Floristic and Soil Organic Matter Changes after Five and Thirty-Five Years of Native Tallgrass Prairie Restoration

Kelly Kindscher[1]
Larry L. Tieszen[2]

Abstract

We studied two tallgrass prairies and adjacent restoration areas in northeast Kansas to analyze (1) the invasion of native tallgrass prairie species from native prairie source populations into replanted areas; (2) the establishment of planted prairie species five and 35 years after being sown; and (3) the effects of native prairie species on soil organic matter. For the majority of dominant species, composition differed statistically between sampled areas even though seed rain was available from the native tallgrass prairie remnants. Plant community differences were statistically different between each native prairie area and all respective restoration sites according to the Multiple Response Permutation Procedure. In addition, species richness was greatly reduced in replanted areas compared to adjacent native prairie remnants. Soil carbon isotope ratios indicated that the planting of warm-season grasses resulted in substantial replacement of old soil organic matter by the newly replanted grasses but that it did not create substantial increases of soil organic matter beyond replacement. The lack of accumulation reflects a nutrient-poor system (nitrogen-poor in particular), and the relative absence of native or introduced nitrogen-fixing plant species on the replanted areas may be a significant factor. It appears that restoration of the original highly diverse vegetation component of the tallgrass prairie ecosystem, even when aided by seeding and an adjacent prairie seed source, will occur on carbon- and nitrogen-depleted soils only over very long periods of time (perhaps centuries), if at all.

[1]Kansas Biological Survey, 2041 Constant Avenue, University of Kansas, Lawrence, KS 66047–2906, U.S.A.
[2]Department of Biology, Augustana College, Sioux Falls, SD 57197, U.S.A.

Introduction

Prairie restoration may "be the oldest ecological restoration of any kind" (Mlot 1990), originating in the 1930s with Norman Fassett's and Aldo Leopold's plan to plant a large tallgrass prairie at the University of Wisconsin Arboretum (Cottam & Wilson 1966; Meide 1988; Sperry 1994). The importance of prairie restoration grew from the tragic Dust Bowl period of the 1930s and subsequent efforts to stabilize the prairie and agricultural ecosystems (Weaver 1943, 1950, 1954, 1968; Worster 1979). Additional interest has arisen because of extensive transformation of the native land cover type to agriculture (Riebsame 1990), resulting in a documented loss of 82–99% of the original tallgrass prairie (Samson & Knopf 1994), and the initiation of the Conservation Reserve Program (CRP) of the U.S. Department of Agriculture (USDA). The CRP resulted in the planting of 14.8 million ha of cropland to native warm-season grasses (Lindstrom et al. 1994). The impacts of management and the effects of CRP on soil carbon are now becoming a subject of active investigation (Burke et al. 1995*a*, 1995*b*; Noll et al. 1995). A better understanding of restoration ecology can offer many insights into basic ecological processes, including succession, competition, and plant population dynamics, and can also provide guidance for management of prairie ecosystems.

The University of Wisconsin–Madison Arboretum's Curtis Prairie is the oldest known prairie restoration and has been studied extensively (Cottam & Wilson 1966; Jordan 1983; Sperry 1983, 1994). It was planted from 1936 through 1941 by the Civilian Conservation Corps under the supervision of the pioneering restorationist Theodore Sperry and the National Park Service (Sperry 1994). During this time, native seed and sod were moved from nearby prairie areas to the prairie restoration area. In a 1990 survey, Sperry noted that 55% of 198 plantings had become successfully established (Sperry 1994). Within these plantings, eight species had spread widely into more than half of the restored prairie and an additional 23 had spread beyond their initial establishment. Successional changes resulted in reduced abundance of weedy, nonnative species.

Of particular interest were nine prairie species that Sperry established by seed but that had not moved from the locations where they were planted more than 50 years previously (Sperry 1994). Sperry considered these "documentary species" (documenting the original plantings), and they included *Amorpha canescens* (lead plant), *Ceanothus americanus* (New Jersey tea), and *Silphium laciniatum* (compass plant) (Sperry 1994). These documentary species, often referred to as conservative species (Mlot 1990), not only demonstrate the difficulty of species establishment and colonization but also the difficulty of establishing proper site conditions (Mlot 1990; Sperry 1994). Although it is considered successful, the restoration at Curtis Prairie has not attained the original species richness or biodiversity of a native tallgrass prairie remnant. This could result from management, length of time required for restoration, absence of grazing and browsing by native ungulates, or other ecosystem processes.

Although indirectly involved in restoration, the USDA's Conservation Reserve Program was established primarily to remove highly erodible and environmentally sensitive cropland from crop production by establishing 10-year contracts with landowners to plant perennial cover crops, including native tallgrass prairie grasses (Berlinger & Knapp 1991). While the program also has had many other environmental benefits, no provision of funding mechanism was established for either agricultural or ecological research (Laycock 1991), so little is known of the success of plant species establishment or the plant biodiversity of the CRP lands.

The purpose of our research was to examine the establishment of prairie plant species and the associated development of soil characteristics at two sites in northeastern Kansas. Few other prairie restoration studies have evaluated the colonization or movement of prairie species over time, although Clarke & Bragg (1994) found that some species moved locally from transplanted prairie sod in Nebraska. The original purpose of this prairie restoration study, started in 1957 at the University of Kansas Rockefeller Experimental Tract, was to determine "whether the native prairie plants and animals could be re-established by seeding adjoining parts of the worn-out cultivated land" (Fitch & Hall 1978). Some results from that experiment are presented here.

We have studied prairie restoration in a favorable context for species establishment: prime farmland replanted to prairie in two areas that have an adjacent native prairie, which serves as a passive seed source. Our tallgrass prairie restoration sites were chosen to evaluate (1) the invasion of native tallgrass prairie species from native prairie source populations into replanted areas; (2) the establishment of planted prairie species (five and 35 years) after being sown; and (3) the effects of native prairie species on soil organic matter.

Methods

Study Area

The study was conducted at two sites in northeast Kansas, the Rockefeller tract and the Fall Leaf tract. These sites were selected because both are composed of a native tallgrass prairie, both are rich in native plant species, and both are immediately adjacent to a replanted area undergoing restoration (Kindscher 1994; Kindscher & Wells 1995). The native prairies were classified as being in the Bluestem Prairie area of Kansas (Küchler 1974). Both native prairies were situated on the western borders of the replanted areas and had the same soil type, local climate, and pre-settlement vegetation. Therefore, the restoration areas were in a similar landscape position related to the prairie remnants, especially in terms of receiving seed rain through gravity and wind dispersal. To limit the growth of weeds, both sites received no fertilizer applications during the restoration.

The Rockefeller tract is located at the University of Kansas, 12 km north of Lawrence, Kansas (Section 33, T11S, R2OE), on Pawnee and Grundy silty clay loams (fine montmorillonitic, mesic Aquic Argiudolls). Since 1956, the four-ha native prairie has been managed by spring burns every 1–3 years (Fitch & Hall 1978). The floristics and plant species composition of this native prairie have been studied extensively (Freeman et al. 1991; Kindscher 1994; Kindscher & Wells 1995).

The 40 ha restoration area adjacent to the native prairie at the Rockefeller tract was farmed (probable crops were wheat, grain sorghum, corn, red clover, and others) until its purchase in 1956. In 1957, the area was disked and sown with a commercial native warm-season grass mixture of *Andropogon gerardii* (big bluestem), *A. scoparius* (little bluestem), *Sorghastrum nutans* (Indian grass), and *Panicum virgatum* (switch grass) (Fitch & Hall 1978). No forbs were planted. Since then, this area has been unmanaged (no grazing or prescribed fire), although one wildfire swept across the area in November 1983. For our study, we selected that portion of the restored grassland which was adjacent to the native prairie and not substantially invaded by trees and shrubs, which were encroaching elsewhere. To determine if there was a distance effect in recruitment of plant species from the native prairie after approximately 35 years, three transects were established in this replanted area of the Rockefeller tract. These transects, labeled "area closest," "area middle distance," and "area farthest," were sampled parallel to the native prairie edge at distances of 6 m, 18 m, and 102 m, respectively.

The second site, Fall Leaf, included a 2 ha native prairie hay meadow and an adjacent 18 ha replanted area undergoing restoration. It is located 16 km southeast of the Rockefeller tract (about 6 km north-northwest of Eudora, Kansas, Section 29, T12S, R21E). Because of differences in establishment time between the two sites, Fall Leaf was sampled as a second independent example, not for comparative purposes. The soils of the Fall Leaf site are Shelby loam and a Vinland-Sibleyville complex (primarily loam, mixed mesic shallow, typic Hapludolls). The native prairie portion is managed through annual haying (except for the edges—about 2 m wide, and a 750 m^2 area left in the center portion in 1988 for seed production purposes). The site has not been grazed during the last 20 years (personal communication with the owner, 1990).

