment strip. In June 1993 and late April 1994–1997, we applied nutrients with a hand-held spreader. The micronutrients included boron (2.3 g/$m^2$), manganese (1.6 g/$m^2$), and zinc (1.2 g/$m^2$). Nitrogen, in the form of 46% urea, was spread at a rate of 40 g/$m^2$ and 46% phosphate at 30 g/$m^2$. During the 1993 and 1994 growing seasons, we attempted no weed control within the treatment strips. However, field thistle (*Cirsium arvense* (L.) Scop.) proved persistent and necessitated spot treatment in May 1995 and each subsequent year.

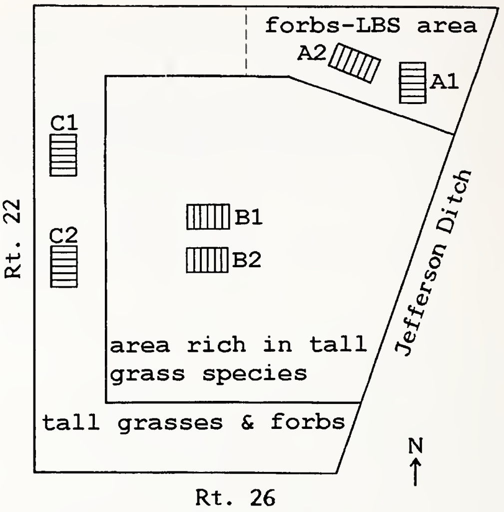


Figure 1.—Schematic showing layout of research plots on the 25-acre (10 ha) Upland Prairie Restoration site. Not drawn to scale. Blocks A1 and A2 are situated in an area rich in forbs and little bluestem (LBS); the grass rich area of block B1 and B2 was planted with less than 10% forbs in the seed mix; blocks C1 and C2 were planted with approximately 20% forbs in the seed mix. Each experimental block encompasses an area of 36 × 17 m.

Starting with the 1993 season, sampling of density and canopy cover of each weed and prairie species took place in late July–early August. During the first two growing seasons, sampling consisted of 15 random 0.25 $m^2$ quadrats per treatment strip. Thus, the total quadrats sampled across the experimental design was 450 per year. As prairie species gained size, their quadrat size was increased to 1 $m^2$.

Total density and total cover of prairie species and of weeds were calculated for each quadrat. In the context of this experiment, we define weeds to mean those species not included in the planted seed mix. Statistical analysis indicated that transect data, even when transformed, did not fulfill the assumption of normal distribution. As a result, statistical comparisons between samples relied upon the non-parametric Mann-Whitney test. In describing the development of the prairie community, mean values for cover and for density were calculated from pooled transects within each block. Effects of soil amendments were tested by pooling similar treatments across the six blocks.

## RESULTS

**Development of the prairie community.**—In the first growing season (1993 or Year I) of the Upland Prairie Restoration, annual weeds dominated. They reached average cover as high as 131% (Fig. 2) in the more moist sites (blocks A1 and A2) located in the northeast corner of field. In the first season (1993), abundant species included flower-of-an-hour (*Hibiscus trionum* L.), nut-sedge (*Cyperus esculentus* L.), and yellow foxtail (*Setaria glauca* (L.) P. Beauv.).

