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Research Article

Twenty Years of Tallgrass Prairie Reconstruction and Restoration at Pawnee Prairie Natural Area, Missouri

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ABSTRACT

In 1996 the Missouri Department of Conservation purchased Pawnee Prairie, a 190-ha mix of remnant tallgrass prairie and formerly row-cropped prairie with varying degrees of *Festuca arundinacea* invasion and past cattle grazing intensities on rolling terrain in the central dissected till plains ecological section. Management actions implemented over the following 20 y included prescribed fire, herbicide treatments of invasive nonnative species, and seeding of local ecotype prairie seed. Concurrently, four vegetation monitoring transects were sampled for plant species composition and cover five times between 1996 and 2017. Each of the transects increased significantly over time in the following per-quadrat means: % native plant species cover, plant species conservatism, and cover-weighted plant species conservatism. At the site level, native grasses increased by 22%, nonnative grasses declined by 76%, native forbs increased by 91%, nonnative forbs declined by 94%, and native sedges declined by 37%. In 1996 the top species in importance value across all transects included weedy native species (e.g., *Dicanthelium lanuginosum*) and nonnative species (e.g., *Daucus carota*). By 2017 the top species had transitioned to characteristic prairie species (e.g., *Schizachyrium scoparium*). Ordination results documented compositional trends across all transects toward greater native species richness, cover, and species conservatism values. At Pawnee Prairie, 20 y of sustained prairie reconstruction and restoration practices applied across an area of differing land use histories resulted in significant gains in the natural quality of the site's vegetation, including a greater abundance of prairie flora matrix species and some conservative species.

Index terms: floristic quality assessment; plant community change; prairie reconstruction and restoration; tallgrass prairie

INTRODUCTION

In Missouri most of the tallgrass prairie has been converted to agriculture (Nelson 2010) as it has throughout the Midwest (Samson and Knopf 1994). A variety of conservation entities and private landowners are planting native prairie species to restore degraded but remnant (i.e., unplowed) tallgrass prairies and formerly cropped lands. Despite many tallgrass prairie restoration and reconstruction projects occurring within the central dissected till plains ecological section (Cleland et al. 2007), few projects have published the results of longer-term vegetation monitoring datasets (Larson et al. 2018). In general, many plant community restoration and reconstruction projects are of relatively short duration with no long-term monitoring (Trowbridge et al. 2017).

In 1996 when this project began, the overall management goal was to restore a more functioning prairie plant community at this site by utilizing a variety of management techniques (e.g., prescribed fire). Success at meeting this over-arching goal was defined (sensu Zedler 2007) as consisting of (1) decreasing the coverage of exotic plant species and (2) increasing the diversity and cover of native prairie plant species (i.e., Success Goals 1 and 2). The objectives of this vegetation monitoring project were to characterize the vegetation composition of Pawnee Prairie Natural Area (NA) across 20 y and to quantify the success (as defined above) of prairie reconstruction and restoration actions on the area. We wished to bridge the knowledge gap in quantitative long-term prairie reconstruction and restoration projects alluded to above with this study. Due to budgetary and staff time constraints the authors were unable to conduct a replicated experiment of these management actions at Pawnee Prairie NA. This is a case study of vegetation monitoring with the statistical scale of inference limited to the study site. However, this case study will provide managers with further guidance on similar tallgrass prairie restoration and reconstruction projects in the region.

METHODS

Study Site Description

Pawnee Prairie NA is a 190-ha state natural area owned and managed by the Missouri Department of Conservation (MDC) and located in northwestern Missouri (40°31′N, 94°8′W). The land was purchased in 1996 and consisted then of four primary vegetation types: formerly row-cropped prairie that had been seeded to tall fescue (*Festuca arundinacea* Schreb.) and heavily grazed by cattle; an admixture of formerly row-cropped prairie on ridges and remnant (untilled) prairie on side slopes that all had been seeded with fescue and moderately grazed by cattle; and remnant prairie with some fescue invasion and a history of either light or moderate cattle grazing. Due to the extreme scarcity of remnant prairie in northern Missouri the area was designated a state natural area in 2004. The site occurs on rolling terrain in the middle of the central dissected till plains ecological section (Figure 1) and is characterized by Adair loam soils (3–9% slopes) on the ridgetops, Adair clay loam (5–9% slopes) and