In April 1989, 16 of the adjacent 18 ha were revegetated under the CRP. This area had previously been in crop production (with wheat, grain sorghum, soybeans, corn, red clover, and other crops). It was planted to the same native, warm-season grasses (purchased from an in-state commercial source) as on the Rockefeller site, except for the addition of *Bouteloua curtipendula* (sideoats grama) and *Eragrostis trichodes* (sand lovegrass). No herbicides were used in the restoration process. Forb seeds were also planted because of the slow nature in which replanted grasslands tend to recruit native species. We chose only local, native prairie species and concentrated on species found on the adjacent Fall Leaf native prairie. Thirty-three species of native prairie plant seed were gathered from local sources (several in quantities of only a few grams) and broadcast with a hand-cranked seeding device in April of 1989. The grasses were no-till drilled into stubble from the previous year's CRP-recommended unharvested sterile sorghum planting. Total rates of seeding were 5.8 kg/ha for grasses and 0.06 kg/ha for forbs.

A second area in the Fall Leaf site, named the "recently untilled area," was not eligible for the CRP because it was not part of the cropland base acreage of the farm. Although this 2 ha area had probably been cropped in the past and is adjacent to the 16 ha CRP area, at planting time it consisted of a mix of nonnative cool-season and native warm-season grasses dominated by *Poa pratense* (bluegrass), *Bromus inermis* (brome grass), and *Tridens flavus* (purple top). This recently untilled area had previously been cut for hay on an irregular basis. This area was thoroughly disked twice and seeded using the same mix as the Fall Leaf CRP.

After planting, the 2 ha recently untilled area and the CRP area were rotary-mowed once in July 1989 to reduce agricultural weed growth and subsequently to encourage the establishment of native, warm-season grasses. During our study, there was no other management of these areas, including burning or grazing.

Vegetation and Soil Sampling

For all areas in this study (Rockefeller Native Prairie, Fall Leaf Native Prairie, and five restored areas labeled Rockefeller area closest, area middle distance, areas farthest, and Fall Leaf recently untilled and Fall Leaf CRP), the vegetation in 30 1.0 m^2 quadrats was sampled, resulting in 210 total quadrats. A stratified random sampling procedure was used with quadrats located 4 m apart in belt transects. Species cover in each quadrat was determined by estimating the percent cover of greatest spread of foliage for each species (Daubenmire 1959). For planned, within-site comparisons, sampling was conducted during the third and fourth weeks of June 1992 at the Rockefeller site and during the third week of September 1992 for the Fall Leaf site. Since only within-site comparisons were to be made, the sampling date differences were not problematic. Careful observation of emerging shoots and dried foliage, along with substantial familiarity of the sites and species (Kindscher 1987, 1992, 1994; Kindscher & Wells 1995), prevented species from being overlooked due to the seasonality of sampling dates. Voucher specimens from these native prairies were deposited in the R. L. McGregor Herbarium (KANU) at the University of Kansas. Nomenclature for all species is from the *Flora of the Great Plains* (Great Plains Flora Association 1991).

Based on previous work (Kindscher 1994; Kindscher & Wells 1995), and similar to Cornelius (Cornelius et al. 1991), species were assigned to the following eight plant guilds: annuals, C_4 grasses, C_3 grasses and sedges, ephemeral spring forbs, spring forbs, summer-fall forbs, legumes, and woody shrubs. In addition, trees and nonnative species were separated from the native prairie plant guilds. The cover data for these guilds were based on composite summations of individual species cover, following the methodology of Kindscher and Wells (1995); they were referred to as cover by guild.

Soil organic matter was obtained from 1 m^2 quadrats located in each native prairie in the replanted area farthest from the native prairie at the Rockefeller site and in the recently untilled area at the Fall Leaf site. Four profiles were sampled randomly near the corner of each quadrat (regardless of the vegetation or bare ground) by driving a coring device (2.5 cm diameter) to depths of 60–100 cm. The four cores from each quadrat were pooled by strata after the horizons were determined and depth-stratified. Four of the pooled samples were taken from each of the sites. Soil samples were derooted, subsampled, and air-dried upon collection. Soil Conservation Service soil scientists verified soil cores as Grundy (Rockefeller site) or Shelby loam (Fall Leaf site). The pooled subsamples were then prepared for isotopic analysis of bulk soil for further particle size and density fractionation.

A homogeneous portion of each bulk soil subsample was decarbonated with 0.5 N HCl and continuous stirring (up to 24 hours) until no effervescence under a vacuum was detected. The treated sample was centrifuged at 10,000 × gravity, resuspended in distilled water, and recentrifuged. The pellet was then dried, pulverized, and loaded into tin cups for combustion under pure oxygen at high temperatures in a Carlo Erba CHN analyzer. Samples of variable sizes were used to provide adequate carbon for isotopic analysis. The combusted sample was separated into CO_2 and N_2 gases and quantified with a gas chromatograph. These provided concentrations of carbon and nitrogen for C:N calculations and for elemental compositions. Separate bulk density estimates enable quantification of these materials on a land area basis.

The combusted products were passed through a drying column, and CO_2 was trapped at liquid nitrogen temperature in the triple trap of a VG SIRA-10 Isotope Ratio Mass Spectrometer (IRMS). Remaining gases were removed under a high vacuum, and the CO_2 was analyzed by the IRMS (Tieszen & Fagre 1993). The isotope ratio is presented as the σ13C value, where σ13C = Rs-Rp/Rp × 1000, where Rs = ratio of 13C in the sample and Rp = ratio of 13C in the standard. This ratio diagnostically distinguishes between C_3 and C_4 species with mean values of −26.7‰ for C_3 species and −12.6‰ for C_4 species in North American native prairie species (Tieszen 1994). This ratio effectively serves as a label for the soil organic matter that accumulates in soil, thereby allowing a reconstruction of past vegetation assemblages (Tieszen & Archer 1990; von Fischer & Tieszen 1995).

Data Analysis

Data for species with cover greater than 5% in at least one of the areas sampled at a site (dominant species) were analyzed by the nonparametric Kruskal-Wallis test in the SPSS/PC+ software package (SPSS 1988). The Kruskal-Wallis test was used to compare the data from the 30 quadrats for individual plant species across areas sampled within each of the two restoration sites, because the variances were not equal between areas sampled, even when the data were transformed (Sokal & Rolf 1995). The nonnormal distributions probably occur because variances were very large. To limit the overall experiment-wise error rate, the Bonferroni method was used to adjust the probability value (Sokal & Rolf 1995). This more conservative value was used because of the repeated comparison among treatments. In addition, a Mann-Whitney *U* test was used for these dominant species to determine if differences occurred between specific treatments. To determine difference in cover by all species combined (a community response pattern), plant species data were compared between treatments by a multiple response permutation procedure in the PC-ORD software package (McCune & Mefford 1995), following Zimmerman et al. (1985) and McCune (1993).

Differences in the number of species per plot between areas sampled within the Rockefeller and Fall Leaf sites were tested by one-way analysis of variance (ANOVA) and the least significant difference procedure as a post-hoc test (SPSS 1988). ANOVA was used because the data were normally distributed and variances were homogeneous. In addition, species diversity (based on quadrat data, $n = 30$/area sampled, according to the Shannon index, H'), evenness of species distribution (Magurran 1988), and soils comparisons ($n = 4$/area sampled) were compared by one-way ANOVA because the basic assumptions of this test were met.

Results

Rockefeller Site

Significant differences for cover among areas sampled were found for five of eight dominant species (species over 5% cover in at least one area sampled) at the Rockefeller site (Appendix 1). Those species that were not significantly different were planted with either native grasses or one of the goldenrods (*Solidago canadensis* and *S. rigida*). Significant differences were also found for individual species between specific treatments, and especially between species on the native prairies and other treatments (Table 1). Fifty-eight species were recorded in the 30 quadrats sampled on the Rockefeller native prairie (Appendix 1). This prairie was dominated by big bluestem and little bluestem, which accounted for 27% and 18% of the total cover, respectively. The forb with the largest cover was *Silphium laciniatum* (compass plant), at 6.3% of the total cover. The legume with the largest cover (also a forb) was *Lespedeza capitata* (roundhead lespedeza), at 0.85% of the cover.

The area sampled closest to the native prairie had 38 species present and was dominated by little bluestem and *Sporobolus asper* (tall dropseed), which together accounted for 58% of the total cover. Tall dropseed did not occur on any native prairie plot, although it did occur in low abundance on the native prairie and is frequently observed locally in areas that are overgrazed or have shallow soil. The forb with greatest total cover (at 4.7%) was *Helianthus rigidus* (stiff sunflower). *Desmodium sessilifolium* (sessile-leaved tickclover) had the greatest cover of any legume but at only 0.1%.

The area sampled at the middle distance from the native prairie had 34 species and was dominated by big and little bluestem, which accounted for 44% of the total cover. Stiff sunflower had the greatest cover of any forb at 9.0% of the total cover. Roundhead lespedeza had the greatest cover of any legume with only 0.1%.