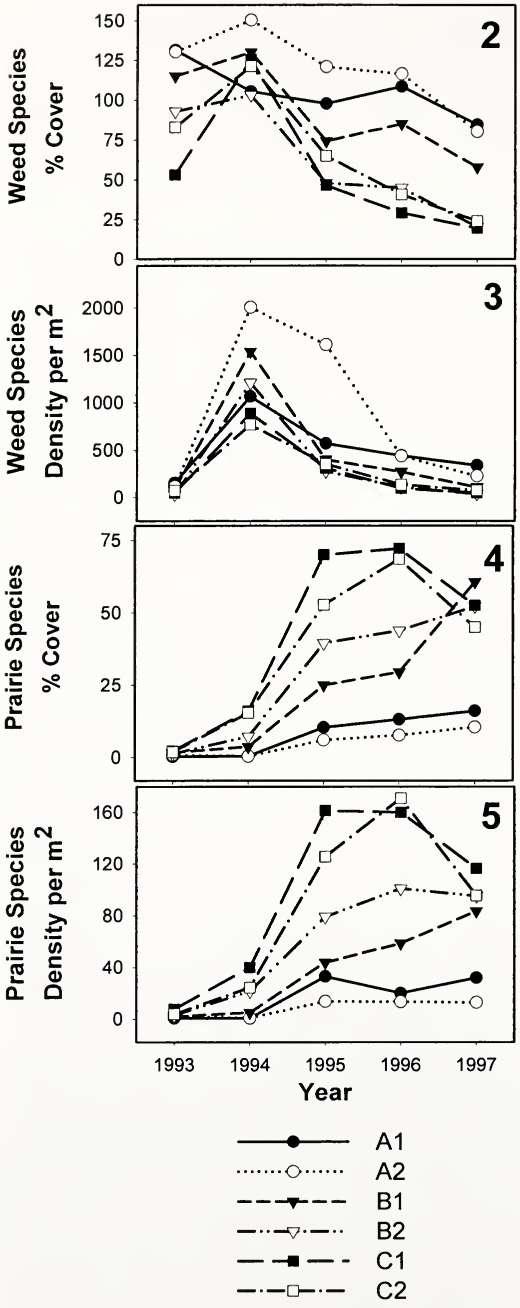
During Year II (1994), the Upland Prairie Restoration site was still heavily dominated by annual weeds (average within block cover ranged from 103–150%) but the species composition changed. Flower-of-an-hour and nut-sedge were replaced by giant foxtail (*Setaria faberi* Herrm.) and common ragweed (*Ambrosia artemisiifolia* L.). Also during Year II, the total density of weed species reached a peaked (Fig. 3); average within block weed densities ranged from 770 plants per m$^2$ in drier sites to 2005 per m$^2$ in moister sites.

By Year III (1995), the Upland Prairie Restoration had undergone dramatic changes. The density of annual weed species in 1995 dropped precipitously (Fig. 3). Except for block A2, average density returned to below 570 per m$^2$. Weed cover (Fig. 2) also fell to less than 75% for blocks B1, B2, C1, and C2 but remained significantly higher ($P <$ 0.0005) for blocks A1 and A2. This overall decline in weed density and cover was accompanied by strong increases in dominance of prairie species (Figs. 4, 5). Average cover by prairie species was as high as 70% (block C1) in the well-drained, forb-enriched areas in the western portion of the planting. Three species were particularly prevalent: black-eyed Susan (*Rudbeckia hirta* L.), big blue-stem (*Andropogon gerardii*), and Indian grass (*Sorghastrum nutans*). In the case of black-eyed Susan, the sharply-increased densities were due to high number of seedlings that sometimes carpeted areas between young grass tussocks. On the other hand, increased grass densities reflect vigorous tiller production in big bluestem and Indiana grass.

Community succession over the remaining two years involved further increases in tillers by perennial grasses accompanied by a decline in forb seedlings such as black-eyed Susan and prairie coneflower (*Ratibida pinnata* (Vent.) Barnhart). As a result, the highest densities, averaging about 160 shoots per m$^2$, occurred in 1996 (Fig. 5). At the end of the five years of observation (1997), the four blocks (B1, B2, C1, and C2) sown with grass rich mixes had an average prairie plant cover of 45–61% (Fig. 4).

The pattern of succession towards high cover and density of prairie species was not uniform across the experimental design. Plots A1 and A2, located on flat ground and planted with a seed mix containing an abundance of forbs and little blue-stem, under-performed over the period from Years III–V. The average cover by prairie species in these plots ranged only from 10.5–16.1% (Fig. 4) and density only reached a maximum of 32 shoots per m$^2$ (Fig. 5). Not surprisingly, the weed cover in these two blocks remained substantially higher than those of blocks B2, C1, and C2 (Fig. 2), although the density of weeds did decline to levels typical of other blocks (Fig. 3).

**Response to soil amendments.**—During each of the five years of observation, soil amendments (micronutrients, nitrogen, phosphate, and phosphate + micronutrient mix) were individually applied to strips within each block. We expected that their addition might stimulate prairie development, i.e., increase the cover and/or density of prairie species. The results indicate that, relative to the control, none of the amendments consistently enhanced the development of the prairie community (Figs. 8, 9). By Year III (1995), cover in the micronutrient, phosphate, and phosphate + micronutrient treatments increased to an average of 37.7–42.5% while the control reached 49% (Fig. 8). Statistically, the strips treated with micronutrients or phosphate alone had slightly lower cover ($P < 0.02$) and density ($P < 0.04$) than the control (Fig. 9). How-

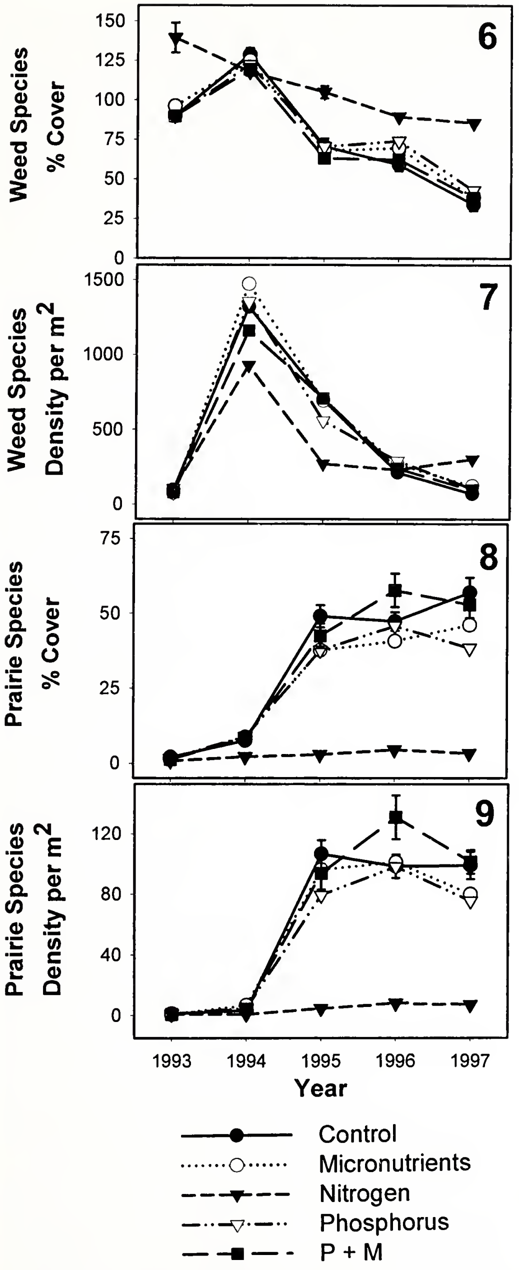


Figures 2–5.—Changes in the Upland Prairie Restoration, 1993–1997. 2. Weed species, mean percent cover; 3. Weed species, mean density; 4. Prairie species, mean percent cover; 5. Prairie species, mean density. Blocks (A1, A2, B1, B2, C1, C2) represent paired locations on the Restoration site (see Fig. 1). For clarity, standard error bars are not shown; variation was consistently less than 10% of the mean value.

