

Relationships between Herbaceous Vegetation and Environmental Factors along a Restored Prairie-Oak Opening Ecotone

Abstract We studied a potential ecotone between a wet-mesic prairie and an oak opening in a restored landscape in southern Wisconsin. We described the relationships between herbaceous vegetation and soil variables along the prairie-oak opening transition using twenty-five 1-m² plots located on five 75-m transects. We identified a total of 46 herbaceous species and analyzed eight environmental variables: seven soil variables and photosynthetically active radiation (PAR). We observed distinct soil gradients along the ecotone: soil organic matter, total N, pH, P, Mg, and Ca levels all exhibited significant reductions when moving along the ecotone from prairie to oak opening. PAR was weakly correlated with vegetation patterns. Using cluster analysis and ordination techniques, we identified few distinct herbaceous community types along the transition, except for a unique assemblage dominated by reed canary grass (*Phalaris arundinacea* L.). Our canonical correspondence analysis (CCA) results indicated strong correlations between herbaceous vegetation and soil N, pH, Ca, and Mg gradients. Herbaceous species richness and Shannon-Wiener diversity increased moving from the prairie into the oak opening. Overall, our results indicated that (1) distinct soil gradients exist at the site, (2) soil gradients are correlated with herbaceous vegetation patterns in the restored area, and (3) while *P. arundinacea* has a strong influence on the composition of vegetation at the site, non-*Phalaris*-dominated plots exhibited continuous rather than discrete ecotonal properties. The potential importance of soil variables and soil gradients should be considered when studying the characteristics of ecotones in restored habitats.

Ecotones are transition zones between two or more distinct community types. The role of ecotones (and ecoclines) in describing and explaining spatial and temporal vegetation patterns has received renewed attention in recent years (Naiman and Décamps 1990, Holland et al. 1991, Hansen and di Castri 1992, Gosz 1993, Risser 1995), although interest in the structure and ecological impact of ecotones is by no means new (Clements 1905, Leopold 1933, Weaver and Albertson 1956). Recent ecotone research has been focused on biodiversity (Pulliam 1988, Hansen and Urban 1992, Leach and Givnish 1996), nutrient and material flows between communities (Johnston 1993, McClaran and McPherson 1995), ecotones in landscapes (Boren et al. 1997, Dyer and Baird 1997, Sagers and Lyon 1997), and regulation and response to large-scale climatic change (Nielson 1993, Rusek 1993). Despite the renewed interest in ecotones, characterization of vegetation in and across ecotones remains problematic (Auerbach and Shmida 1993, Jarvis 1995, Stohlgren et al. 1997).

Rates of spatial change in vegetation are scale-dependent, and ecotones can be characterized over a wide range of spatial scales (di Castri 1993, Gosz 1991, Crumley 1993). Assigning boundary classifications can be difficult at larger scales because of the tendency of small-scale differences to average out at larger levels of observation (Allen and Hoekstra 1992). Ecotone studies at the population level encompass the spatial distribution of individuals in a small habitat and facilitates analysis at smaller scales (Fahrig and Merriam 1985, Gosz 1993). In both large and small scale ecotonal landscapes, specific environmental variables can strongly influence the distribution and abundance of vegetation and be correlated with the spatial distribution of ecotones (Gosz

and Sharpe 1989, Risser 1990, van der Maarel 1990, Neilson 1993). Grassland and prairie vegetation, in particular, have been shown to be sensitive to changes in soil nutrient status and balance (Wedin and Tilman 1996), and soil gradients have been shown to have a strong influence on the composition of prairie and savanna vegetation (Curtis 1959, Anderson 1968, Jastrow 1987, Zak et al. 1990, Leach 1994).

We studied a suspected ecotone between a restored prairie community and a remnant oak opening. The study was conducted in the Curtis Prairie, a prairie restoration project at the University of Wisconsin-Madison Arboretum. The restoration effort at the Curtis Prairie has been studied from a variety of perspectives, including land use history (Blewett and Cottam 1984), fire (Anderson 1972, Peet et al. 1975), vegetation dynamics (Cottam and Wilson 1966, Blewett 1981), and organic matter incorporation into soils (Nielsen and Hole 1963). However, no studies have assessed potential linkages between underlying soil gradients and composition of vegetation along the restored prairie-oak opening ecotone. Our overall objective was to determine how herbaceous vegetation was distributed in the ecotonal region and if vegetation patterns were correlated with soil variables and/or photosynthetically active radiation (PAR). Specifically, we wanted to determine:

- (1) if and how the environmental variables changed across the prairie-oak opening boundary;
- (2) if the boundary between the two vegetation zones was discrete or continuous;
- (3) if any of the environmental variables were correlated with vegetation composition;
- (4) if a plant diversity gradient existed between the adjacent vegetation zones.

Study Site

The 0.45-ha study site was located in the northwestern portion of the Curtis Prairie, a prairie restoration project within the University of Wisconsin-Madison Arboretum. Presettlement vegetation in the area consisted of an oak opening intermixed with patches of tallgrass prairie (Curtis 1959, Sachse 1965, Cottam and Wilson 1966, Blewitt and Cottam 1984). The area was settled and converted into farmland in the 1850s. By the 1920s, the agricultural fields were abandoned, and the area was used as a horse pasture. In 1932 the Arboretum acquired the land, and in 1935 the prairie restoration project at Curtis Prairie was initiated. By 1948 the first prescribed burning was conducted (Curtis and Partch 1948). Current management of the Curtis Prairie includes a two-year cycle of prescribed burning; two-thirds of the prairie are burned one year, and the remaining third is burned the next (Anderson 1972). Occasional brushing and mowing also have been used as management tools. A detailed history of the site is provided by Blewitt and Cottam (1984).

Methods

Herbaceous Vegetation Sampling

Five 75-m transects were established at intervals of 15 m running parallel across the prairie-oak opening border. The transects started at a small drainage channel running southwest to northeast across the site (a topographical low point). Position 1 was in the prairie while position 5 was in the oak opening. All transects were set up at an azimuth of 310°. Sampling plots were located at 15 m intervals along the transect. Herbaceous vegetation was sampled using 1-m² quadrat constructed from PVC pipe. Vegetation samples were taken at each 15 m

interval along each of the five transects for a total of 25 plots. The quadrat shape and size are appropriate for this type of vegetation (Brummer et al. 1994).

Herbaceous vegetation within each plot was clipped at the base of the plant (plant-soil interface) and separated according to species. Nomenclature follows Gleason and Cronquist (1991). The species samples were then dried by placing them in a drying oven at 65°C for 48 hours or until a constant weight was obtained. Dry weight biomass was determined for each species (g m⁻²) (Appendix A). Photosynthetically active radiation (PAR) was measured on each plot using a Li-Cor LI-192SA Quantum Sensor (Lincoln, NE). Paired light measurements were taken in full sunlight adjacent to the study area, above the herbaceous canopy (approximately 1.3 m) as a measure of light interception by oak opening burr oaks (*Quercus macrocarpa* Michx.), and at approximately 8 cm above the ground surface beneath the herbaceous canopy.

Soils

A composite soil sample was taken from each plot to a depth of approximately 10 cm from three arbitrary locations within each plot. Leaf litter was removed from the sample area prior to soil collection. Soil samples were stored in plastic bags and kept refrigerated until analysis. Soils were analyzed at the University of Wisconsin-Madison's Soil Testing, Plant Analysis and Feed and Forage Analysis Laboratory in Madison, WI. Soils were analyzed for pH, organic matter, total N, available P, and exchangeable K, Ca, and Mg.

Soil pH was measured using a glass electrode pH meter in a 1:1 w/v aqueous solution following the methods of Corey and Tanner (1961). Calcium was measured as lime (CaOH₂) using a glass electrode Ca

meter in a 1:1 w/v aqueous solution. Available phosphorous was measured after the methods of Bray and Kurtz (1945). Available potassium was measured according to the methods outlined in Wilde et al. (1979). Percent organic matter (OM) was determined following the methods of Schulte (1980). Total nitrogen was measured using the semi-micro Kjeldahl procedure (Bremner and Mulvaney 1982)

Vegetation Analysis

Classification of herbaceous vegetation was conducted using Cluster Analysis performed by program PC-ORD (McCune and Mefford 1995). To evaluate the variation in herbaceous vegetation and environmental variables along the transects, analysis of variance tests were performed using the general linear model (GLM) procedure in Minitab 8.2 (Minitab 1991). Mean separations across transect position groups were conducted using Fisher's test at $P < 0.05$. Species density was defined as the total number of species found in a sample plot and was used as an estimate for species richness (Magurran 1988). Species diversity was determined using the Shannon-Wiener diversity index, $H' = -\sum p_i \ln p_i$, where p_i is the proportion of importance value of the i th species. These values were based on dry-weight biomass.

To evaluate relationships between vegetation and environmental variables, we performed multivariate analyses, namely detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) ordinations on herbaceous species-environmental variable matrices. We conducted the ordinations using the programs PC-ORD (McCune and Mefford 1995) and CANOCO 3.10 (ter Braak 1990). Herbaceous species biomass was used in the plant matrix as an indicator of plant abundance. Plant dry weight biomass was used in all the

ordination and classification methods described. The DCA procedure used segment detrending, nonlinear rescaling of axes, and rare species downweighting (Hill and Gauch 1980). The CCA procedure involved linear combination of variables for site scores, no transformation of species abundance matrices, and the use of a Monte Carlo permutation to test the significance of the first axis eigenvalue (ter Braak 1990). In all CCA ordinations performed, the Monte Carlo test indicated that the eigenvalues for the first axis were significant ($P < 0.05$). Given the influence of noisy environmental data on CCA (McCune 1997), CCA was used and interpreted in the limited context of describing plant community variation with respect to the limited set of measured environmental variables in the study. Soil and environmental variables were transformed, when necessary, to meet the assumptions of normality. Significance is reported at the $\alpha = 0.05$ level, unless otherwise noted in the text.

Results

A total of 46 herbaceous species were found on the study plots (Appendix A). Standing crop, dry weight biomass on the plots ranged from 69 to 2117 g m⁻² (mean = 533 g m⁻²). A distinct biomass gradient was also observed along the prairie-oak opening transition; mean plot biomass was 642 g m⁻², 1046 g m⁻², 437 g m⁻², 307 g m⁻², and 231 g m⁻², at transect positions 1, 2, 3, 4, and 5, respectively. Herbaceous species density on plots ranged from 2 to 11 species (mean = 5.9). Note that the species density totals do not include a limited number of spring ephemeral species. A summary of the overall fidelity of the herbaceous species encountered in the study indicated that the majority of the species sampled were uncommon; cumulative totals of species fidelity show that

64.6% of the species were found on three or fewer plots, 29.1% were found on from four to eight plots, and the remaining 6.3% were found on nine or more plots.

Soil Chemical Gradients

Table 1 provides a comparison of the means, standard deviations, and ranges of the environmental variables in the study. The relatively wide ranges of environmental variables depicted in Table 1 indicate the existence of soil heterogeneity at the site. Table 2 summarizes the correlations between environmental variables in the study. Moving from prairie towards the oak opening, seven of the eight environmental variables under

examination were found to be negatively and significantly correlated with distance along the transects: pH ($r = -0.81$), organic matter ($r = -0.73$), N ($r = -0.75$), P ($r = -0.63$), Ca ($r = -0.82$), Mg ($r = -0.88$), and PAR above the herbaceous canopy ($r = -0.53$) (Figure 1). Table 2 shows that K was not significantly correlated with distance or any of the environmental variables measured. Furthermore, PAR above the herbaceous canopy was weakly correlated with all other environmental variables, and PAR beneath the herbaceous canopy exhibited even weaker correlations (Table 2). Table 2 also shows that many of the soil nutrient variables were strongly correlated.

Table 1. Means, standard deviations, and ranges (minimum and maximum) of environmental variables along a prairie-oak opening ecotone in the Curtis Prairie.

Variable ^a	Mean	Standard Deviation	Range
pH	6.6	0.7	5.3 - 7.5
Organic matter	5.3	1.2	2.6 - 7.1
N	0.23	0.06	0.11 - 0.34
P	24.6	6.8	13.0 - 35.5
K	0.34	0.07	0.23 - 0.48
Ca	5.5	1.7	2.8 - 7.7
Mg	4.0	1.4	1.9 - 6.2
PAR	76.1	34.5	8.6 - 97.6

^aVariables shown are in the following units: organic matter (OM) %; Total N %; available P (P) mg/l; exchangeable K (K) cmol+kg⁻¹; exchangeable Ca (Ca) cmol+kg⁻¹; exchangeable Mg (Mg) cmol+kg⁻¹; photosynthetically active radiation (PAR) $\mu\text{mol s}^{-1}\text{m}^{-2}$.

Table 2. Pearson correlation coefficients between variables measured in the study.

Variable ^a	D	pH	OM	N	P	K	Ca	Mg	PAR over	PAR under
Distance (D)	-	-.81	-.73	-.75	-.63	.06	-.83	-.88	-.53	-.14
pH		-	.54	.68	.41	.10	.87	.89	.49	.20
OM			-	.92	.80	.19	.76	.76	.43	.14
Total N				-	.74	-.02	.46	.43	.40	.17
P					-	.08	.28	.67	.20	-.05
K						-	-.03	.01	.13	.11
Ca							-	.94	.46	.13
Mg								-	.43	.07

^aVariables shown are in the following units: distance (D) m; organic matter (OM) %; Total N %; available P (P) mg/l; exchangeable K (K) cmol+kg⁻¹; exchangeable Ca (Ca) cmol+kg⁻¹; exchangeable Mg (Mg) cmol+kg⁻¹; photosynthetically active radiation (PAR) $\mu\text{mol s}^{-1}\text{m}^{-2}$.

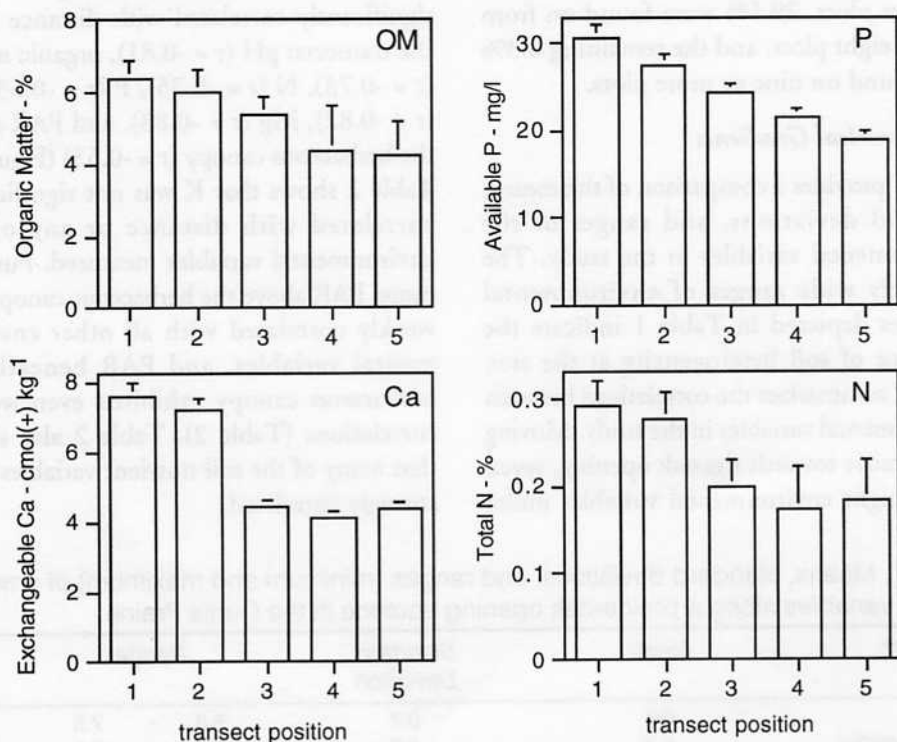


Figure 1. Graphs show relationships between transect position and soil nutrient levels. Transect position 1 corresponds to prairie and 5 corresponds to oak opening in the Curtis Prairie. Bars represent one standard deviation.

Figure 1 is a composite graph of transect position plotted versus measured soil levels of total N, available P, exchangeable Ca, and percent OM. Significant reductions in soil N ($P < 0.001$), Ca ($P < 0.001$), P ($P = 0.030$), and OM ($P = 0.002$) were noted moving from prairie (position 1) to oak opening (position 5). The Mg results (not shown) were highly similar to the Ca results. These results indicate strong underlying soil gradients on the study site moving across the prairie restoration-oak opening transition zone.

Vegetation along the Transition

Cluster analysis identified six weak clusters in the dataset. However, only a single dis-

tinct herbaceous assemblage was found in the study area. Reed canary grass (*Phalaris arundinacea* L.) dominated the plant assemblages found in transect positions 1 and 2 along the ecotone. The DCA ordination results (not shown) also indicated this pattern. Figure 2 shows that positions 1 and 2 had significantly lower DCA mean scores than positions 3 to 5 ($P < 0.001$). No significant differences in mean DCA scores were found between positions 3, 4, and 5. However, the standard deviation was highest for position 3. This latter result indicates the vegetation at position 3 (between the prairie restoration and oak opening) shows a high rate of species change at that location. The five remain-

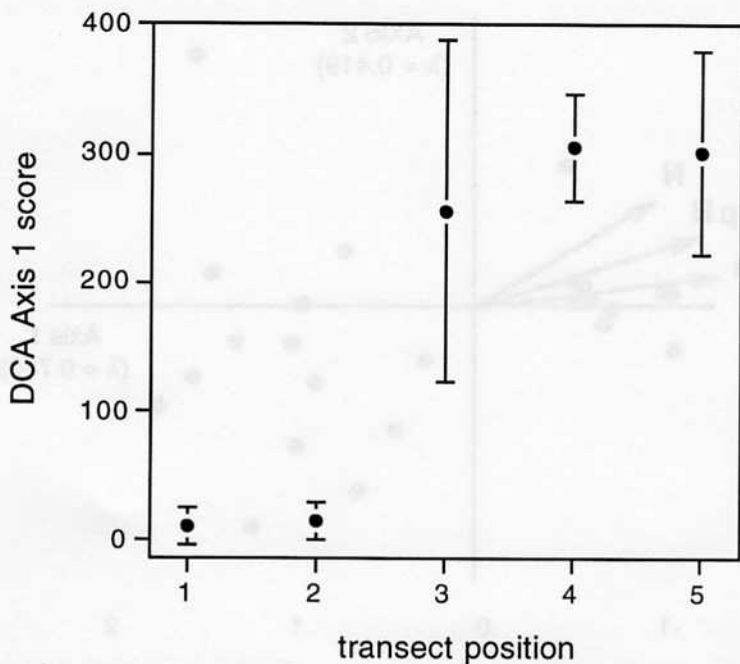


Figure 2. A plot of DCA axis 1 scores (± 1 SD) versus plot position along the five study transects.

ing non-*Phalaris*-dominated clusters were located in plots spread out along the three remaining transect positions. No clear patterns of prairie versus oak opening vegetation were found.

Vegetation-Environmental Relationships

Ordinations were used to detect relationships between vegetation and measured environmental variables. Both DCA and CCA were run, but because the two ordinations produced similar results, only the CCA results are presented in detail. Figure 3 is a summary CCA ordination showing plot ordination on a biplot for the 25 vegetation plots with eight environmental variables. The first three axes of the CCA ordination explained 35.2% of the variation in the species matrix. The three vectors shown in Figure 3 correspond to the environmental vari-

ables showing strong correlations with the first CCA axis, namely Ca ($r = -0.88$), N ($r = -0.72$), and pH ($r = -0.71$). Mg also exhibited a strong correlation ($r = -0.78$) as did OM ($r = -0.58$); however, a vector for Mg wasn't included in Figure 3 because Mg results were similar to those of Ca. The results in Figure 3 parallel the results presented in Table 2. The CCA correlations also closely paralleled the correlations between environmental variables and the DCA ordination axes. While CCA may be sensitive to noise in environmental data (McCune 1997), the results provide corroboration of the soil gradient analysis and the DCA results.

The distribution of plots in Figure 3 also shows a separation of the plots dominated by *Phalaris*, with all *Phalaris*-dominated plots located exclusively on the left side of the ordination. No clear segregation of plots

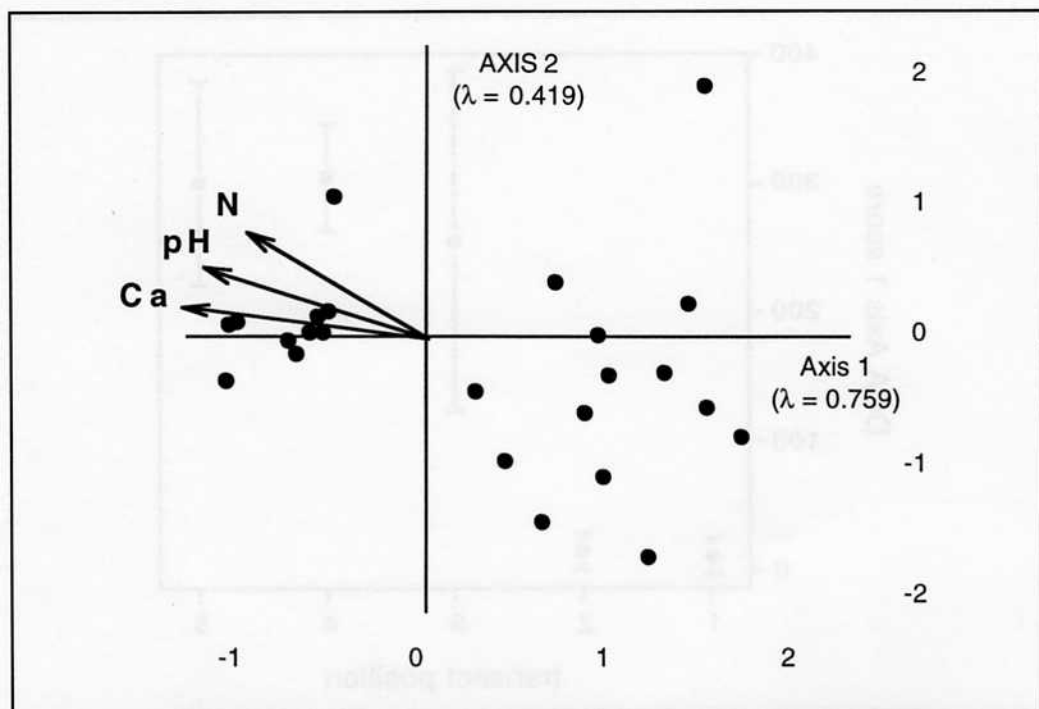


Figure 3. A CCA ordination biplot of 25 plots and 9 environmental variables. The environmental variables with the strongest correlation with the vegetation matrix are shown in the biplot.

was observed on the right half of the CCA biplot, indicating more of a continuous distribution than discrete gradation of herbaceous assemblages in the non-*Phalaris*-dominated plots.

Diversity Gradients

In addition to soil chemical gradients, a herbaceous plant diversity gradient also was found along the prairie-oak opening transition. Plant diversity was calculated for each transect position using both species richness (S) and the Shannon-Weiner Diversity Index (H'). The results in Table 3 show that both species richness and Shannon-Weiner diversity were positively correlated with distance along the transition zone; as prairie graded into oak opening, species richness and diversity increased. Diversity estimates were

strongly correlated with Ca ($r = -0.90$), N ($r = -0.84$), OM ($r = -0.72$), and pH ($r = -0.67$). Interestingly, no significant relationships were found between any of the PAR measurements and species diversity measures.

There was a strong negative correlation between *Phalaris* and species richness ($r = -0.75$) and diversity ($r = -0.78$) along the ecotone transition. While the cause-effect relationship between *Phalaris* and plant diversity is beyond the scope of this study, the results suggest that *Phalaris* dominance reduces diversity.

Discussion

The term ecotone was first used by Clements (1905) to describe the "tension zone" between plant communities where the major

Table 3. Correlations between Shannon-Weiner diversity (H'), species density (S), and distance and environmental variables. Values represent Pearson's correlation coefficients (r).

Variable ^a	S	H'
Distance (D)	.60	.73
pH	-.44	-.67
OM	-.66	-.72
N	-.74	-.84
P	-.82	-.53
K	.12	.13
Ca	-.62	-.90
Mg	-.67	-.80
PAR	-.25	-.46

^aVariables shown are in the following units: distance (D) m; organic matter (OM) %; Total N %; available P (P) mg/l; exchangeable K (K) cmol+kg⁻¹; exchangeable Ca (Ca) cmol+kg⁻¹; exchangeable Mg (Mg) cmol+kg⁻¹; photosynthetically active radiation (PAR) $\mu\text{mol s}^{-1}\text{m}^{-2}$.

dominant species in adjacent communities overlapped in their distribution. In recent years, the term ecotone has been used interchangeably with the terms "transition zone" and 'landscape boundary' (van der Maarel 1990; Shugart 1990; Holland et al. 1991; Hansen and di Castri 1992). The presence of ecotones and their manifestation are influenced by a host of factors, including edaphic conditions, geomorphology, disturbance, and climate (Risser 1990, van der Maarel 1990, Gosz 1993).

The results of our study indicate distinct ecotonal characteristics in both vegetation and soil variables in the Curtis Prairie. The herbaceous layer exhibited sharp ecotonal boundaries only at the transition between *Phalaris*-dominated communities and prairie-oak opening vegetation. Cluster analysis and CCA ordinations showed little distinct separation between plots on non-*Phalaris*-dominated plots; herbaceous vegetation assemblages were more continuous than discrete across the prairie-oak opening

transition. