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Local Ecology Research Papers

Influence of Edge Effects on Tallgrass Prairie Species Diversity and Distribution

Miranda Lentz 2021

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Field Ecology 361 Professor Kathleen Shea December 15, 2021 Revised January 11, 2022

Abstract

North American tallgrass prairies are highly diverse ecosystems that have experienced near wholesale degradation over the last 200 years and now exist as highly-disturbed, fragmented patches. These edges are correlated with detrimental changes to community dynamics, plant community composition, invading species frequency, and abiotic variables like soil health and carbon storage, the effects of which mainly occur along the transition between adjacent habitats and extend into the habitat. This study sought to answer whether the St. Olaf Natural Lands prairie flora or their abiotic influencers experienced commonly-detrimental edge effects. Ultimately, biotic variables of species diversity and distribution were not influenced by the presence of an habitat edge, though the height of the most common species showed a significant reaction to edge distance. The year of site restoration was a strong influence on several abiotic factors (maximum wind speed and soil moisture) and points to the sites acting as unique microcommunities with differing species composition and richness but similar species diversity values and stem densities. The prairie communities in the St. Olaf Natural Lands currently do not experience the widescale negative edge effects from fragmentation, likely due to the careful management practices that include regular prescribed burnings to rejuvenate biodiversity.

Introduction

Anthropogenic land use frequently causes fragmentation in natural ecosystems, creating hard edges between forests or prairies with roads, agricultural fields, or highly-managed green spaces that do not resemble the natural biota. The frequency and severity of these edges are correlated with changes in physical or biotic response variables, occurring along the transition between adjacent habitats, a concept known as "edge effects" (López-Barrera et al. 2007). The mere presence of an edge to a habitat has been found to reduce species diversity and abundance as well as alter behavioral patterns and distribution of plants (Cully et al. 2003), birds (Beck et al. 2016), arthropods (Kuli-Révész et al. 2021), and a host of other invertebrates (Laurance et al. 2007). Edges also influence atmospheric and soil variables, like nutrient cycling, compaction, pollution, and availability of water (Piper 1995, Fletcher Jr 2005, Eckert 2016, Smith et al. 2016, Knee 2017). As ongoing fragmentation causes existing habitat patches to shrink, they experience an increase in the ratio of edge to total area, reducing the community's resilience to common disturbances like fire (Laurance et al. 2007), surrounding land use (Cully et al. 2003), predation (Kuli-Révész et al. 2021), species invasion (Koper et al. 2010), and extreme weather events

(Laurance et al. 2000). Outside of active prevention of further fragmentation, understanding how existing edges will affect unique ecosystems can lead to more effective and counteractive management strategies.

The tallgrass prairies of the North American Great Plains covered approximately 100 million hectares in the early 1880s, about 7 million ha of which existed in Minnesota, but less than 1% of that land remains intact after Euro-American settlement (Samson and Knopf 1994). Since then, historically homogenous tallgrass prairie communities have seen extreme fragmentation and invasion by alien species (Cully et al. 2003). This shrinkage signifies a massive loss in the abundance of seasonal species and carbon sequestration services (Okerman 1997, Eckert 2016). Dominant native tallgrass species include the C₄ grasses Andropogon gerardi (Big Bluestem), Sorghastrum nutans (Indian Grass), and Panicum virgatum (Switchgrass) (Cully et al. 2003). After a disturbance like fire, modern tallgrass prairies experience large shifts in diversity within the first three growing seasons. The first year post-fire is dominated by non-native weedy forbs, followed in the second year by native perennial composite forbs, and then stabilizing in species composition with C₄ grasses (Camill et al. 2004).

This study sought to determine the effects of interior habitat edges (not along the bordering highways) of the restored St. Olaf Natural Lands tallgrass prairie. I compared biotic metrics of grass and forb species diversity and health to determine the strength of edge effects on our current prairie composition. I also compared abiotic atmospheric and soil characteristics to determine if they had any possible influence on the biotic trends above or below-ground. Each of these variables were measured on a distance gradient from edge to center of three prairie patches distinguished by their year of restoration. The specific objectives of this study were to determine if the Natural Lands prairie species diversity and distribution or their abiotic influencers were influenced significantly by 1. the distance from a natural or manufactured prairie edge and/or 2. the site location, differentiated by the year of restoration.

Methods

Site Description and Method Overview

The St. Olaf Natural Lands in Northfield, MN (44.4703 N., 93.1925 W) include about 61 acres of restored prairie that house 25.40 native forb species, 10 native grass species, and a host of other non-native invaders (Knee, 2017). The lands were restored over time in patchwork sections from corn and soy agricultural use to a plant community resembling historic assemblages. Each section undergoes patchwork burnings every 2-5 years to maintain species diversity and deter invader takeover. This study investigated the biotic and abiotic qualities in three sections of the prairie that were restored in four-year increments: 1994, spring 1998, and spring 2002 (Figure 1). The 1994 and 2002 study sites shared edges with forest while the 1998 study site shares its edge with a wide recreational trail that itself borders forest.

The experiment followed line transect and plot methods described by Brower et al. (1998). At each restoration site, two 50 m transect lines were laid perpendicular to the closest edge (although the 1994 site had to run diagonal in order to avoid compounded edge effects from the second nearby recreational trail edge). During October 22–24, study plots were marked at 16.67 m increments (0, 16.67, 33.33, 50) and 1 m² quadrat frames were used to quantify grass and forb species density, stem density, and average species heights. Unidentifiable species were sampled, pressed, and identified at a later date. Abiotic measurements of maximum wind speed (knots), relative atmospheric humidity (% moisture), and temperature (°C) were taken at each plot with a Kestrel 3000 device during November 7–8. By this date, temperature was highly dependent on the sun's position and could not be controlled for with sampling time, so it was later dropped from analysis. Soil samples were also taken with a soil corer (sample volume was a consistent 47.752 cm³) and analyzed on November 13 in lab for percent moisture, bulk density (g/cm³), and percent organic matter.

Data Analysis

Soil samples were weighed before and after being oven-dried for over 48 hours at 105°C. Percent moisture determination used the following equation: $\frac{\text{weight of water}}{\text{dry weight of soil}} \times 100$. Water weight was calculated by subtracting the dry soil sample weight from the original soil sample weight. Bulk density determination used the following equation: $\frac{\text{dry weight of soil}}{\text{volume of sample (47.752 cm}^3)}$. Each of the soil samples were then put through 2 mm sieves and new samples between 4.5 g and 9.0 g were weighed before going into a muffle furnace at 500°C for four hours. The final weights were taken after the duration. Percent organic matter determination used the following equation: $\frac{\text{(weight after 105°C-weight after 500°C)}}{\text{weight after 105°C}} \times 100$. All final soil weights used in the above equations have subtracted the weight of the tin boats that held the samples.

The data were analyzed in RStudio 3.6.0 and Excel 16.54. All biotic and abiotic variables were subject to a 1-way ANOVA test with either the effect by edge or by site location as well as 2-way ANOVA tests investigating any interactions between the two explanatory variables. Post-hoc Tukey's HSD tests were used when ANOVAs suggested significant effects. The results of these relationships were visualized with overlaid box-whisker and violin plots or more streamlined line plots using the means from each variable. Shannon (H') and Simpson (Ds) biodiversity indices, and pairwise variance of Ds t-tests were conducted in excel.

Results

Biotic Variables

Fifteen species were identified across all sites, 46% of which were forbs and 54% of which were grasses. The forbs included Ambrosia artemisiifolia (Ragweed), Asclepias syriaca (Common Milkweed), Aster spp. (Aster flowers), Cirsium arvense (Canada Thistle), Helianthus spp. (Sunflowers), Monarda fistulosa (Wild Bergamot), and Solidago canadensis (Goldenrod). The grasses included Andropogon gerardi (Big Bluestem), Bouteloua curtipendula (Side Oats Grama), Elymus

canadensis (Canada Wild Rye), *Phalaris arundinacea* (Reed Canary Grass), *Schizachyrium scoparium* (Little Bluestem), *Sorghastrum nutans* (Indian Grass), and two unidentified Brome species dubbed spp. 1 and spp. 2.

Biotic measurements of species density, stem density, and average height were compared using all 15 species (Figure 2) as well as with only the four most common species. The variety of species present was not affected significantly by the plot distance from edges though there does seem to be a somewhat positive trend in mean species density from 2.5 to 4 as distance increases (Figure 2A, ANOVA, F-val = 1.046, df = 3, 20, p-val = 0.394). Species density was also not affected significantly by the year of site restoration (Figure 2C, ANOVA, F-val = 1.796, df = 2, 21, p-val = 0.191). The mean density of individual stems revealed non-significant positive trends for both distance from edge (Figure 2B, ANOVA, F-val = 1.783, df = 3, 20, p-val = 0.183) and year of site restoration (Figure 2D, ANOVA, F-val = 2.572, df = 2, 21, p-val = 0.1).

A look at the stem density and average species height with only the four most common species, two forbs and two grasses—Aster spp., S. canadensis, A. gerardi, and P. arundinacea—revealed strong effects by species, but not necessarily by edge or site (Figure 3, 4). S. canadensis occurrence was consistently more dense than A. gerardi by both edge (Figure 3A, 2-way ANOVA, F-val = 0.557(edge)/ 4.226(spp.), df = 3, 3, 38, p-val = 0.6466(edge)/ 0.0113(spp.)) and site (Figure 4A, 2-way ANOVA, F-val = 2.009(site)/ 3.395(spp.), df = 2, 3, 39, p-val = 0.1478(site)/ 0.0272(spp.)). Differences in average height were driven by A. gerardi outgrowing the other three species and had a significantly associated effect by edge (Figure 3B, 2-way ANOVA, F-val = 4.794(edge)/ 8.505(spp.), df = 3, 3, 38, p-val = 0.00627(edge)/ 0.00019(spp.)), but not by site (Figure 4B, 2-way ANOVA, F-val = 2.483(site)/ 11.283(spp.), df = 2, 3, 39, p-val = 0.0966(site)/ 1.82e-05(spp.)). The peak growing heights for both A. gerardi and S. canadensis occurred at moderate distances from the edges in the 16.6 and 33.3 m plots.

Diversity measures of species richness and the Shannon (H') and Simpson (Ds) indices were not significantly driven by distance from edge or year of site restoration. Flat counts of individuals showed a positive trend with increased edge distance and nearly every plot distance supported a larger percent of grass species than forb species (with the exception of 16.6 m) (Table 1). Species richness and Simpson diversity values were relatively even across edge distances, though Shannon diversity values suggested slightly lower diversity at the 0 m plots (Table 2). Pairwise comparisons of the Ds values confirmed in no strong effects by edge distance (Table 3). Summaries of individuals by site location showed no trends, but the ratio of grasses to forbs was quite different: the 1998 site was 26% forbs to 74% grasses, the 2002 site was 42% forbs to 58% grasses, and the 1994 site was 59% forbs to 41% grasses (Table 4). Species richness was also more uneven: the 1998 site supported 10 species, the 2002 site supported 9 species, and the 1994 site supported 7 species. However, those sites' Simpson diversity values were nearly identical (0.88, 0.88, 0.87, respectively) and the Shannon values were relatively close (0.90, 0.86, 0.81, respectively) (Table 5). Pairwise comparisons of the Ds values confirmed no strong effects on community diversity by site location, even with these trends in species composition differences (Table 6).

<u>Abiotic Variables</u>

The five abiotic variables relating to soil and atmospheric characteristics showed no trends influenced by edge distance (Figure 5). Edge effects were not present for soil moisture (Figure 5A, ANOVA, F-val = 0.255, df = 3, 20, p-val = 0.857), soil bulk density (Figure 5B, ANOVA, F-val = 0.082, df = 3, 20, p-val = 0.969), soil percent organic matter (Figure 5C, ANOVA, F-val = 0.561, df = 3, 20, p-val = 0.647), maximum wind speed (Figure 5D, ANOVA, F-val = 0.308, df = 3, 20, p-val = 0.819), or relative humidity (F-val = 0.014, df = 3, 20, p-val = 0.998). Similarly, site location effects were not present for soil bulk density (Figure 6B, ANOVA, F-val = 0.363, df = 2, 21, p-val = 0.7) or soil percent organic matter (Figure 6C, ANOVA, F-val = 1.368, df = 2, 21, p-val = 0.276).

The same five abiotic variables showed some significant differences driven by site location (Figure 6). The forest-edged 1994 and 2002 sites had soil that was significantly more moist than the recreational trail-edged 1998 site (Figure 6A, ANOVA, F-val = 9.757, df = 2, 21, p-val = 0.00101). The relationship between edge and site on mean soil percent moisture is visualized in Figure 7. In contrast, the recreational trail-edged 1998 site experienced significantly higher wind speeds than the forest-edged 1994 site (Figure 6D, ANOVA, F-val = 4.864, df = 2, 21, p-val = 0.0184). The relationship between edge and site on mean wind speed is visualized in Figure 8. Atmospheric relative humidity was also shown to be significantly higher in the 1998 site than the 1994 site, which in turn was significantly more humid than the 2002 site (Figure 6E, ANOVA, F-val = 250.4, df = 2, 21, p-val = 2.24e-15). Although the comparison between first two sites could be considered sound data, the drastic change between them and the 2002 site is likely due to the data being collected on different days, resulting in a confounding weather effect that cannot be accounted for reasonably.

Investigations into the possibility of an interaction effect between edge distance and site location resulted in some success, where soil moisture and bulk density both had p-values < 0.05 for interaction terms. However, upon using Tukey HSD tests on both 2-way ANOVAs, there were only a couple plot-site interactions, so it is more likely that the 2-way ANOVAs registered false positives due to the sheer number of variable relationship tests run.

Summary

In this study, edge effects were only detected in relation to the biotic changes in height of select species. Effects by site location were only detected in the abiotic characteristics of maximum wind speed and soil moisture content. Though comparisons of species richness and abundance through stem counts or diversity indices yielded no significant effects from edge or site, they suggested that the sites had notable changes in species compositions in terms of both forb-to-grass coverage and the types of forbs or grasses present.

Discussion

This study sought to answer whether the St. Olaf Natural Lands prairie species diversity and distribution or their abiotic influencers experienced commonly-detrimental edge effects. Across all eight variables measured, distance from an edge only had a significant effect on average species height, represented by optimal growth occurring at an intermediate distance from edge and center (Figure 3B). Ultimately, the Natural Lands prairie is not at risk of detrimental edge effects on species diversity, distribution, and health at its interior edges (not bordering the adjacent highways). In contrast, effects by site location were only present on the two abiotic variables soil percent moisture (Figure 6A) and maximum wind speed (Figure 6D), with the more-exposed recreational-trail-edged 1998 site experiencing significantly less soil moisture and higher wind speeds. These results are relatively consistent with past student research on the Natural Lands prairie, though the absence of any effects on species diversity contrasts wider literature.

Edge effects

Common concern over the severity of edge effects arises from smaller patches, which have a higher edge to area ratio and thus more exposure to detrimental land-use effects and invading species. Additionally, double-edged plots, like this study's 1994 plot, experience a four-fold increase in the magnitude of observed edge effects, also increasing the distance of edge influence 11-33% further than in single-edged plots (Fletcher Jr. 2005). Similarly, greater numbers of edges give foreign species an advantage over native species, which further endangers native prairie composition (Koper et al. 2010). That trend was not supported by this study. While the double-edged 1994 site had a lower species richness, only one out of the five dominating species was non-native (Table 4). This study's lack of effects on species diversity contrasts these two studies, but confirms previous research conducted on the Natural Lands prairie itself (Okerman 1997, Eckert

2016, Knee 2017). Notably, distance from trail edges had no effect on mean plant biomass, but soil percent moisture and organic matter increased with distance from the trail, possibly due to increased soil compaction from tail-use to prevent water absorption (Eckert 2016). Height being driven by edge distance in this study may be driven by the natural variation in stem heights (Figure 3B) and greater abundance of all four common species having more individuals in the intermediary-distance plots than the edge and center, even though there was a greater total species abundance in the further distances from the edge (Table 1). An analysis of soil nutrients and below-ground competition could provide insight into this unexpected trend.

Site effects

The year of site restoration was a strong influence on several abiotic factors and points to the different sites acting as unique micro-communities with quite different species composing the bulk of the biomass, but ending up with similar species diversity values and stem density. Camill et al. (2004) noted that community composition tends to change drastically in the first three growing seasons after prescribed burnings. Specifically, annual or biennial forbs were early successional species in the first growing season, followed by native perennial forbs the next year, and finally C₄ grasses, which remained dominant after year three but continued to struggle in competition with C₃ grasses. Strangely, all three sites in this study represent different stages of Camill et al.'s successional theory. The 1994 site represented the first growing season dominated by forbs (60%) with some C₄ grasses, the 2002 site represented the second growing season dominated by an invasive C₃ grass and forbs, and the 1998 site represented the growing seasons past year three dominated by C₄ grasses (74%) (Table 4). This relation is peculiar considering the last burn years for each site. The greater 1994 site was last burned 3.5 years ago in the spring of 2018, the 2002 site was last burned 1.5 years ago in the spring of 2020, and the 1998 site was last burned 4.5 years ago in the spring of 2017 (Patterson 2014, Shea correspondence 2022). While the 2002 site composition aligned with the expected last burn time and Camill et al.'s

successional theory, the 1994 and 1998 sites should have had more C₄ grass-dominated compositions to fit the theory. This difference indicates an additional influencing factor.

Though the species composition and richness were quite different, each site supported approximately the same number of individuals and near identical Simpson diversity values, indicating a compensatory species evenness for the sites with lower species richness (Table 5). Previous St. Olaf student research is in agreement on the effect by site, but rather than year of restoration, the cause is more likely the timing of prescribed burnings (Okerman 1997, Eckert 2016, Knee 2017). Growth without regular burning intervals leads to reduced diversity and abundance, though each of this study's exact plot locations may not have experienced much burning due to their heightened proximity to flammable forest cover and daily public access.

Possible Confounders

There are a host of additional influencers to site-specific changes besides fire regularity (Eckert 2016, Knee 2017). Matrix effects arise from different types of adjacent edges (Koper et al. 2010). For example, a forest edge may be a denser barrier to invading species migration compared to a recreational trail edge. Proximity to urban centers and urban land use inherently alter predation and herbivory patterns (Fletcher Jr. 2005, Kuli-Révész et al. 2021). Species-specific responses to edge effects are also highly variable (Laurance et al. 2007). Larger abiotic effects like season, severe weather events, number of edges, size of plot, existing soil organic composition and community, and soil nutrient deposition via management practices have varying magnitudes of influence (Laurance et al. 2000, Cully et al. 2003, López-Barrera et al. 2007). Each of these variables must be considered in the context of suitable testing sites for future study.

Conclusions and Future Studies

The St. Olaf Natural Lands prairie hosts a diverse array of grass and forb species and may be composed of many micro-communities of varying compositions depending on the year of patch restoration and frequency of prescribed burning. These community shifts are associated with slightly differing soil characteristics and abiotic conditions. Future studies could determine whether soil nutrients play a part in influencing community composition as well as the state of below-ground competition between dominant forbs and grasses. Studies on the progression of plant composition after instances of burning would also be insightful in comparison to the sites presented in this study.

While the prairie interior edges near other natural ecosystems do not affect species diversity and distribution, or are simply experiencing a beneficial matrix effect, the same cannot be said yet about the exterior edges that face widely used roads. Future studies may build on this study's concept and compare the differences between these interior and exterior edge effects, possibly in the northern 2004 site or between the 2003 sites to compare road vs agricultural edges. Additionally, studying which plants may be more resilient against edge effects could provide useful information for prairie management planning to protect more sensitive native species from being outcompeted.

Acknowledgements

I thank Professor Kathleen Shea for her advice and encouragement through each step of this project. I also thank Professor Charles Umbanhowar for his assistance in prairie grass and forb identification. Finally, thank you to my field ecology classmates for always offering me their support throughout the semester.

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Tables and Figures



Figure 1. GPS coordinates of the transect-based plots (circled in yellow) located in the different restoration year sites (outlined in white) of 1994, 1998, and 2002 within the St. Olaf Natural Lands. The coordinates are within 2 m of accuracy and are displayed using ArcGIS Pro Field Maps.

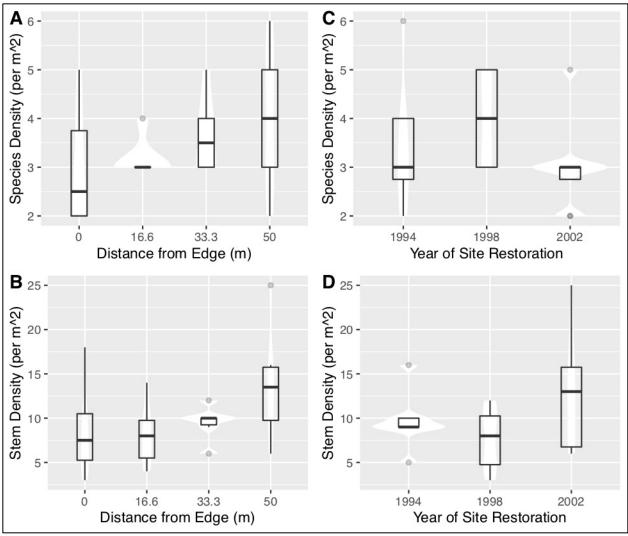
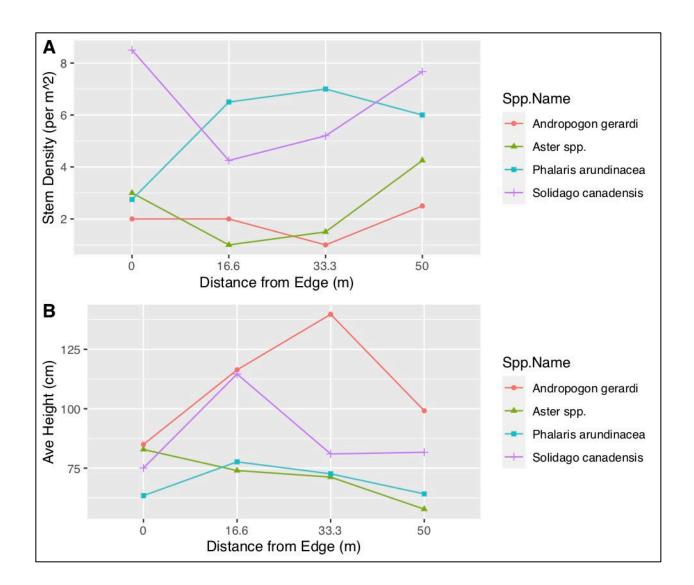


Figure 2. Comparisons of plot distance from edge (in meters) (Fig 2 A & B) or year of site restoration (1994, 1998, 2002) (Fig 2 C & D) and the biotic variables species density (per 1 m^2) and stem density (total number of individuals per 1 m^2). No relationships were significant (all p-values > 0.1).



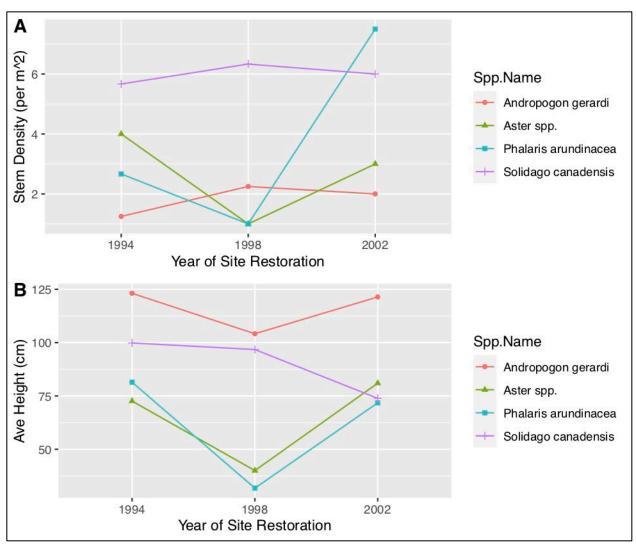


Figure 4. Comparisons of year of site restoration (1994, 1998, and 2002) and the biotic variables (A) stem density (total number of individuals per 1 m²) and (B) average height (cm) of the four most prevalent species across plots: *Andropogon gerardi* (Big bluestem), *Aster spp.* (Asters), *Phalaris arundinacea* (Reed canary grass), and *Solidago canadensis* (Goldenrod). Both relationships had significant species-driven differences (both p-values < 0.02) but neither had a significant site-driven effect (both p-values > 0.09).

Table 1. Species counts in plots of varying distances from the prairie edge (m). The percent of forb and grass species were calculated with the total number of individuals at each plot distance.

	0 m	16.6 m	33.3 m	50 m
Ambrosia artemisiifolia	1			
Andropogon gerardi	1	2	4	4
Asclepias syriaca		1		
Aster spp.	2	1	2	4
Bouteloua curtipendula			1	
Cirsium arvense				1
Elymus canadensis				1
Helianthus spp.		1		
Monarda fistulosa	2	2	1	1
Phalaris arundinacea	4	2	1	4
Schizachyrium scoparium	2	1	1	1
Solidago canadensis	2	4	5	3
Sorghastrum nutans	2	2	2	2
Brome spp. 1			3	2
Brome spp. 2		1	2	
Total individuals	16	17	22	23
Percent forb species	43.75	52.94	36.36	39.13
Percent grass species	56.25	41.18	63.64	60.87

Table 2. Diversity indices (Shannon (H') and Simpson (Ds)) accounting for species richness and evenness by distance from the prairie edge (m).

	0 m	16.6 m	33.3 m	50 m
Richness	8	10	10	10
Shannon (H')	0.87	0.95	0.93	0.93
Simpson (Ds)	0.91	0.93	0.90	0.91
Variance Ds	0.000961	0.000980	0.000785	0.000457

Table 3. Pairwise comparisons of Simpson (Ds) diversity values (t-values are shown) by distance from the prairie edge (m). No pairwise comparisons were significantly different (P<0.05).

	0 m	16.6 m	33.3 m	50 m
0 m				
16.6 m	-0.4116065			
33.3 m	0.0854524	0.5166032		
50 m	-0.0201131	0.4583477	-0.1227935	

Table 4. Species counts in prairie sites from different restoration years. The percent of forb and grass species were calculated with the total number of individuals at each site.

	1994	1998	2002
Ambrosia artemisiifolia		1	
Andropogon gerardi	4	4	3
Asclepias syriaca	1		
Aster spp.	4	2	3
Bouteloua curtipendula		1	
Cirsium arvense		1	
Elymus canadensis			1
Helianthus spp.			1
Monarda fistulosa	5		1
Phalaris arundinacea	3	2	6
Schizachyrium scoparium		5	
Solidago canadensis	6	3	5
Sorghastrum nutans		7	1
Brome spp. 1	4	1	
Brome spp. 2			3
Total individuals	27	27	24
Percent forb species	59.26	25.93	41.67
Percent grass species	40.74	74.07	58.33

Table 5. Diversity indices (Shannon (H') and Simpson (Ds)) accounting for species richness and evenness by site restoration years.

	1994	1998	2002
Richness	7	10	9
Shannon (H')	0.81	0.90	0.86
Simpson (Ds)	0.87	0.88	0.88
Variance Ds	0.000275	0.000923	0.000884

Table 6. Pairwise comparisons of Simpson (Ds) diversity values (t-values are shown) by site restoration years. No pairwise comparisons were significantly different (P<0.05).

	1994	1998	2002
1994			
1998	-0.3292298		
2002	-0.2310458	0.083039	

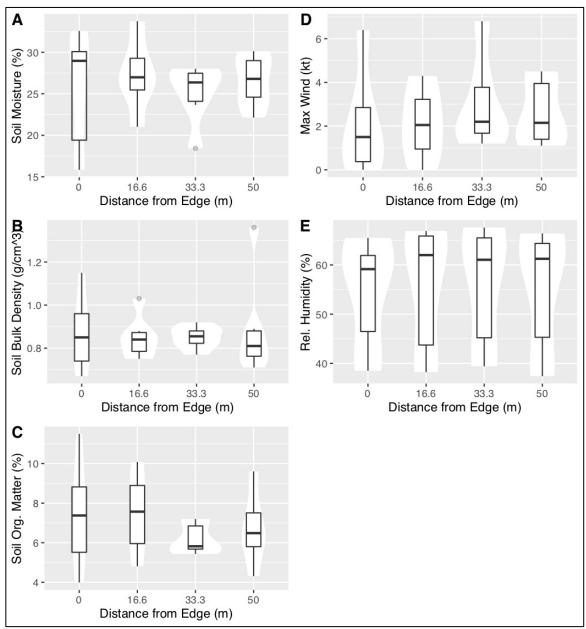


Figure 5. Comparisons of plot distance from edge (in meters) and the abiotic variables (A) soil percent moisture, (B) soil bulk density (g/cm^3), (C) soil percent organic matter, (D) maximum wind speed (kt), and (E) relative humidity (in percent moisture). No relationships were significant (all p-values > 0.6).

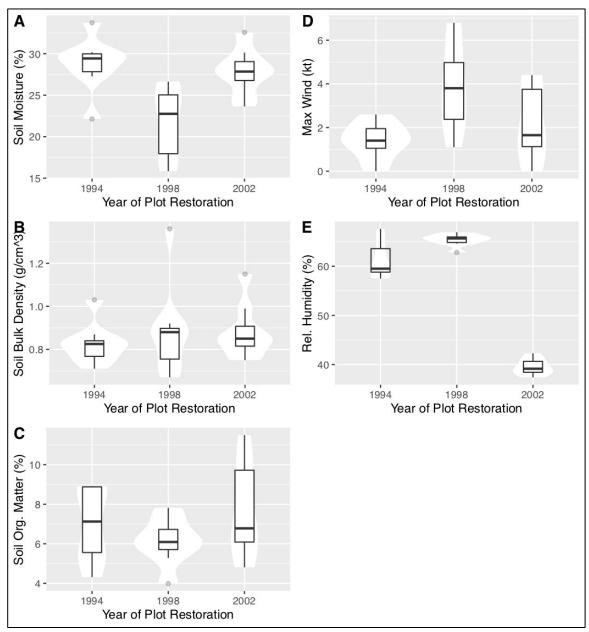


Figure 6. Comparisons of year of site restoration (1994, 1998, and 2002) and the abiotic variables (A) soil percent moisture, (B) soil bulk density (g/cm³), (C) soil percent organic matter, (D) maximum wind speed (kt), and (E) relative humidity (in percent moisture). Soil percent moisture, maximum wind speed, and relative humidity had significant site-driven effects (all p-values < 0.01).

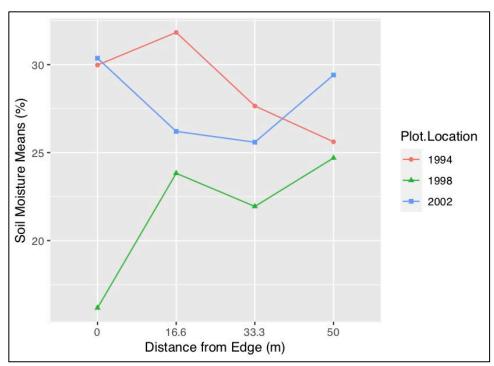


Figure 7. A closer look at the interacting effects of edges and year of restoration on soil percent moisture by comparing the means from each group. There was an effect both by plot location (p-value ≤ 0.001) by the geographic interaction of distance from edge and site location (p-value = 0.043105).

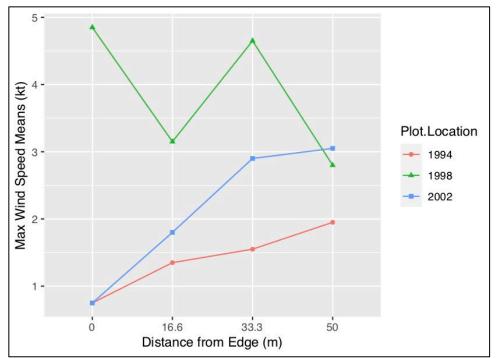


Figure 8. A closer look at the interacting effects of edges and year of restoration on maximum wind speed (kt) by comparing the means from each group. While there was an effect by site location (p-value = 0.0184), there was no significant interaction (p-value = 0.7554).