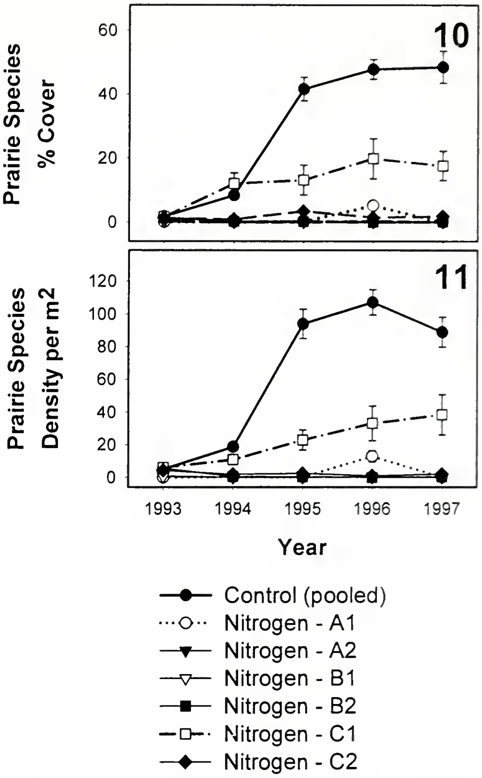
ever, during the last two seasons of observation (Years IV–V), these differences largely disappeared. When compared to the control, no significant differences in cover or density of prairie species were observed in Year IV (1996) and only cover within the phosphate treatment was statistically lower ($P < 0.02$) than the control in Year V (1997).

While no fertilizer amendment provided sustained, meaningful enhancement of the developing prairie community, the negative response to nitrogen application was unequivocal. In nitrogen treated strips, average cover and density of prairie species remained near nil to extremely low throughout the duration of the study (Figs. 8, 9). Instead, the areas receiving nitrogen applications retained a community dominated by annual weed species. These weeds included common and giant ragweed (*Ambrosia trifida* L.), giant foxtail, lamb's quarter (*Chenopodium album* L.), and knotweeds (*Polygonum* spp.). Their dominance in nitrogen-enriched plots was not usually due to increases in density. In fact, in Years II–III (1994 and 1995) the density of annual weeds was actually lower where nitrogen had been applied (Fig. 7). Clearly, however, the luxuriant nitrogen supply modified the size and, therefore, cover of individual weed plants (Fig. 6). This response was particularly evident in the first year of the experiment (1993) when weed cover under nitrogen enriched conditions averaged near 140%. Even at the end of the observation period (i.e., Years IV–V), the cover of weeds was still approximately 85% and substantially composed of annual as opposed to perennial weed species.

To clarify further the observed relationship between nitrogen enrichment and prairie species, we plotted the five-year response to nitrogen for each individual block against the pooled results from control plots (Figs. 10, 11). Among five of the six blocks, cover of prairie species in nitrogen treatment plots consistently remained below 6% (compared to 50% for control plots) throughout the study period (Fig. 10). At the same time, density remained below 14 shoots per $m^2$ (Fig. 11) compared to up to 107 shoots per $m^2$ in control plots. The cover and density of prairie species in block C1, located in the well-drained western sector of Upland Prairie Restoration site, was somewhat exceptional. By



Figures 6–9.—Changes in response to soil amendment treatments, 1993–1997. 6. Weed species, mean percent cover; 7. Weed species, mean density; 8. Prairie species, mean percent cover; 9. Prairie species, mean density. P + M = phosphate plus micronutrients. Some standard error bars omitted for clarity.



Figures 10–11.—Response of prairie species to nitrogen enrichment versus pooled control (1991–1997). 10. Mean per cent cover; 11. Mean density. The control is pooled from across the six blocks. Individual nitrogen enrichment treatments are shown for each block – A1, A2, B1, B2, C1, and C2. Note the low and strongly overlapping values for each nitrogen transect except the one from block C1.

1997, this block had average cover of nearly 18% and density of 38 shoots per m$^2$. Although these values are significantly higher than those of other nitrogen plots, they are still significantly lower than those observed for non-nitrogen treatments (e.g., for cover data: $P < 0.0008$). Of interest, this same block supported a low weed cover during the first year (1993) of the experiment, with an average of only 53% (Fig. 2). However, in other years its weed cover and density were not exceptional.

## DISCUSSION

In the Upland Prairie Restoration, annual species dominated the early successional community (Years I–II). Seedlings of prairie species were present within the substantial weed stands but did not become readily visible until Year III. By the end of the five-year study period, the overall Upland Prairie Restoration had a high cover and density of planted prairie grasses and forbs, including substantial populations of about 15 species. Subsequent sampling (unpubl. data for 1998–2000) indicates that this species diversity and quality has changed little.

The use of phosphate, micronutrients, or a combination of phosphate + micronutrients proved ineffective in enhancing establishment of prairie grass and forb seedling and overall community development. Instead, one of the most critical factors was simply the location. Within the topographic diversity of the site, a gentle east-facing slope proved most favorable. On lower, flat areas, heavy June rainfall during Year I held the silt-loam soils at saturation for a prolonged period. These moister micro-sites had lower density and cover of prairie species through most of the five-year observation period. Some portions of the 25-acre (10 ha) site (outside the experimental area) actually experienced short-term flooding and, as a result, only developed a sparse cover of big blue-stem.

Our inability to demonstrate effects due to phosphorus fertilization supports the findings of Gibson et al. (1993) on natural Konza Prairie. In general, tallgrass species are obligate mycotrophs (Hetrick et al. 1994; Knapp et al 1998). In a study of the obligate mycotroph, big blue-stem, Hetrick et al. (1989) found no increase in biomass with phosphate. This lack of responsiveness extends to other warm-season grasses (Hetrick et al. 1990). According to Hetrick et al. (1994), these obligate symbionts would have less competitive advantage in a phosphate-enriched environment (although we were unable to demonstrate clear detrimental effects of phosphate enrichment in our field experiment). Forbs as well as cool-season grasses, on the other hand, often lack a dependence upon mycorrhizal fungi. Yet, again in our restoration, phosphate failed to enhance growth even in areas where forbs were abundant. This was unexpected given the results of Hetrick et al. (1990) in which facultative symbionts responded to either phosphate enrichment or mycorrhizae.

In contrast to the neutral response to phosphate or micronutrient enrichment, nitrogen fertilization clearly had detrimental impact. This took the form of increased dominance and persistence of annual weeds and a concomitant reduction in prairie species. The nitrogen effects we observed have been reported for other herbaceous communities such as old fields (Carson & Barrett 1988; Goldberg & Miller 1990), hay-meadows (Silvertown 1980), flatwood range (Kalmbacker & Martin 1996) as well as tundra and short-grass prairie (Gough et al. 2000). In our case, nitrogen enrichment compromised establishment of prairie grasses as well as forbs. Under conditions of nitrogen enrichment, individual weed plants may attain greater biomass and cover, resulting in strong light attenuation at ground level (Wilson & Tilman 1993; Piper 1995; Foster & Gross 1998). These low-light conditions may, in turn, suppress seed germination, as seen in winter wheat (Valenti & Wicks 1992), and/or the ability of seedlings to endure strong interspecific competition. Regardless of the specific mechanism, the negative effects of nitrogen enrichment may be of more consequence in this early stage of restoration. As somewhat of a contrast to the observations on the Upland Prairie Restoration, Seastedt et al. (1991), in their study of nitrogen addition to mature Konza Prairie, did not report increases in weed content but rather a change in the competitive environment that favored forb species over $C_4$ grasses.

Our results demonstrate the negative impact of acute nitrogen enrichment of a restoration site. Can we also expect lower or chronic nitrogen enrichment to be a problem? Bobbink et al. (1998) suggest that even air-borne nitrogen deposition can alter community function. Nitrogen-fixing shrubs in California coastal prairie (Maron & Connors 1996) and *Trifolium repens* L. in grasslands (Warren 2000) facilitate invasion by weedy exotics. These observations suggest a need to alter management strategies for nutrient-rich prairie restoration sites. One suggested strategy is soil impoverishment, through the addition of saw-dust (Török et al. 2000; Morgan 1994; Wilson & Gerry 1995), to immobilize nitrogen. Or, Collins et al. (1998) recommend high mowing in order to increase light at ground level and the enhancement of seed germination and seedling development.

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