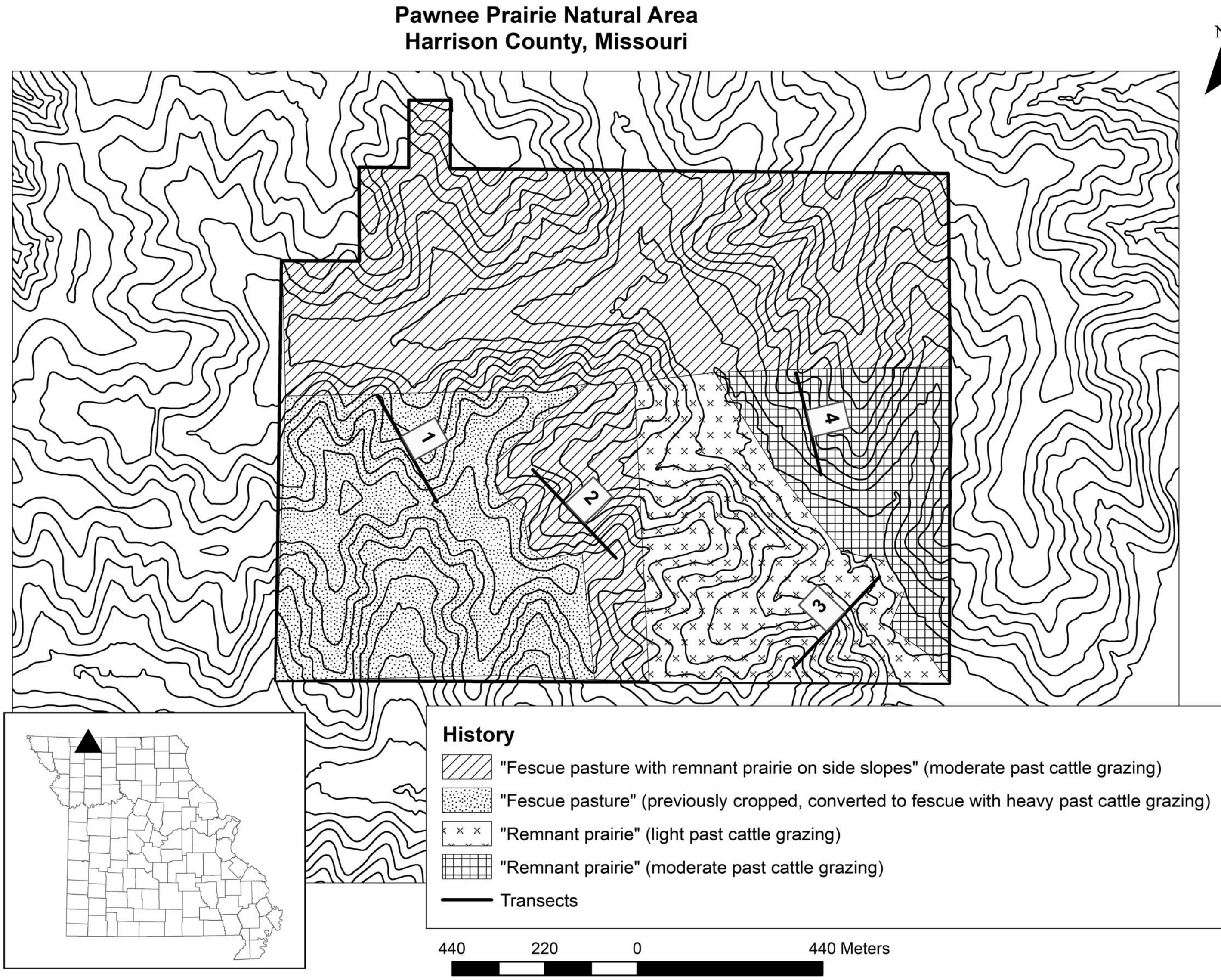

Figure 1.—Pawnee Prairie Natural Area in Harrison County, Missouri, showing locations of the sampling transects (3-m contours).

Shelby loam (9–20% slopes) on the side-slopes, and Zook-Colo silty clay loams in the valley bottoms (NRCS 2018).

A variety of typical prairie restoration and reconstruction practices (Packard and Mutel 1997) were applied to Pawnee Prairie NA over the last 20 y (Table 1). Across the area trees were cut and stump treated with triclopyr and fence row tree lines were removed by dozer between 1997 and 2002. Broadcast spraying of glyphosate and clethodim from vehicle-mounted boom sprayers typically in the fall and occasionally in the early spring when most native vegetation was still dormant was used to deaden tall fescue. Across Pawnee Prairie NA most of the prescribed fires occurred in March and April to effectively combat the tall fescue invasion across large areas of the site. However, one August and a few October and November burns did occur. These were utilized to prepare a seedbed for native plant seedings in the winter. Most of the area received at least 8 prescribed fires over the 20-y period. No wildfires occurred, and the prescribed fires were of moderate intensity. Native seedings were utilized both to establish prairie vegetation on formerly cropped lands and to enhance degraded remnant prairies. Native seed was typically broadcast in the winter. All native seed utilized was either from remnant prairie plants on site or from Helton Prairie NA (38 km away). Prairie seedings were typically high-mowed (approximately 15–30 cm) at least once the growing season following planting. A portion of the area was treated with a system of patch-burn cattle grazing in May to August of 2011–2013 (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006; Hovick et al. 2015; Briggler et al. 2017). Stocking rates ranged from 4 to 6 animal units/0.4 ha. This was done with the goal of increasing the vegetative structural heterogeneity of the prairie to provide more ideal habitat conditions for the greater prairie-chicken (*Tympanuchus cupido* L.), which is listed as state-endangered in Missouri. The aggressive nonnative sericea lespedeza (*Lespedeza cuneata* [Dum. Cours.] G. Don) has been spot-treated from all-terrain vehicles in the summer, primarily with triclopyr and fluroxypyr, across most of the area beginning in 2005 and continuing through 2017.

Vegetation Sampling

Four permanent 300 m long transects were established in 1996 that covered the same range of soil types and landforms, but areas of different land management histories (Figure 1, Table 1). Transect beginnings were chosen and not randomly assigned. Sampling points were located at 15-m intervals along the transect, and at each sampling point a 0.25-m^2 quadrat was established on a random perpendicular side of the transect, 2 m offset from the line, for a total of 20 quadrats per transect. Quadrats were randomized with respect to the transect in this way each sampling year. Within each quadrat all vascular plant species were identified to species or genera (Yatskievych 1999, 2006, 2013). The quadrats were sampled five times, always in August, in 1996, 2001, 2013, 2015, and 2017. In 1996 taxa in the genera *Carex*, *Dicanthelium*, *Juncus*, and *Rubus* were only identified to the generic level, and Daubenmire (1959) cover classes were used to estimate the aerial cover of all vascular plant species rooted in the quadrat. Beginning in 2001, all species were identified to the specific level and straight percent cover estimates were utilized.

Data Analyses

Plant species cover and frequency data were used to calculate relative importance values (RIVs, sensu Curtis 1959) as follows:

$$Relative\ cover = \frac{cover\ of\ species\ i}{\sum(cover\ of\ all\ species\ per\ 0.25\ m^2\ per\ transect)} * 100$$

$$Relative\ frequency = \frac{frequency\ of\ species\ i}{\sum(frequency\ of\ all\ species\ per\ 0.25\ m^2\ per\ transect)} * 100$$

$$Relative\ Importance\ Value\ (RIV)\ of\ species\ i = \frac{Relative\ cover + Relative\ frequency}{2}$$

To address specific species' level response in relation to Success Goals 1 and 2, we calculated RIVs for species commonly found within each sampling event. Descriptive statistics for the percent native vegetation cover per quadrat and the number of native species per quadrat were calculated for different transect and year combinations. For the 1996 data we utilized cover class midpoints for the analyses. For example, a species with Daubenmire cover class one (0–5%) was reassigned a cover value of 2.5%. For the univariate analyses, taxa identified only to the generic level in 1996 were assigned a "best fit" species based on field notes from subsequent years.

To further address vegetation quality and measure Success Goal 2, we utilized a floristic quality assessment approach (Matthews et al. 2015; Freyman et al. 2016). Coefficients of Conservatism (C values) assigned to Missouri's flora (Ladd and Thomas 2015) were used to examine changes in the natural quality of the plant communities on the study site. Remnant-dependent, habitat-specialist species have higher C values whereas ruderal species have lower values. For example, *Ambrosia artemisiifolia* L. has a C of 0 whereas *Drymocallis arguta* Pursh has a C of 10. For each of the 0.25-m^2 quadrats, we calculated species richness, the mean Coefficient of Conservatism (mean C), and the cover-weighted mean C, as follows:

$$Species\ Richness\ (S) = Number\ of\ species\ (native + adventive)\ per\ 0.25\ m^2$$

$$Mean\ C = \frac{\sum C}{S}$$

$$Total\ Cover\ (T) = \sum\left(cover\ of\ all\ species\ per\ 0.25\ m^2\right)$$

$$Cover - Weighted\ Mean\ C = \frac{\sum_{i=0}^{n}(C\ value\ species\ i * cover\ species\ i)}{T}$$

where C is the C value for each unique species (both native and adventive) encountered in the quadrat. Adventive species were assigned a C value of 0 (Francis et al. 2000).

One-way analysis of variance (ANOVA) and Tukey's honestly significant difference test (HSD) were used to test changes in vegetation metrics across years within a transect as well as among transects for 1996 and 2017. Nonmetric multidimensional scaling (NMS) using PC-ORD (McCune and Mefford 2011) was used to ordinate each sampling year's species or taxa group's occurrence data. Each species' or taxa group's occurrence count per transect and year combination (four transects, five years of sampling) was used as a presence surrogate in the ordination matrix. Species that occurred in less than 1% of the data set were removed prior to analysis, leaving 138 of the 254 species. We selected 500 runs of real and 500 runs of simulated data and the Bray-Curtis/Sorensen distance measure in PC-ORD. Variables of interest in the secondary matrix included the mean C value, mean native cover, and mean native richness for each transect and year combination. For taxa groups not identified to the species level in 1996 we assigned the mean C value for all species identified in that genera in later sampling years.

Multiple response permutation procedure (MRPP) was used in PC-ORD to determine if the average of the within-group compositional variation was less than the average of the dissimilarities between random samples drawn from the entire population (McCune and Mefford 2011). We used the Bray-Curtis/Sorensen distance measure and the default weighting option (the number of unique distances calculated among *n* sampling units: *n/sum*(*n*)). MRPP provides a chance-corrected within-group agreement (*A*) value, where *delta* is the overall weighted mean of within-group averages of the pairwise dissimilarity among sample units and *E* is the expected *delta*, calculated as an average of all permutations:

$$A = 1 - delta/E(delta)$$

A values close to 1 indicate higher within-group homogeneity, and *P* values are commonly interpreted to refer to differences between group comparisons (McCune and Mefford 2011).

Table 1.—Initial site conditions and land management history of the transects.

	Transect 1 (T1)	Transect 2 (T2)	Transect 3 (T3)	Transect 4 (T4)
Starting Land Condition in 1996	"Fescue pasture" (previously cropped, converted to fescue with heavy past cattle grazing)	"Fescue pasture with remnant prairie on side slopes" (moderate past cattle grazing)	"Remnant prairie" (light past cattle grazing)	"Remnant prairie" (moderate past cattle grazing)
Year				
1996	April - land purchased	April - land purchased	April - land purchased	April - land purchased
1997	September - trees removed	September - trees removed	September - trees removed	September - trees removed
1998	April - prescribed fire	April - prescribed fire	April - prescribed fire	April - prescribed fire
1999	April - prescribed fire; October - broadcast sprayed with glyphosate	April - prescribed fire	April - prescribed fire	April - prescribed fire
2000	March - prescribed fire; April - broadcast sprayed with glyphosate; May - planted seed from Helton Prairie NA (38 km away); Summer - mowed	April - prescribed fire	April - prescribed fire	April - prescribed fire
2001		April - prescribed fire; October - broadcast sprayed with glyphosate; November - prescribed fire		
2002	March - prescribed fire	January - broadcast seed from on-site nursery and Pawnee Prairie NA; August - mowed	October - prescribed fire	October - prescribed fire; November - sprayed with clethodim
2003				January - broadcast seed from Helton and Pawnee Prairie NAs
2005	March - prescribed fire; Summer - spot sprayed sericea lespedeza[a] with triclopyr and fluroxypyr	March - prescribed fire	March - prescribed fire	March - prescribed fire; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr
2006		Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr		
2007		November - broadcast sprayed with glyphosate	April - prescribed fire; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	April - prescribed fire
2008	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr; August - prescribed fire; November - broadcast sprayed with glyphosate		Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr
2009	April - prescribed fire	January - broadcast seed from Pawnee Prairie NA		
2010	March - prescribed fire; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr; November - broadcast sprayed with glyphosate	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr; mowed	March - prescribed fire; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	March - prescribed fire; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr
2011	May to August - grazing with cattle (stocking rate of 4-6 animal units/0.4 ha); Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	April - prescribed fire; May to August - grazing with cattle (stocking rate of 4-6 animal units/0.4 ha); Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	May to August - grazing with cattle (stocking rate of 4-6 animal units/0.4 ha) on part of site; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr
2012	May to August - grazing with cattle (stocking rate of 4-6 animal units/0.4 ha); Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	May to August - grazing with cattle (stocking rate of 4-6 animal units/0.4 ha); Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	April - prescribed fire; May to August - grazing with cattle (stocking rate of 4-6 animal units/0.4 ha) on part of site; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr; November - broadcast sprayed with glyphosate	April - prescribed fire; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr

Table 1.—Continued.

	Transect 1 (T1)	Transect 2 (T2)	Transect 3 (T3)	Transect 4 (T4)
2013	April - prescribed fire; May to August - grazing with cattle (stocking rate of 4-6 animal units/0.4 ha); Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	May to August - grazing with cattle (stocking rate of 4-6 animal units/0.4 ha); Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	May to August - grazing with cattle (stocking rate of 4-6 animal units/0.4 ha) on part of site; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr
2014	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr
2015	March - broadcast sprayed with glyphosate; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	February- broadcast seed from Pawnee Prairie NA; March- sprayed with glyphosate; April - prescribed fire; Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr; mowed	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr
2016	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr
2017	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr	Summer - spot sprayed sericea lespedeza with triclopyr and fluroxypyr
Total # of prescribed fires	8	9	8	8

[a] *Lespedeza cuneata* [Dum. Cours.] G. Don

RESULTS

Mean percent native vegetation cover per quadrat significantly increased between 1996 and 2017 for all of the transects (Figure 2; ANOVA, Tukey's HSD; T1 $F_{4,95} = 14.66$, $P < 0.01$; T2 $F_{4,94} = 5.40$, $P < 0.01$; T3 $F_{4,87} = 5.02$, $P < 0.01$; T4 $F_{4,95} = 9.55$, $P < 0.05$). At the site level, the mean percent native vegetation cover per quadrat went from 45.34% (SE = 3.14) in 1996 to 83.30%

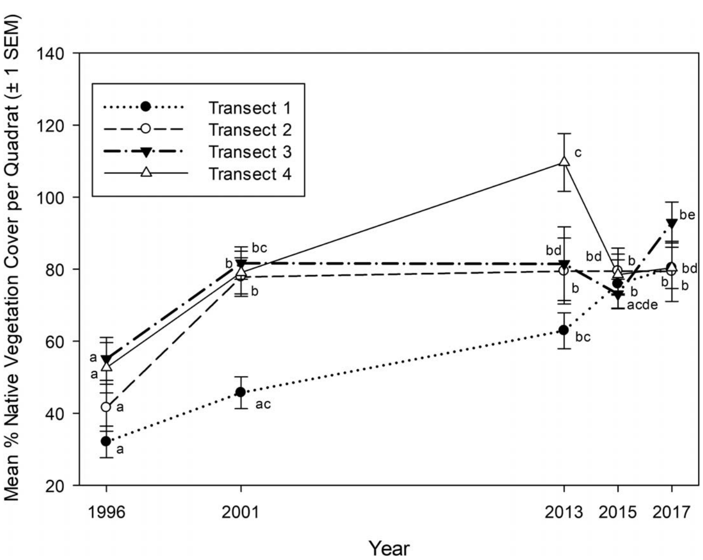

Figure 2.—Mean percent native vegetation cover per quadrat (± SE). Mean comparisons made within a transect across years. Year pairs that do not share at least one letter in common are significantly different (ANOVA and Tukey's HSD, $P < 0.05$).

(SE = 3.24) in 2017, an 84% increase. For T1 mean percent native vegetation cover per quadrat did not significantly ($P < 0.01$) increase until 2013 whereas this metric significantly ($P \leq 0.05$) increased for the other transects by 2001. There were some significant ($P \leq 0.05$) fluctuations in cover for T4 between years in the period 2013–2017 but 2017 cover was significantly greater than in 1996 and was not significantly different than 2015 cover. T1 increased the most in cover between 1996 and 2017 (+151%) and T4 increased the least (+53%). Mean percent native vegetation cover per quadrat differed significantly between the transects in 1996 (ANOVA; $F_{3,76} = 3.11$, $P = 0.03$) but not in 2017 (ANOVA; $F_{3,76} = 0.99$, $P = 0.40$). By 2017, transects 1, 2, and 4 were all at or close to 80% cover and T3 was at 93% cover.

The mean number of native plant species per quadrat significantly increased between 1996 and 2017 for T1 and T3 (Figure 3; ANOVA, Tukey's HSD; T1 $F_{4,95} = 18.43$, $P < 0.01$; T3 $F_{4,87} = 8.56$, $P < 0.01$). For T2 only 1996 versus 2015 native plant species density was significantly different (ANOVA, Tukey's HSD; $F_{4,94} = 5.03$, $P < 0.01$). T4 was significantly different in native species density between 1996 versus 2013 and 2015 (ANOVA, Tukey's HSD; $F_{4,95} = 8.29$, $P < 0.05$) but not 2017. At the site level, the mean number of native species per quadrat went from 7.5 (SE = 0.3) in 1996 to 11.46 (SE = 0.35) in 2017, a 53% increase. T1 increased the most in native species density between 1996 and 2017 (+100%) and T4 increased the least (+27%). In 1996 the mean number of native plant species per quadrat significantly differed between the transects (ANOVA; $F_{3,76} = 7.03$, $P < 0.01$) but not in 2017.

Mean C per quadrat significantly increased between 1996 and 2017 across all transects (Figure 4; ANOVA, Tukey's HSD: T1 $F_{4,95} = 83.66$, $P < 0.01$; T2 $F_{4,94} = 24.54$, $P < 0.01$; T3 $F_{4,87} = 24.62$, $P < 0.01$; T4 $F_{4,95} = 49.47$, $P < 0.01$). Mean C per quadrat

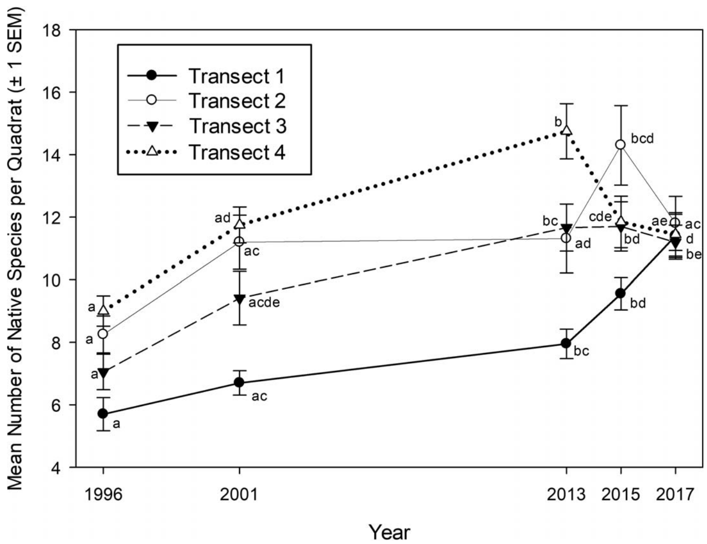

Figure 3.—Mean number of native plant species per quadrat (± SE). Mean comparisons made within a transect across years. Year pairs that do not share at least one letter in common are significantly different (ANOVA and Tukey's HSD, $P < 0.05$).

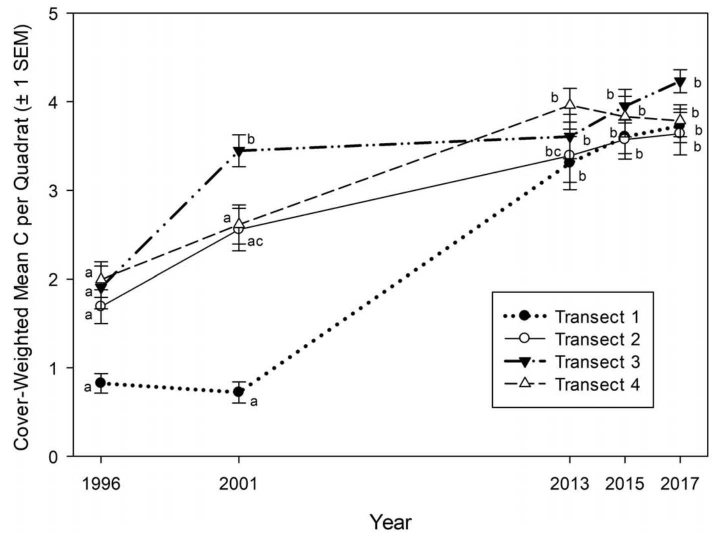

Figure 5.—Cover-weighted mean C per quadrat (± SE). Mean comparisons made within a transect across years. Year pairs that do not share at least one letter in common are significantly different (ANOVA and Tukey's HSD, $P < 0.05$).

did not significantly increase for any of the transects until 2013 (Figure 4). The time period between 2001 and 2013 was when significant increases occurred across all the transects in mean C. After 2013, mean C leveled off and no significant increases occurred from 2013 to 2017 for all of the transects. At the site level mean C went from 1.85 (SE = 0.25) in 1996 to 3.58 (SE = 0.11) in 2017, an increase of 94%. T1 increased the most in mean C (+193%) over the 20 y while T4 increased the least (+71%). Mean C per quadrat differed significantly between the transects in 1996 (ANOVA; $F_{3,76} = 16.1$, $P < 0.01$) and 2017 (ANOVA; $F_{3,76} = 3.01$, $P = 0.03$), with T1 significantly lower than all other transects (Tukey's HSD; $P < 0.01$) in 1996 and significantly lower than T3 in 2017 (Tukey's HSD; $P = 0.03$).

Cover-weighted mean C per quadrat significantly increased between 1996 and 2017 across all transects (Figure 5; ANOVA, Tukey's HSD: T1 $F_{4,95} = 65.57$, $P < 0.01$; T2 $F_{4,95} = 11.83$, $P < 0.01$; T3 $F_{4,87} = 21.12$, $P < 0.01$; T4 $F_{4,95} = 18.15$, $P < 0.01$). Cover-weighted mean C per quadrat did not significantly increase for transects 1, 2, and 4 until 2013, whereas T3 significantly increased in this metric between 1996 and 2001 (Figure 5). Between 2013 and 2017 none of the transects increased significantly in cover-weighted mean C, having leveled off. At the site level, cover-weighted mean C went from 1.60 (SE = 0.27) in 1996 to 3.85 (SE = 0.13) in 2017, an increase of 141%. T1 increased the most in cover-weighted mean C (+353%) over the 20 y while T4 increased the least (+90%). Cover-weighted mean C per quadrat significantly differed between the transects in 1996 (ANOVA; $F_{3,76} = 7.76$, $P < 0.01$) with T1 lower than the other transects (Tukey's HSD; $P < 0.05$). In 2017 the transects did not significantly differ in this metric.

In 1996, 74% of the RIV across all transects was represented by species that were either nonnative or had C values in the range of 0–3 (Figure 6). By 2017, only 37% of the relative importance value was represented by such species. Likewise, the share of relative importance value for species with C values in the 4–6 range ("matrix prairie species" sensu Taft et al. 2006) doubled between 1996 and 2017, increasing from 24% to 57%. Even conservative species ($C \geq 7$) increased from 1% to 5% of the share of relative importance value during this time period. There was a general decrease in the relative importance of nonnative species during this time period (Figure 6). Weedy native species with annual life histories and C values of 0–1 such as *Erigeron annuus* (L.) Pers. and *Aristida oligantha* Michx., along with exotic species (C value 0), had greater representation of RIV across the transects in sampling years 1996, 2001, and 2013 (Figure 6). Likewise, shorter-lived more ruderal perennials

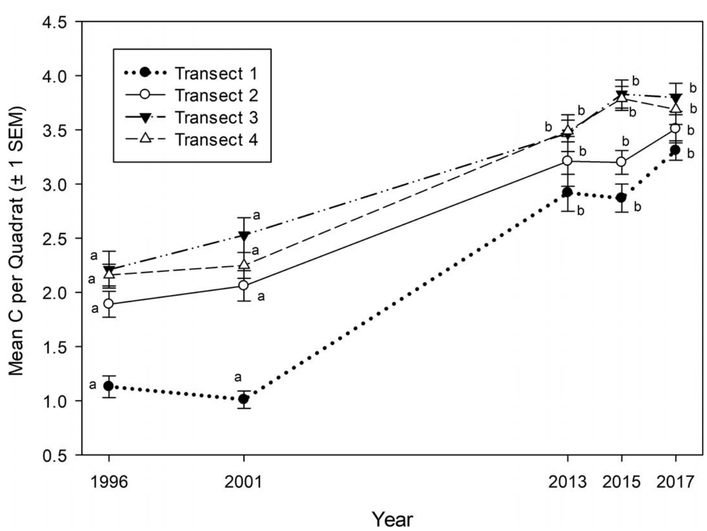

Figure 4.—Mean C per quadrat (± SE). Mean comparisons made within a transect across years. Year pairs that do not share at least one letter in common are significantly different (ANOVA and Tukey's HSD, $P < 0.05$).

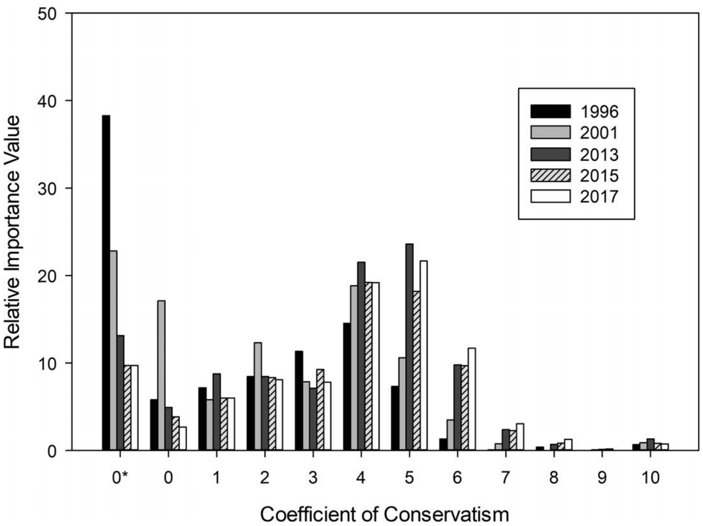

Figure 6.—Distribution of plant species' relative importance values by sampling year pooled across transects for C values. Note that the asterisk indicates nonnative species. The importance value for species with a particular C value is the sum of relative cover and relative frequency for those species divided by 2 for a transect by year combination. Relative importance values shown here are those values averaged across all transects for any year.

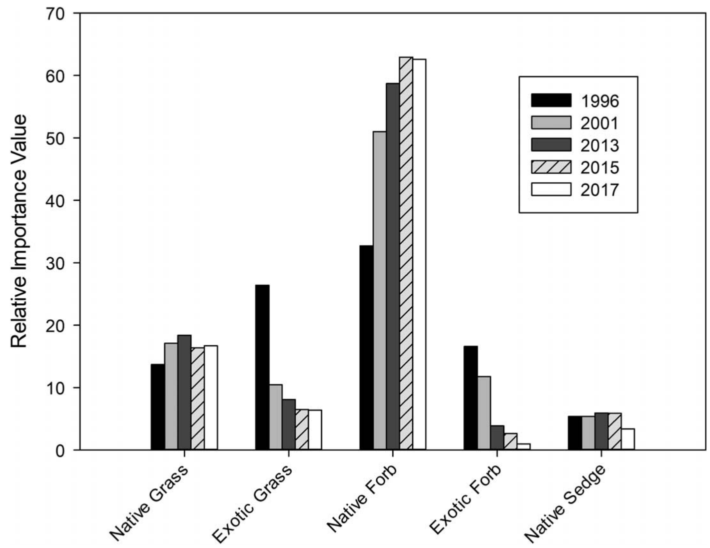

Figure 7.—Relative importance values of different plant species physiognomic groups by sampling year pooled across transects. The importance value for species within a physiognomic group is the sum of relative cover and relative frequency for those species divided by 2 for a transect by year combination. Relative importance values shown here are those values averaged across all transects for any year.

with C values of 2–3 such as *Dichanthelium lanuginosum* (Elliott) Gould and *Potentilla simplex* Michx. had greater abundances in the earlier years of this project. In contrast, matrix species (e.g., *Oligoneuron rigidum* [L.] Small, C value 5) increased in relative importance over the 20 y. Even some conservative species increased across time. For example, on T3, *Symphyotrichum oolentangiense* [Riddell] G.L. Nesom (C value 7), had an RIV of 0.3% in 1996 that increased to 5.9% by 2017. Trends in the RIVs of vegetation physiognomic groups across all four transects between 1996 and 2017 (Figure 7) showed a 22% increase in native grass RIV, a 76% decrease in exotic grass RIV, a 91% increase in native forb RIV, a 94% decrease in exotic forb RIV, and a 37% decrease in native sedge (i.e., *Carex* spp.) RIV. Table 2 demonstrates the shift in plant species composition across the transects for this sampling period.

The NMS ordination showed a 3-dimensional solution that achieved a stress value of 0.086, which is suitable for interpretation (Clarke 1993; Figure 8 shows the ordination in 2 dimensions). Mean C value, mean native cover, and mean native richness were all positively correlated with the *x* axis. Species *r* values negatively correlated with the *x* axis included *Daucus carota* L. (nonnative) and *Symphyotrichum pilosum* (Willd.) G.L. Nesom (C value 0). *Silphium integrifolium* Michx. (C value 4) and *Schizachyrium scoparium* (Michx.) Nash (C value 5) were positively correlated with the *x* axis. For the *y* axis, *Dichanthelium lanuginosum* (Elliott) Gould (C value 2) and *Oxalis stricta* L. (C value 0) were negatively correlated whereas *Carex* species (average C value 4) and *Sporobolus heterolepis* (A. Gray) A. Gray (C value 6) were positively correlated.

Based on the results of the MRPP, the site's composite species composition in 1996 was significantly different than in all the

Table 2.—The average relative importance values (across all transects) for those species constituting the top 50% of RIV. Asterisk indicates nonnative species.

1996 (all transects)			**2017 (all transects)**		
Species/Taxa Group	C Value	I.V.	Species/Taxa Group	C Value	I.V.
Poa pratensis L.	0*	12.5	*Schizachyrium scoparium* (Michx.) Nash	5	6.5
Festuca pratensis Schreb.	0*	9.7	*Sorghastrum nutans* (L.) Nash	4	5
Carex spp.	4	5.4	*Monarda fistulosa* L.	4	4.6
Daucus carota L.	0*	5	*Solidago altissima* L.	1	4.5
Symphoricarpos orbiculatus Moench	1	3.2	*Poa pratensis* L.	0*	4.5
Trifolium repens L.	0*	3.2	*Helianthus grosseserratus* M. Martens	4	4.1
Muhlenbergia frondosa (Poir.) Fernald	3	2.8	*Oligoneuron rigidum* (L.) Small	5	4
Agrimonia parviflora Aiton	5	2.6	*Ratibida pinnata* (Vent.) Barnhart	4	3.5
Dichanthelium lanuginosum (Elliott) Gould	2	2.6	*Symphyotrichum ericoides* (L.) G.L. Nesom	5	2.8
Teucrium canadense L.	2	2.5	*Rudbeckia subtomentosa* Pursh	5	2.5
			Pycnanthemum tenuifolium Schrad.	4	2.3
			Coreopsis tripteris L.	6	2
			Rubus ablatus L.H. Bailey	2	1.9
			Silphium integrifolium Michx.	4	1.9

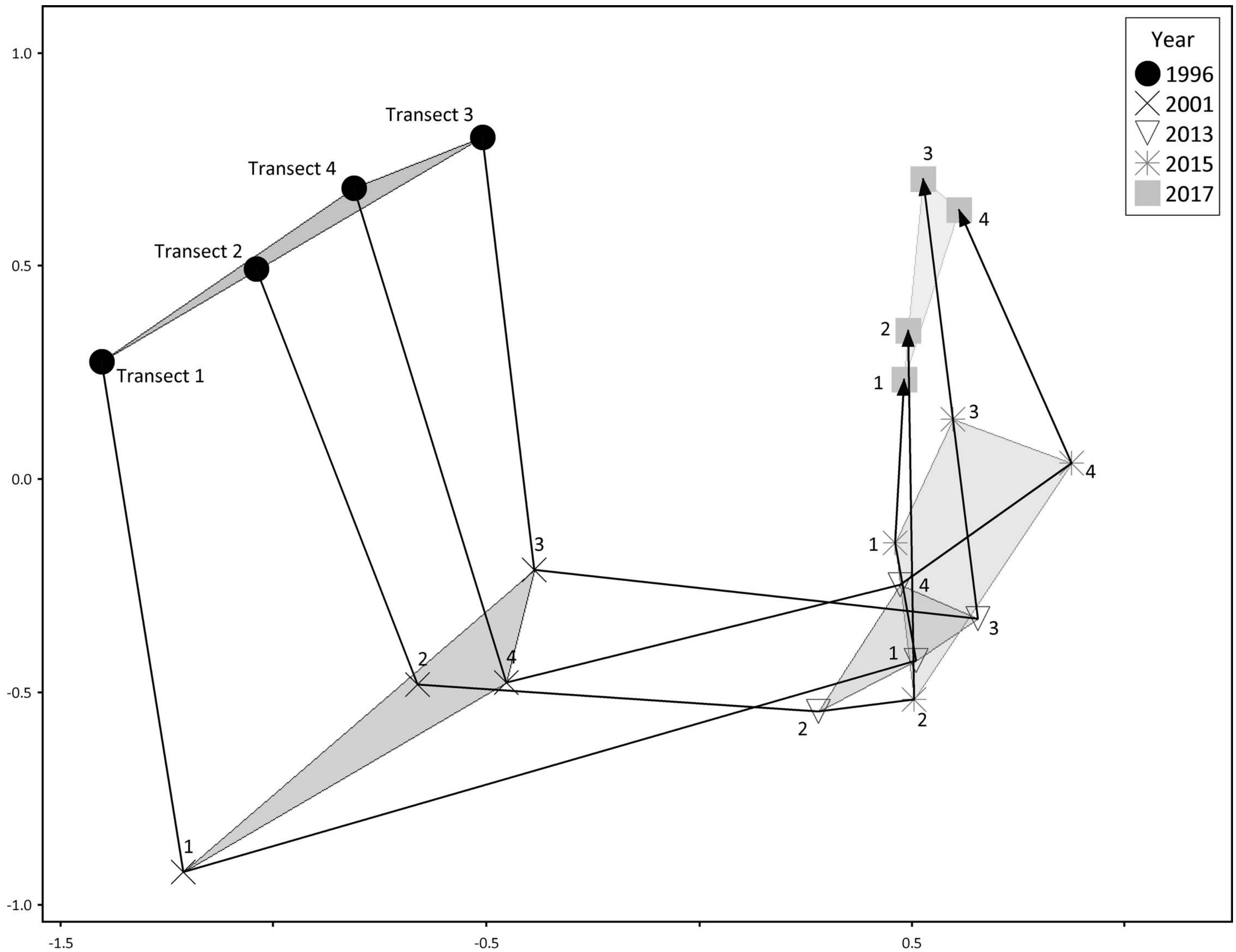

Figure 8.—Nonmetric multidimensional scaling (NMS) ordination of species'/taxa group's occurrence count per transect and year combination. A 3-dimensional solution was found with a final stress value of 0.086. Mean C, mean native cover, and mean native richness were all positively correlated with the *x* axis (r^2 values of 0.496, 0.566, and 0.918, respectively). Species *r* values negatively correlated with the *x* axis included *Daucus carota* (–0.948) and *Symphyotrichum pilosum* (–0.808). *Silphium integrifolium* and *Schizachyrium scoparium* were positively correlated with the *x* axis (0.722 and 0.705, respectively). For the *y* axis, *Dicanthelium lanuginosum* (–0.805) and *Oxalis stricta* (–0.733) were negatively correlated whereas *Carex* species (0.733) and *Sporobolus heterolepis* (0.700) were positively correlated.

other years ($P < 0.05$; Table 3). The 2001 species composition was also significantly different than the later sampling years. The 2015 and 2017 species composition were not significantly different. Across all sampling years, T1 was significantly different in species composition from T3 and T4 but not in relation to T2; T3 and T4 were not significantly different; T2 and T4 were not significantly different whereas T2 and T3 were.

DISCUSSION

Across a wide variety of metrics, the trend for all transects was a greater proportion of native vegetation composed of more matrix prairie species. All of the transects recorded significant increases in mean percent native vegetation cover (Figure 2), mean C (Figure 4), and cover-weighted mean C (Figure 5). By 2017 the transects did not significantly differ in terms of the mean percent native vegetation cover, mean number of native plant species, and cover-weighted mean C. This suggests, at least for this site, that despite the differing land use histories and initial site conditions of the transects, the management techniques applied here all resulted in improvements in the quality of the plant community (i.e., meeting Success Goals 1 and 2). Weedy native and nonnative plant species declined in abundance through time with a concomitant increase in characteristic native prairie species (Table 2; Figures 6 and 7) as described in Success Goal 1. However, despite the quantative similarities discussed above, qualititave differences in cover and composition exist, such that the remnant prairies are still easily distinguishable from the other areas to many practitioners. This illustrates a need for more sophisticated evaluation tools, and the

Table 3.—Multiple response permutation procedure (MRPP) results. For each comparison between year (A) and transect (B), the top value is the *A* statistic and the bottom value is the *P* value. (Values with $P < 0.05$ are in **bold**).

(A)	1996	2001	2013	2015	2017
1996		0.1560	0.1952	0.1781	0.1769
		0.0061	**0.0056**	**0.0055**	**0.0058**
2001	0.1569		0.1224	0.1421	0.2070
	0.0061		**0.0052**	**0.0057**	**0.0053**
2013	0.1952	0.1224		0.0060	0.0595
	0.0056	**0.0052**		0.5830	**0.0322**
2015	0.1781	0.1421	0.0060		0.0449
	0.0055	**0.0057**	0.5830		0.0625
2017	0.1769	0.2070	0.0595	0.0449	
	0.0058	**0.0053**	**0.0322**	0.0625	

(B)	Transect 1	Transect 2	Transect 3	Transect 4
Transect 1		0.0241	0.0756	0.0559
		0.1923	**0.0048**	**0.0331**
Transect 2	0.0241		0.0413	0.0011
	0.1923		**0.0483**	0.4283
Transect 3	0.0756	0.0413		0.0005
	0.0048	**0.0483**		0.4597
Transect 4	0.0559	0.0011	0.0005	
	0.0331	0.4283	0.4597	

importance of incoporating these monitoring tools at the beginning of a restoration project.

The ordination results show the transects changed in species composition through time and moved along the *x* and *y* axes toward an increasingly conservative flora. The MRPP demonstrated that these shifts in species composition were significant (Table 3). MDC described success for this prairie reconstruction and restoration project in 1996 as decreased cover of exotic plant species and an increased diversity and cover of native prairie plant species. Based on these goals the data from this study point to a successful project of restoring and reconstructing prairie at this site.

By 2017, transects 2, 3, and 4 all had mean C values $\geq$3.5, meeting Swink and Wilhelm's (1994) benchmark value for a plant community to be considered marginal natural area quality. However, these mean C values are relatively low compared to vegetation transects sampled on floristically rich prairie sites in Missouri's unglaciated prairie region, which often exceed values of 4.5 (Thomas 2016). Mean C values and cover-weighted mean C values appear to be leveling off after 2013 (Figures 4 and 5). Similar asymptotic trajectories of mean C have been reported for prairie (McIndoe et al. 2008) and wetland (Matthews et al. 2009) reconstructions in Indiana and Illinois, respectively. It is likely that due to the land use history and isolated nature of this site, future gains in floristic quality will be much slower and of smaller increments (Matthews et al. 2017). The use of cover-weighted mean C is more recent in the literature (Carter and Blair 2012; Bourdaghs 2014; Freyman et al. 2016), and benchmark values for this metric for Midwestern prairies are currently unavailable. It may be true that cover-weighted mean C does not add additional information that simple mean C offers. We report our values in an effort to contribute to future research despite our data's ultimate similarity in response by these two metrics.

One point of concern we note from the impacts of the various management actions is the decrease in native sedge RIV (Figure 7). This was the only native species physiognomic group to display a decline in abundance over the 20 y. We offer two possible alternate explanations for this. It could be that this decrease is related to glyphosate treatments of tall fescue in the fall and early spring when many sedges are green but most other native plants are dormant. Also, repeated spring (April) prescribed burns that were targeted against reducing tall fescue dominance may have negatively affected sedges. An alternate explanation would be that more weedy, low C value sedge species such as *Carex blanda* Dewey (C value 2) dominated the areas in the early years and were replaced by more conservative *Carex* and/or non-*Carex* flora. Sedges were often not targeted by early MDC seed harvest hand collection efforts, and many species shatter before traditional mechanical seed collection efforts occur, so they were likely underrepresented in the seed mixes. Since sedges were only identified to the generic level in the early years of the study, it is impossible to know the true cause of this decline. Future research should experimentally test the impacts of typical tall fescue control measures used in prairie restorations on sedges. In this case, increases in vegetation quality contingent upon reducing fescue via prescribed fire and herbicides may have resulted in a decline in native sedge cover.

Some studies have documented declines in ecological integrity with time after restoration, or especially, reconstruction (Camill et al. 2004; McLachlan and Knispel 2005; Hansen and Gibson 2014). To date this does not seem to be the case at Pawnee Prairie NA. Future monitoring may elucidate future changes in the plant communities of the site. Current infestations of nonnative sericea lespedeza and scattered areas of *Lotus corniculatus* L. (not reflected in the transect data yet) may stymie future gains in natural quality on the area. At Pawnee Prairie NA, 20 y of sustained and typical prairie reconstruction and restoration practices applied across an area of differing land use histories resulted in significant gains in the natural quality of the site's vegetation. Based on the initial management goals for the site, we can state that thus far this project appears to be a success in promoting native prairie species.

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