The area sampled farthest from the native prairie had 37 species and was dominated by big and little bluestem, which accounted for 49% of the total cover. *Aster praeal-*

Table 1. Comparisons of percent cover by dominant species.*

Species	*Native Prairie*	*Area Closest*	*Area Middle Distance*	*Area Farthest*
Rockefeller Site				
Andropogon gerardii	27.3 a	12.6 a	17.0 a	15.2 a
Andropogon scoparius	17.9 a	32.3 b	27.9 c	34.2 b
Aster praealtus	5.9 ab	0.6 c	3.3 b	2.5 ac
Helianthus rigidus	5.3 a	4.7 b	9.0 c	0.1 a
Panicum virgatum	0.4 a	2.0 b	6.1 c	14.8 d
Sorghastrum nutans	2.4 a	3.4 ab	5.7 b	9.6 b
Sporobolus asper	0.0 a	25.3 b	12.6 c	18.1 c
Sporobolus heterolepis	8.8 a	0.0 b	0.0 b	0.0 b
Fall Leaf Site				
Species	*Native Prairie*	*Area Recently Untilled*	*CRP*	
Andropogon gerardii	26.5 a	3.6 b	9.3 b	
Andropogon scoparius	33.9 a	7.2 b	16.6 c	
Bouteloua curtipendula	9.3 a	2.8 b	3.1 c	
Heterotheca latifolia	0.0 a	0.0 a	5.9 b	
Muhlenbergia schreberi	0.0 a	5.5 b	0.0 a	
Panicum virgatum	0.4 a	9.6 b	4.7 a	
Setaria viridis	0.0 a	0.0 a	19.7 b	
Sorghastrum nutans	5.0 a	49.3 b	20.6 c	
Tephrosia virginiana	6.4 a	0.0 b	0.0 b	

*Cover of at least 5% for at least one treatment, according to the Mann-Whitney *U* test, $p < 0.05$. Numbers with the same letters are not significantly different from one another.

tus (willow-leaved aster) had the greatest cover of any forb (2.5%). The most important legume was *Baptisia lactea* (white wild indigo) with only 0.1% of the total cover.

At the Rockefeller site, differences between areas sampled for six out of the eight prairie guilds (Table 2) on the native prairie (Kindscher 1994) were statistically significant. The C_4 grass guild also dominated the cover of all areas sampled but was not statistically different between areas sampled. Not surprisingly, woody species and nonnative species, both with low cover values, were not statistically different in the prairie areas sampled.

The native prairie had considerably greater cover of the legume guild, with *Amorpha canescens* (lead plant), *Baptisia bracteata* (yellow wild indigo), and *Lespedeza capitata* and *L. violacea* (lespedezas); the summer/fall forb guild, with willow leaf aster, *Eryngium yuccifolium* (rattlesnake master), stiff sunflower, compass plant, and *Solidago rigida* (stiff goldenrod); and the woody guild, with *Rhus glabra* (smooth sumac) and *Rubus ostryfolius* (blackberry), although the woody guild was not statistically significant. The ephemeral spring forb guild was found only on the native prairie, but even there at very low cover, as discussed in our previous work (Kindscher & Wells 1995). The two areas sampled closest to the native prairie were generally similar to each other in composition by guild and were intermediate between the native prairie and the area sampled farthest from the native prairie. Of the three replanted areas sampled, the area farthest from the prairie had the greatest cover of the annual guild, with ragweed and *Croton capitatus* (wooly croton), C_3 grass and sedge guild (*Carex brevior*), and the planted C_4 grass guild.

Fall Leaf Site

Significant differences for cover of dominant species (species over 5% cover in at least one area sampled) between areas sampled were found for seven of nine species at the Fall Leaf site (Appendix 2). Significant differences were also found for individual species between treatments (Table 1). Forty-nine species were present on the 30 quadrats sampled on the native prairie at the Fall Leaf site (Appendix 2). These quadrats were dominated by big bluestem and little bluestem, which together accounted for more than 60% of the total cover. In addition, the native prairie had the largest cover of the forb *Rudbeckia hirta* (black-eyed Susan) and the legume *Tephrosia virginiana* (goat's rue), which accounted for more than 6% of the total cover. Nonnative species accounted for only 0.15% of the total cover of the native prairie area.

The replanted area that was recently untilled had 48 species in its sampled quadrats and was dominated by the planted Indian grass and switch grass (49.4% and 9.7%, respectively, of the total cover; Appendix 2). The forb with the largest cover was an unplanted, widely dispersed legume, *Desmodium illinoense* (Illinois tickclover), at 2.4% of the total cover. Nonnative species accounted for only 0.3% of the total cover. This area also

Table 2. Average percent cover (standardized to 100%) for plant guilds for the areas sampled at the Fall Leaf and Rockefeller sites.*

Guilds	*Native Prairie (% Cover)*	*Area Closest (% Cover)*	*Area Middle Distance (% Cover)*	*Area Farthest (% Cover)*	*Significance*
			Rockefeller Site (areas sampled)		
Annual	1.7	0.2	0.2	0.4	*
C_3 grasses and sedges	0.7	0.6	0.1	0.7	*
C_4 grasses	58.9	75.6	71.1	91.9	
Ephemeral forbs	0.2	0.1	0.0	0.0	*
Summer-fall forbs	27.0	14.8	19.1	5.4	*
Legumes	2.6	0.2	0.1	0.1	*
Spring forbs	6.2	8.1	9.1	1.5	*
Woody species	1.5	0.5	0.1	0.1	
Nonnative	0.0	0.0	0.0	0.0	
Total	100.00%	100.00%	100.00%	100.00%	
Percent C_4 signal	58.9%	75.6%	71.1%	91.9%	
			Fall Leaf Site (areas sampled)		
Guilds	*Native Prairie*	*Area Recently Untilled*	*CRP*		
Annual	0.2	0.3	10.3		*
C_3 grasses and sedges	6.1	3.4	0.8		*
C_4 grasses	78.7	81.1	55.9		*
Ephemeral forbs	0.2	0.1	0.0		*
Summer-fall forbs	2.5	2.8	4.8		*
Legumes	7.5	3.3	0.9		*
Spring forbs	2.0	0.2	5.7		*
Woody species	1.6	8.3	0.4		*
Nonnative	0.2	0.3	21.3		*
Total	100.00%	100.00%	100.00%		
Percent C_4 signal	78.7%	81.1%	55.9%		

*Percent C_4 signal is the ratio of C_4 photosynthetic pathway species to total cover. The nonparametric Kruskal-Wallis test was used to test for significant differences among treatments ($p < 0.05$ marked with an asterisk).

had greater cover than the other Fall Leaf sampled areas of the following species: sand lovegrass and Indian grass, both planted native grasses, *Dichanthelium acuminatum* (panic grass, which probably remained in the seed bank during tillage prior to restoration), *Cassia chamaecrista* (partridge pea, a planted native annual legume), and *Symphoricarpos orbiculatus* (buckbrush, a native woodland shrub that most likely was a root sprout but may have persisted in the seed bank or invaded from the adjoining brushy land). These species with large cover values indicate the importance of site history and other factors that influence the establishment of planted species.

The CRP area had 41 species present on the sampled quadrats, but the summed cover of all species was less than that of the native prairie or other replanted area. Indian grass and little bluestem were the dominant native species and accounted for 37% of the total cover. The annual *Heterotheca latifolia* (camphor weed) had the largest cover of any forb at 5.9%. The legume with the largest cover was partridge pea at only 0.5% of the total cover. Nonnative species were conspicuous, especially *Setaria viridis* (green foxtail) and *S. faberi* (Chinese foxtail), and totaled 21.3% of the total cover.

Significant differences were found among the three Fall Leaf areas sampled for all guilds (Table 2). As on the Rockefeller site, the C_4 native grass guild (primarily big bluestem, little bluestem, Indian grass, and switch grass) was the dominant cover for all areas sampled. The Fall Leaf native prairie also had a considerably greater cover than the other treatments of the C_3 native grass and sedge guild, including *Stipa spartea* (needle and thread grass), and by the legumes goat's rue and lead plant. The recently untilled area had the greatest number of woody species, including blackberry, *Cornus drummondii* (rough-leafed dogwood), buckbrush, *Ulmus rubra* (red elm), *Maclura pomifera* (Osage orange), *Juglans nigra* (black walnut), and *Gleditsia triacanthos* (honey locust), which, from observed size and vigor during the first year, apparently persisted as root sprouts from the former pasture. The CRP, the only area sampled to have recently been in till agriculture, had the greatest cover of nonnative species and annuals, including green foxtail, *Ambrosia artemisiifolia* (annual ragweed) and camphor weed. These indicate that the recent history of agricultural land use—only five years previous—provides a large and persistent seed bank for these species.

Number of Species per Plot, Diversity Index, and Community Differences

Both native prairie areas had significantly more species per plot than their respective replanted areas (Fig. 1). At the Rockefeller site, all areas sampled were different, except for the areas closest and at middle distance, which had intermediate values between the native prairie and the area farthest from the native prairie. The greatest number of species in any one plot was also greater for the native prairie areas than for the replanted areas.

There was no statistical difference in diversity between areas sampled at the Fall Leaf site (Table 3). At the Rockefeller site, in contrast, there were significant differences in diversity between the native prairie and the areas at middle and farther distance from the native prairie. No differences were seen in evenness between areas sampled at either site (Table 3).

There were also significant differences in the cover of all species when combined in a multiple response permutation procedure (Table 4). This indicates that there is a community response pattern, resulting in differences in cover of the combined species in these plant communities.

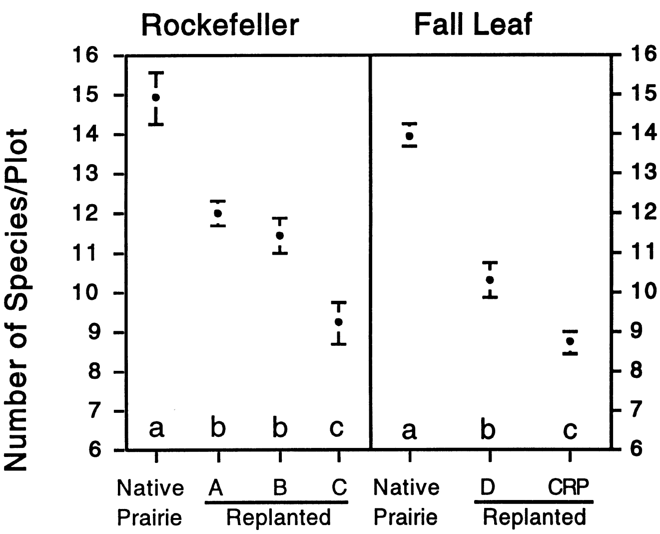

Figure 1. Average number of species per quadrat (30 quadrats/area sampled) and standard errors for the Rockefeller and Fall Leaf sites. Least significant difference post hoc test used with analysis of variance. Means sharing same lowercase letters at each site are not significantly different ($p < 0.05$). Area closest to the native prairie (a); area middle distance (b); area furthest from the native prairie (c); recently untilled area (d).

Table 3. Comparisons of number of species found in 30 1-m^2 sampled quadrats, diversity (H'), standard error of the mean associated with H' (SE), and evenness for the areas sampled at the Rockefeller and Fall Leaf sites.*

Area Sampled	*No. of Species*	H′	*SE*	*Evenness*
Rockefeller Site				
Native prairie	58	3.56 ab	0.006	0.893
Area closest	38	3.27 ac	0.009	0.885
Area middle distance	34	3.05 ac	0.011	0.881
Area farthest	37	3.11 a	0.011	0.864
Fall Leaf Site				
Native prairie	49	3.47 a	0.007	0.892
Area recently tilled	48	3.38 a	0.009	0.873
Conservation Reserve Program	41	3.27 a	0.010	0.881

*Following analysis of variance, we conducted a least significant difference post hoc test, $p < 0.05$. Lowercase letters designate significant differences between these areas sampled.

Soil Carbon Isotopes and Soil Organic Matter

The patterns of soil carbon (C) were similar for the native prairie and replanted treatments at the Rockefeller and Fall Leaf sites (Fig. 2). The one-way ANOVA, testing for treatment effects on total soil carbon, was highly significant ($p = 0.0001$, $F = 163$), with the Rockefeller replanted treatment possessing the least soil C and the Rockefeller native prairie the most, but only slightly (though significantly) more than the Fall Leaf native prairie. As is suggested by the curves in Figure 2, the patterns of the soil C concentrations with depth were consistent at the two sites. In the upper four layers of the profile, the Rockefeller native prairie possessed slightly higher C concentrations than Fall Leaf native prairie, and both areas had higher concentrations than the replanted treatments, which possessed statistically similar low values (one-factor ANOVA, $p < 0.05$), whereas in the lower two strata all treatments possessed similar low C concentrations ($p > 0.05$). The total nitrogen concentrations of these soils followed a pattern in each site that was nearly identical to that of the carbon concentrations at the Fall Leaf site, with similar patterns of statistical significance. Very low total nitrogen amounts were found throughout the profile in the replanted Rockefeller site, however, and the upper surface sample contained only one-third the nitrogen found in the adjacent native prairie.

The patterns of the distribution of carbon isotopes with depth were similar in the native prairies at the two sites (Fig. 2). Depth was a significant determinant of the stable isotopic value in both native prairies (Rockefeller, $p < 0.0001$, $F = 104$; Fall Leaf, $p < 0.0001$, $F = 11.3$). In both cases, the isotope values were more negative in the surface soils (−18.5‰ at Rockefeller and nearly −19.5‰ at Fall Leaf). Both native prairies became more positive

Table 4. Comparison of combined species cover for all areas sampled at the Rockefeller and Fall Leaf sites by the multiple response permutation procedure.

Comparison	T *Statistic*	*Observed*	*Expected*	*Variance*	*Significance*
Rockefeller Site					
Native prairie vs. area closest	−25.055	0.893	1.035	0.319E−04	0.000
Native prairie vs. area middle distance	−13.462	0.877	0.940	0.217E−04	0.000
Native prairie vs. area farthest	−20.826	0.920	1.028	0.268E−04	0.000
Area closest vs. area middle distance	−7.469	0.843	0.882	0.271E−04	0.000
Area closest vs. area farthest	−7.034	0.900	0.937	0.273E−04	0.000
Area middle distance vs. area farthest	−4.970	0.879	0.903	0.227E−04	0.001
Fall Leaf Site					
Native prairie vs. area recently tilled	−29.048	0.700	0.899	0.469E−04	0.000
Native prairie vs. Conservation Reserve Program	−20.602	0.663	0.755	0.210E−04	0.000
Area recently tilled vs. Conservation Reserve Program	−33.456	0.668	0.839	0.260E−04	0.000

with depth, attaining values near −14 to −15‰ at similar depths between 25 and 45 cm. The most positive isotope values differed from the surface 1 cm values by 4.5‰. Carbon isotope values became more negative, again at greater depths, approaching −18‰ at a depth of 1 m at the Fall Leaf native prairie. The depth patterns in the native prairies were similar.

The Rockefeller replanted area showed no effect of depth on carbon isotope values ($p = 0.09$; $F = 2.2$) and differed from the native prairie by having very positive carbon isotope values in the near-surface soils. It was similar to the native prairie at other depths. This pattern was similar at the Fall Leaf site. There was no depth effect ($p = 0.08$, $F = 2.5$) across all profile samples, although the top two strata were more negative when tested alone than the 15–55 cm depths. When the native prairies were compared to the replanted treatments, only the top two samples at the Rockefeller replanted treatments differed significantly from and more positively than (0–1 cm, $p < 0.006$, $F = 27.5$; 1–5 cm, $p = 0.001$, $F = 67.9$) from the Rockefeller native prairie.

Discussion

The lack of establishment success of native prairie species five and 35 years after planting was evident from the

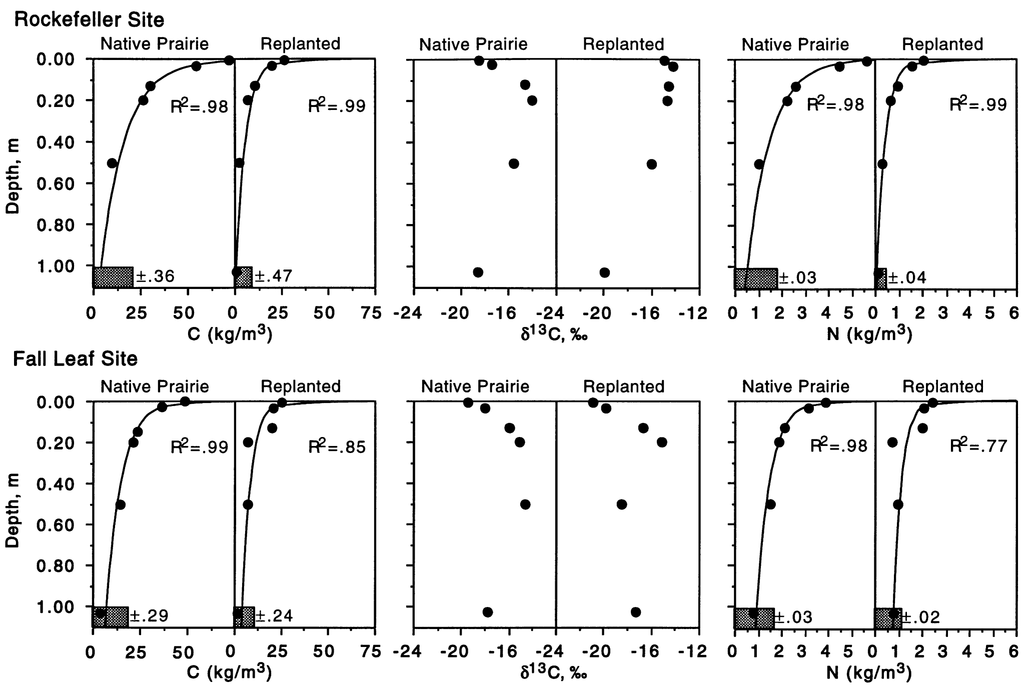

Figure 2. Change in the concentration of carbon, σ13C, and nitrogen with depth in native and farthest replanted prairies at the Rockefeller and Fall Leaf sites. Values are corrected for bulk density and are means of four samples. Each sample consists of four randomly selected and pooled samples. Bar indicates the amount of carbon or nitrogen (with standard errors) per 1 m² to a depth of 1 m. Equation: $y = a + b\,(\log(x))$.

data, which show statistical differences in cover for the majority of dominant species among native and replanted treatments at both the Rockefeller and Fall Leaf sites. These results are consistent with studies of other tallgrass prairie restoration sites (Cottam & Wilson 1966; Mlot 1990; Schramm 1990; Thompson 1992; Sperry 1994).

The lack of difference in plant species diversity (H') between areas sampled at the Fall Leaf site was likely caused by the large variability in the number of quadrats where species were located. Some species were widely common; others were locally rare. While the Fall Leaf native prairie had considerable cover by many conservative prairie species, the replanted areas had a higher proportion of cover by nonnative, early-successional species (in the CRP area, for example, the following weeds occurred: *Bromus japonicus* (cheat grass), *Conyza canadensis* (horseweed), *Ipomea lacunosa* (morning glory), and green and yellow foxtail. These early-successional species, which do not persist in prairie restorations (Mlot 1990; Schramm 1990; Sperry 1994), indicate that after five years the site is still undergoing significant colonization and successional competition. In contrast, there were significant differences in diversity at the Rockefeller tract between the native prairie and the replanted areas, which had insignificant numbers of annuals and nonnative species. It appears that, after the early-successional phase of restoration, some annual and nonnative species that are more adapted to the soil disturbance phase fail to survive. But they may not be replaced quickly by conservative native prairie species. Again, this is consistent with the findings of others (Cottam & Wilson 1966; Mlot 1990; Schramm 1990; Thompson 1992; Sperry 1994).

Analysis of Cover of Prairie Plant Guilds

The dominant cover of all areas sampled at both sites was by the C_4 grass guild. There were statistical differences between areas sampled at both the Rockefeller and Fall Leaf sites. For both big and little bluestem, it appears that these landscape-dominating planted C_4 grass species have not reached rates of cover comparable to those of the native prairies, perhaps due to long-term management differences such as the lack of burning or grazing.

The analysis of cover by guild is useful because species that may replace each other functionally or have small cover values can be combined into meaningful groups for analysis (Cornelius et al. 1991; Kindscher 1994; Kindscher & Wells 1995). Also, when major and minor species within a guild were grouped together for comparison, some chance distributions by individual species were essentially averaged, thus reducing the variance of the data.

The native prairie had statistically greater cover than the replanted areas for all forb guilds whose cover was more than a trace (Table 2). The differences between guilds for the areas sampled at both sites are not surprising, especially because the restored areas were reseeded relatively recently (to grasses at the Rockefeller site in 1957 and to grasses and forbs at the Fall Leaf site in 1989). When the Fall Leaf site was planted, the late-spring precipitation was below normal and the grass and forb seedlings did not establish well. Because a much greater amount of native grass than forb seed was planted, a considerably greater cover of native grasses was established. Nonetheless, our data from both sites show the slow rate of movement of native plant propagules from an adjacent or nearby source. It appears that the replanted areas have not yet reached a condition in which they can support as many native prairie species, which is evident from the significantly different plant community cover. They also are not receiving an equal number of propagules. In a study of seed rain and the seed bank at the Rockefeller site, the native prairie had significantly greater seed rain (700%), seed bank (300%), and seed rain diversity, than the adjacent replanted area (Schott 1993). This raises questions about the effects of the soil and nutrients on plant establishment. It should be noted that seed rain from the Fall Leaf native prairie is greatly reduced because of annual July haying of 98% of the native prairie, which significantly lowers its establishment potential for most species.

Carbon Isotope Data

The carbon isotope data for the native prairies at both sites suggest that the present vegetation is not in a long-term, steady state with the soil organic matter (SOM) at these sites. Under long-term conditions of stable climate and similar growth form or species composition, the carbon isotopic composition of SOM should be similar with depth and among particle sizes (Andreux et al. 1990; Tieszen & Archer 1990; Balesdent et al. 1993; von Fischer & Tieszen 1995). These are not the results we found (Fig. 2). We interpret our isotopic signals to document a relatively recent (perhaps decades) shift toward a C_3-derived signal in the carbon entering SOM. Such a recent shift is reflected in the signal from the portions of SOM that turn over the most rapidly, that of the near-surface samples (von Fischer & Tieszen 1995). In this study the carbon isotope values of the uppermost soil fractions (top 1.0 cm) should reflect the most recent input. A portion of this more negative signal is accounted for by the anthropogenic alteration of the atmospheric isotopic composition (Marino & McElroy 1991; Tieszen & Fagre 1993). As shown by von Fischer and Tieszen (1995), however, with actual data and simulated results based on the CENTURY model (Parton et al. 1987), this anthropogenic depletion can account only for a maximum of 1.5‰ depletion, or only one-third of the difference we have found.

We suggest that the carbon isotopic signal at a depth around 25 cm is closest to the undisturbed prehistoric prairie signal, because turnover at this depth should be slower than that near the surface. If we assume that the surface 1.0 cm has incorporated 100% of the anthropogenic signal in its SOM, we must still account for a difference of about 3‰. The only remaining explanation for this greater C_3 signal is that it resulted from a substantial increase in depleted carbon from C_3 plants. A carbon isotope value of -14‰ would suggest a C_3 composition of around 11% (1‰ = ca. 7.2% C_3 departure from the C_4 equilibrium value). The near-surface value of -17.0‰ (-18.5 corrected for 1.5‰ anthropogenic incorporation) represents a C_3 composition of around 32%. The difference between 11% and 32% should approximate the additional carbon signal coming into the SOM from C_3 sources. This increase is supported by the cover estimates (Table 2), in which C_3 species account for 41% of the cover at the Rockefeller native prairie and 22% at the Fall Leaf native prairie. Thus, this interpretation of the change in the native prairies from what we interpret to be an isotopic value approaching the recent prehistoric signals is in broad agreement with the cover estimates.

The return to more negative values at depths greater than 25 cm in the native prairies probably records some earlier Holocene signal in which the dominance of C_3 plants was greater. Confirmation of this interpretation requires C^{14} dating to determine a mean residence time for the SOM. These results are not yet available.

The isotope data from the replanted areas sampled at the Rockefeller site were especially interesting because they were very positive in the near-surface horizons, in contrast to those of the native prairies. This results from recent (in the last years to decades) isotopic input, which has been largely C_4. This recent signal would possess around 12% C_3 input to account for an isotopic value around -14‰. The cover estimates suggest an 8.1% C_3 input (Table 2, farthest area sampled), again in close agreement with our isotopic values.

If this interpretation is correct, however, it suggests some important relationships occurring in this replanted prairie grass system. It appears that this particular system did not sequester significant net carbon during the 35 years that it has been allowed to develop. The carbon values remain very low in this system, suggesting that during this period of recovery the carbon signal in the active SOM fractions may have been replaced (more recently showing a clear C_4 signal) but that very little if any net carbon accumulation occurred. This system also still has very low nitrogen content in the mineral components of the soil system (Fig. 2), which suggests that if nitrogen is strongly limiting, carbon accumulation in CRP lands is unlikely to develop even if carbon turnover is occurring. This has serious ramifications for any efforts aimed at managing these lands for carbon sequestration as a means of mitigating atmospheric CO_2 levels and climate change.

The isotopic pattern at the Fall Leaf site, unlike that of the Rockefeller replanted site, shows a near-surface pattern similar to that of the native prairies. This may be a direct reflection of the greater forb component in the Fall Leaf replanted areas (18.9% in the recently tilled area in Table 2) or the history of C_3 pasture and past C_3 agricultural crops. This greater forb component is probably caused by a mixture of the seed bank, planted seeds, and early-successional patterns of plant establishment.

Conclusions

The Rockefeller replanted areas show an influence of the native prairie as a source of propagules for species establishment. It appears that there is a distance effect, with the closest area sampled having greater establishment of propagules. This distance effect is being explored by ongoing research. Although site differences prevent statistical comparisons between the native prairies at the Rockefeller and Fall Leaf sites, both sites show difficulties in the establishment of native prairie species. Our data indicate that the substantially older Rockefeller replanted areas are more stable and have much less cover of agricultural weeds (primarily nonnative annuals on the Fall Leaf site). Difficulties in establishing forb richness by seed in restoration areas, especially at larger restoration sites (Warkins & Howell 1983; Thompson 1992), further emphasize the problems of achieving highly successful prairie restorations and raise many questions about the best management practices to encourage biodiversity. Specifically, would mowing, burning, or fertilizer treatments have sped up the restoration process?

In addition, the data on plant species composition remain statistically different between native and replanted areas at the two sites for many species, especially for conservative, "high-quality" prairie species (Schramm 1976; Mlot 1990). These differences occur at the Fall Leaf site, even though seeds of these species were planted. Differences in guild cover between native prairie and replanted areas offer insights that cannot be explained by individual species alone. Perhaps most telling is that the legume guild cover on the Rockefeller native prairie is more than 1000% larger than on any replanted area, while on the Fall Leaf native prairie it is more than 200% larger than on any replanted area. These legume species, many of them conservative, are believed to add nitrogen to the system (Weaver 1954, 1968). This indicates that the absence of native legumes on the replanted tracts may significantly delay the recovery of these systems. Finally, the community composition of plant species cover between treatments shows that the replanted treatments have not returned to a condition similar to that of the native prairie in terms of plant species composition. It is possible that these replanted prairies are reaching alternative stable states.

The isotopic data suggest a prehistoric prairie system that was dominated by a higher proportion of C_4 species than occurs today. The modern signal of the native prairie has shifted significantly toward the C_3 species and reflects the high incidence of C_3 forbs in these prairie relicts. This high percentage of forbs likely results from management practices that favored their expansion and enhanced their contribution to the near-surface soil organic matter isotopic signal. Adjacent CRP-like replanted areas do not show this forb abundance (with the exception of Fall Leaf CRP, which had a sizeable percentage of weedy annuals and planted forbs; Table 2). It has been assumed that ecosystem recovery, especially improvements to the soil, plant, and animal ecosystems, should occur as a side benefit of the CRP (Lindstrom et al. 1994). Our soil data show incorporation of the C_4 isotopic signal in the soils, but, even after 35 years following reseeding, increases in the soil organic matter content appear limited, since the values are substantially lower than those of the undisturbed prairie.

It appears that restoration of the originally highly diverse vegetation component of the tallgrass prairie ecosystem through the establishment of only four or five native warm-season grasses (such as has occurred through the CRP) will occur only over long periods of time (perhaps centuries) even when native prairies are adjacent. When no native prairies are nearby to serve as a seed source, recovery of native species to these recreated prairie communities will take even longer. With the increasing fragmentation of most of today's tallgrass prairie biome, complete vegetation restoration may not occur at all without thoughtful human assistance. From the perspective of prairie biodiversity, even efforts to substantially speed up the restoration process, such as at the 50-year-old Curtis Prairie (Sperry 1994) or the Fermi Lab prairie restoration in Illinois (Warkins & Howell 1983), have been slow at best. Policy makers and resource managers must realize that results from the longest-studied restoration attempts—tallgrass prairies in North America—indicate that we do not yet know if we can completely restore the biodiversity of an ecosystem. With questions remaining concerning the success of restoration of ecosystems, it is important to increase our efforts to protect the remaining tallgrass prairie and other threatened ecosystems.

Acknowledgments

The following people assisted us in the field or lab: J. Campbell, C. Picher, M. Chapman, D. DeJong, A. Fraser, and H. Loring. Helpful reviews of the manuscript were provided by D. Egan, D. Kettle, L. Kahn, M. Mehaffey, C. Lauver, and S. Taliaferro.

LITERATURE CITED

Andreux, F., C. Cerri, P. B. Vose, and V. A. Vitorello. 1990. Potential of stable isotope, 15N and 13C, methods for determining input and turnover in soils. Pages 259–275 in A. F. Harrison, P. Ineson, and D. W. Heal, editors. Nutrient cycling in terrestrial ecosystems. Elsevier Applied Science, London.

Balesdent, J., C. Girardin, and A. Mariotti. 1993. Site-related 13C of tree leaves and soil organic matter in a temperature forest. Ecology **74:**1713–1721.

Berlinger, B. P., and J. A. Knapp. 1991. Impacts of the conservation reserve program in the central Great Plains. Pages 46–49 in L. A. Joyce, J. E. Mitchell, and M. D. Skold, editors. The conservation reserve—yesterday, today and tomorrow. General technical report RM-203. U.S. Forest Service, Fort Collins, Colorado.

Burke, I. C., E. T. Elliott, and C. V. Cole. 1995*a*. Influence of macroclimate landscape position, and management on soil organic matter in agroecosystems. Ecological Applications **5:** 124–131.

Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995*b*. Soil organic matter recovery in semiarid grasslands: implications for the conservation reserve program. Ecological Applications **5:** 793–801.

Clarke, W. M., and T. B. Bragg. 1994. Movement of tallgrass prairie plant species from sod transplant into adjacent reestablished grassland. Prairie Naturalist **26:**67–81.

Cornelius, J. M., P. R. Kemp, J. A. Ludwig, and G. L. Cunningham. 1991. The distribution of vascular plant species and guilds in space and time. Journal of Vegetation Science **2:** 59–72.

Cottam, G., and H. C. Wilson. 1966. Community dynamics on an artificial prairie. Ecology **47:**88–96.

Daubenmire, R. F. 1959. Canopy coverage method of vegetation analysis. Northwest Science **33:**43–64.

Fitch, H. S., and E. R. Hall. 1978. A 20-year record of succession on reseeded fields of tallgrass prairie on the Rockefeller experimental tract. Special publication 4. Museum of Natural History, University of Kansas, Lawrence, Kansas.

Freeman, C. C., W. D. Kettle, K. Kindscher, R. E. Brooks, V. C. Varner, and C. M. Pitcher. 1991. Vascular Plants of the Kansas ecological reserves. Pages 23–47 in W. D. Kettle and D. O. Whittemore, editors. Ecology and hydrogeology of the Kansas Ecological Reserves and the Baker University wetlands. Open-file report 91–35. Kansas Geological Survey, Lawrence, Kansas.

Great Plains Flora Association. 1991. Flora of the Great Plains. University Press of Kansas, Lawrence, Kansas.

Jordan, W. R. 1983. Looking back: a pioneering restoration project turns fifty. Restoration and Management Notes **1(3):**4–10.

Kindscher, K. 1987. Edible wild plants of the prairie: an ethnobotanical guide. University Press of Kansas, Lawrence, Kansas.

Kindscher, K. 1992. Medicinal wild plants of the prairie: an ethnobotanical guide. University Press of Kansas, Lawrence, Kansas.

Kindscher, K. 1994. Rockefeller prairie: a case study of plant guild classification of a tallgrass prairie. Pages 123–140 in P. D. Lewis, editor. Proceedings of the 13th North American Prairie Conference, Windsor, Ontario, Canada. Ontario Parks and Recreation Department, Windsor, Ontario, Canada.

Kindscher, K., and P. V. Wells. 1995. Prairie plant guilds: an ordination of prairie plant species based on ecological and morphological traits. Vegetatio **117:**29–50.

Küchler, A. W. 1974. A new vegetation map of Kansas. Ecology **55:**586–604.

Laycock, W. A. 1991. The conservation reserve program: How did we get where we are and where do we go from here? Pages 1–6 in L. A. Joyce, J. E. Mitchell, and M. D. Skold, editors. The conservation reserve—yesterday, today and tomorrow. General technical report RM-203. U.S. Forest Service, Fort Collins, Colorado.

Lindstrom, M. J., T. E. Schumacher, and M. L. Blecha. 1994. Management considerations for returning CRP lands to crop production. Journal of Soil and Water Conservation **49:**420–425.

Magurran, A. E. 1988. Ecological diversity and its measurement. University Press, Princeton, New Jersey.

Marino, B. D., and M. B. McElroy. 1991. Isotopic composition of atmospheric CO_2 inferred from carbon in C_4 plant cellulose. Nature **349:**127–131.

McCune, B. 1993. Multivariate analysis on the PC-ORD system. August 1993 version. Biology Program. Oregon State University, Corvallis, Oregon.

McCune, B., and M. J. Mefford. 1995. PC-ORD. Multivariate analysis of ecological data. Version 2.0. MjM Software Design, Glenden Beach, Oregon.

Meide, C. 1988. Aldo Leopold. Univesity of Wisconsin Press, Madison, Wisconsin.

Mlot, C. 1990. Restoring the prairie. BioScience **40:**804–809.

Noll, M. G., C. J. Sorenson, and C. W. Rice. 1995. Biological condition of an agricultural soil six years after conservation reserve. Transactions of the Kansas Academy of Science **98:** 102–112.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal **51:**1173–1179.

Riebsame, W. E. 1990. The United States Great Plains. Pages 561–575 in B. L. Tuner, II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Marhews, and W. B. Meyer, editors. The Earth as transformed by human action: global and regional changes in the biosphere over the past 300 years. Cambridge University Press, Cambridge, United Kingdom.

SPSS, Inc. 1988. Statistical package of the social sciences. Chicago, Illinois.

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

Schott, G. W. 1993. Characterization of a native prairie and old-field implications for plant species invasibility. Unpublished M.S. thesis. University of Kansas, Lawrence, Kansas.

Schramm, P. 1976. The "do's and don'ts" of prairie restoration. Pages 139–150 in D. C. Glenn-Levin and R. Q. Landers, Jr., editors. Proceedings of the Fifth Midwest Prairie Conference. Iowa State University Extension, Ames, Iowa.

Schramm, P. 1990. Prairie restoration: a twenty-five year perspective on establishment and management. Pages 169–177 in D. D. Smith and C. A. Jacobs, editors. Proceedings of the 12th North American Prairie Conference. University of Northern Iowa, Cedar Falls, Iowa.

Sokal, R. R., and F. J. Rolf. 1995. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Company, New York.

Sperry, T. M. 1983. Analysis of the University of Wisconsin–Madison prairie restoration project. Pages 140–147 in R. Brewer, editor. Proceedings of the Eighth North American Prairie Conference. Department of Biology, Western Michigan University, Kalamazoo, Michigan.

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

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

Tieszen, L. L. 1994. Stable isotopes in the Great Plains: vegetation analyses and diet determinations. Pages 261–282 in D. W. Owsley and R. L. Jantz, editors. Skeletal biology in the Great Plains: a multidisciplinary view. Smithsonian Press, Washington, D.C.

Tieszen, L. L., and S. Archer. 1990. Isotopic assessment of vegetation changes in grassland and woodland systems. Pages 293–321 in C. B. Osmond, editor. Plant biology of the basin and range. Ecological studies 80. Springer Verlag, New York.

Tieszen, L. L., and T. Fagre. 1993. Carbon isotopic variability in modern and archaeological maize. Journal of Archaeological Science **20:**25–40.

von Fischer, J. C., and L. L. Tieszen. 1995. Carbon isotope characterization of soil organic matter from four tropical forests in Luquillo, Puerto Rico. Biotropica **27:**138–148.

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

Weaver, J. E. 1943. Replacement of true prairie by mixed prairie in eastern Nebraska and Kansas. Ecology **24:**421–434.

Weaver, J. E. 1950. Stabilization of Midwestern grasslands. Ecological Monographs **21:**39–60.

Weaver, J. E. 1954. North American prairie. Johnsen Publishing, Lincoln, Nebraska.

Weaver, J. E. 1968. Prairie plants and their environment. University of Nebraska Press, Lincoln.

Worster, D. 1979. Dust bowl: the southern plains in the 1930s. Oxford University Press, Cambridge, United Kingdom.

Zimmerman, G. M., H. Goetz, and P. W. Mielke, Jr. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology **66:**606–611.

Appendix 1. Average percent cover by species for three areas sampled at the Rockefeller site (30 plots/area).*

Species	Guild	Native Prairie (%)	Area Closest (%)	Area Middle Distance (%)	Area Furthest (%)	Significance
Acalypha virginica	annual	0.9	0.0	0.0	0.0	
Acer negundo	woody	0.0	0.0	0.1	0.0	
Achillea millefolium	spring ephemeral	0.0	0.1	0.0	0.0	
Agrostis hyemalis	C_3 grass	0.1	0.0	0.0	0.0	
Ambrosia artemisiifolia	annual	0.3	0.1	0.2	0.3	
Amorpha canescens	legume (woody shrub)	0.4	0.0	0.0	0.0	
Andropogon gerardii	C_4 grass	27.3	12.6	17.0	15.2	NS
Andropogon scoparius	C_4 grass	17.9	32.3	27.9	34.2	NS
Antennaria neglecta	spring forb	0.0	0.0	2.6	0.6	
Apocynum cannabinum	summer-fall forb	0.4	0.1	0.9	0.4	
Asclepias meadii	spring forb	0.1	0.0	0.0	0.0	
Asclepias tuberosa	spring forb	0.0	0.0	0.0	0.1	
Asclepias verticillata	summer-fall forb	0.0	0.2	0.0	0.0	
Asclepias viridiflora	spring forb	0.0	0.0	0.0	0.2	
Asclepias viridis	spring forb	0.0	0.0	0.1	0.0	
Aster oolentangiensis	summer-fall forb	0.2	0.0	0.0	0.0	
Aster pilosus	summer-fall forb	0.2	1.1	0.7	0.1	
Aster praealtus	summer-fall forb	5.9	0.6	3.3	2.5	**
Baptisia bracteata	legume	0.4	0.0	0.0	0.0	
Baptisia lactea	legume	0.0	0.0	0.0	0.1	
Bidens polylepis	annual	0.6	0.0	0.0	0.0	
Carex brevior	C_3 grass	0.4	0.0	0.0	0.7	
Carex sp.	C_3 grass	0.1	0.1	0.0	0.0	
Cassia chamaecrista	legume (annual)	0.4	0.0	0.0	0.0	
Ceanothus herbaceous	woody shrub	0.4	0.0	0.0	0.0	
Commandra umbellata	spring forb	0.4	0.6	0.3	0.0	
Cornus drummondii	woody shrub	0.2	0.0	0.0	0.1	
Croton capitatus	annual	0.0	0.0	0.0	0.1	
Dalea candida	legume	0.1	0.0	0.0	0.0	
Desmodium illinoense	legume	0.1	0.0	0.0	0.0	
Desmodium sessilifolium	legume	0.0	0.1	0.0	0.0	
Dichanthelium acuminatum	C_3 grass	0.1	0.4	0.1	0.1	
Dichanthelium oligosanthes	C_3 grass	0.2	0.1	0.0	0.0	
Echinacea pallida	spring forb	0.0	0.1	0.1	0.0	
Erigeron strigosus	annual	0.1	0.3	0.5	0.1	
Eryngium yuccifolium	summer-fall forb	4.7	4.6	4.4	0.0	
Eupatorium altissimum	summer-fall forb	0.1	0.0	0.0	0.0	
Eupatorium rugosum	summer-fall forb	0.1	0.0	0.0	0.0	
Euphorbia corollata	spring forb	0.7	0.2	0.1	0.1	
Euthamia gymnospermoides	summer-fall forb	0.0	0.0	0.3	0.5	
Fraxinus americana	woody	0.0	0.2	0.0	0.0	
Gentiana puberulenta	summer-fall forb	0.1	0.1	0.1	0.4	

(Continued)

Appendix 1. Continued.

Species	*Guild*	*Native Prairie (%)*	*Area Closest (%)*	*Area Middle Distance (%)*	*Area Furthest (%)*	*Significance*
Gnaphalium obtusifolium	annual	0.0	0.1	0.0	0.0	
Hackelia virginiana	summer-fall forb	0.0	0.0	0.0	0.1	
Helianthus annuus	annual	0.1	0.0	0.0	0.0	
Helianthus hirsutus	summer-fall forb	0.0	0.0	0.0	0.5	
Helianthus rigidus	summer-fall forb	5.3	4.7	9.0	0.1	***
Hypericum punctatum	summer-fall forb	0.0	0.0	0.1	0.1	
Hypoxis hirsuta	spring ephemeral	0.0	0.0	0.0	0.0	
Koeleria cristata	C_3 grass	0.1	0.0	0.0	0.0	
Lactuca serriola	nonnative	0.0	0.0	0.0	0.0	
Lespedeza capitata	legume	0.9	0.1	0.1	0.0	
Lespedeza violacea	legume	0.0	0.0	0.0	0.0	
Linum sulcatum	annual	0.0	0.0	0.0	0.1	
Muhlenbergia racemosa	C_4 grass	0.5	0.0	0.0	0.0	
Oenothera villosa	annual	0.1	0.0	0.0	0.0	
Oxalis dillenii	spring forb	0.1	0.0	0.1	0.1	
Panicum virgatum	C_4 grass	0.4	2.0	6.1	14.8	***
Physalis pumila	summer-fall forb	0.0	0.0	0.0	0.0	
Plantago virginica	annual	0.0	0.0	0.0	0.0	
Polygala verticillata	annual	0.1	0.0	0.0	0.0	
Pycnanthemum tenuifolium	summer-fall forb	0.3	2.0	0.4	0.1	
Rhus glabra	woody shrub	1.2	0.0	0.0	0.0	
Rosa arkansana	woody shrub	0.0	0.1	0.1	0.0	
Rubus ostryifolius	woody shrub	0.3	0.0	0.0	0.0	
Ruellia humilis	spring forb	0.1	0.2	0.0	0.1	
Salvia azurea	summer-fall forb	0.2	0.1	0.0	0.0	
Scleria triglomerata	C_3 grass	0.0	1.0	1.9	0.0	
Silphium laciniatum	summer-fall forb	6.3	3.7	1.8	0.0	
Solanum carolinense	summer-fall forb	0.0	0.0	0.0	0.0	
Solidago canadensis	summer-fall forb	3.4	0.4	0.4	0.2	
Solidago missouriensis	summer-fall forb	0.8	0.3	0.7	0.1	
Solidago rigida	summer-fall forb	4.7	2.7	2.6	0.9	
Sorghastrum nutans	C_4 grass	2.4	3.4	5.7	9.6	NS
Sporobolus asper	C_4 grass	0.0	25.3	12.6	18.1	***
Sporobolus heterolepis	C_4 grass	8.8	0.0	0.0	0.0	***
Toxicodendron radicans	woody	0.0	0.0	0.1	0.0	
Tridens flavus	C_3 grass	0.0	0.0	0.0	0.0	
Tripsacum dactyloides	C_4 grass	1.6	0.0	0.0	0.0	
Ulmus rubra	woody	0.0	0.1	0.0	0.0	
Vernonia baldwinii	summer-fall forb	0.0	0.0	0.1	0.0	
Viola pedatifida	spring ephemeral	0.2	0.0	0.0	0.0	
Total		100.0	100.0	100.0	100.0	

*For all species with cover over 5% in at least one treatment (in bold), we performed analysis of variance using the nonparametric Kruskal-Wallis test and a Bonferroni correct.
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.
NS = not significant. Species names from the Flora of the Great Plains (Great Plains Flora Association 1991).

Appendix 2. Average percent cover by species for three areas sampled at the Fall Leaf site (30 plots/area).*

Species	*Guild*	*Native Prairie (%)*	*Area Recently Untilled (%)*	*Conservation Reserve Program (%)*	*Significance*
Acalypha virginica	annual	0.2	0.1	0.2	
Achillea millefolium	spring ephemeral	0.1	0.0	0.0	
Ambrosia artemisiifolia	annual	0.0	0.0	3.8	
Ambrosia trifida	annual	0.0	0.1	0.0	
Amorpha canescens	legume (woody shrub)	0.6	0.0	0.0	
Ampelopsis cordata	woody	0.0	0.0	0.1	
Andropogon gerardii	C_4 grass	26.5	3.6	9.3	NS
Andropogon scoparius	C_4 grass	33.9	7.2	16.6	NS
Andropogon virginicus	C_4 grass	0.0	0.1	0.1	
Antennaria neglecta	spring forb	0.9	0.0	0.0	
Aristida basiramea	C_4 grass	0.3	0.0	0.0	
Aster ericoides	summer-fall forb	0.5	0.0	0.0	
Aster pilosus	summer-fall forb	0.2	0.4	3.3	
Aster sericeus	summer-fall forb	0.2	0.0	0.0	
Baptisia bracteata	legume	0.1	0.0	0.0	
Bidens polylepis	annual	0.0	0.1	0.1	
Bouteloua curtipendula	C_4 grass	9.3	2.8	3.1	***
Bromus japonicus	nonnative	0.0	0.1	0.0	
Carex sp.	C_3 grass	0.1	0.1	0.0	
Cassia chamaecrista	legume (annual)	0.0	0.6	0.5	
Ceanothus herbaceous	woody shrub	0.7	0.0	0.0	
Cirsium altissimum	summer-fall forb	0.0	0.0	0.1	
Conyza canadensis	annual	0.0	0.1	0.2	
Coreopsis palmata	spring forb	1.5	0.0	0.1	
Cornus drummondii	woody shrub	0.0	2.0	0.1	
Crotolaria sagittalis	legume (annual)	0.0	0.0	0.1	
Cyperus sp.	C_4 grass	0.0	0.1	0.0	
Dalea candida	legume	0.2	0.0	0.0	
Dalea purpurea	legume	0.1	0.1	0.0	
Desmodium illinoense	legume	0.5	2.4	0.0	
Desmodium sessilifolium	legume	0.2	0.3	0.0	
Dichanthelium acuminatum	C_3 grass	0.0	0.9	0.0	
Dichanthelium oligosanthes	C_3 grass	0.0	0.1	0.0	
Echinacea pallida	spring forb	0.7	0.0	0.0	
Eragrostis spectabilis	C_4 grass	0.9	0.0	0.0	
Eragrostis trichodes	C_4 grass	0.0	2.2	1.2	
Erigeron strigosus	annual	0.4	0.2	4.8	
Euphorbia corollata	spring forb	0.2	0.0	0.0	
Euphorbia dentata	annual	0.0	0.0	0.1	
Euphorbia nutans	annual	0.0	0.0	0.1	
Fragaria virginiana	spring forb	0.1	0.0	0.7	
Geum canadense	spring ephemeral	0.0	0.2	0.0	
Gleditsia triacanthos	woody	0.0	0.0	0.3	
Gnaphalium obtusifolium	annual	0.0	0.1	0.0	
Helianthus tuberosus	summer-fall forb	0.0	0.0	0.2	
Heterotheca latifolia	annual	0.0	0.0	5.9	***
Ipomoea lacunosa	annual	0.0	0.0	0.1	

(Continued)

Appendix 2. Continued.

Species	Guild	Native Prairie (%)	Area Recently Untilled (%)	Conservation Reserve Program (%)	Significance
Juglans nigra	woody	0.0	0.9	0.0	
Lactuca sp.	spring forb	0.1	0.0	0.0	
Leptoloma cognatum	C_4 grass	0.7	0.9	0.2	
Lespedeza capitata	legume	0.0	0.1	0.4	
Lespedeza sericea	nonnative	0.0	0.1	0.0	
Lespedeza stipulacea	nonnative	0.1	0.0	0.0	
Linum sulcatum	annual	0.2	0.0	0.0	
Maclura pomifera	woody	0.0	1.5	0.0	
Muhlenbergia schreberi	C_4 grass	0.0	5.5	0.0	***
Oxalis dillenii	spring forb	0.1	0.0	0.0	
Panicum virgatum	C_4 grass	0.4	9.6	4.7	***
Parthenocissus quinquefolia	woody	0.0	0.1	0.0	
Paspalum setaceum	C_3 grass	0.1	0.0	0.0	
Physalis pumila	summer-fall forb	0.0	0.1	0.0	
Potentilla arguta	spring forb	0.3	0.0	0.0	
Potentilla recta	nonnative	0.1	0.0	0.0	
Potentilla simplex	spring forb	0.1	0.0	0.0	
Prunus serotina	woody	0.1	0.0	0.0	
Pycnanthemum tenuifolium	summer-fall forb	0.1	0.0	0.0	
Rosa arkansana	woody shrub	0.3	0.1	0.2	
Rubus ostryifolius	woody shrub	0.0	2.2	0.0	
Rudbeckia hirta	summer-fall forb	0.8	0.0	0.9	
Ruellia humilis	spring forb	0.1	0.0	0.0	
Rumex acetosella	nonnative	0.0	0.0	0.1	
Rumex altissimus	spring forb	0.0	0.0	1.0	
Rumex crispus	nonnative	0.0	0.1	0.0	
Salvia azurea	summer-fall forb	0.6	0.0	0.0	
Scleria thriglomerata	C_3 grass	0.1	0.0	0.0	
Setaria faberi	nonnative	0.0	0.0	1.4	
Setaria viridis	nonnative	0.0	0.0	19.7	***
Solanum carolinense	summer-fall forb	0.0	0.2	0.2	
Solidago canadensis	summer-fall forb	0.0	0.1	0.1	
Sorghastrum nutans	C_4 grass	5.0	49.3	20.6	***
Sporobolus asper	C_4 grass	0.1	0.1	0.0	
Sporobolus heterolepis	C_4 grass	1.2	0.0	0.0	
Stipa spartea	C_3 grass	0.7	0.0	0.0	
Symphoricarpos orbiculatus	woody shrub	0.1	0.2	0.0	
Tephrosia virginiana	legume	6.4	0.0	0.0	***
Teucrium canadense	summer-fall forb	0.0	2.0	0.0	
Toxicodendron radicans	woody	0.0	1.0	0.0	
Tridens flavus	C_3 grass	4.4	2.4	0.8	
Ulmus rubra	woody	0.0	0.3	0.0	
Viola pedatifida	spring ephemeral	0.1	0.0	0.0	
Vitis sp.	woody	0.0	0.1	0.0	
Total		100.0	100.0	100.0	

*For all species with cover over 5% in at least one treatment (in bold), we performed analysis of variance using the nonparametric Kruskal-Wallis test and a Bonferroni correct.
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.
NS = not significant. Species names from the Flora of the Great Plains (Great Plains Flora Association 1991).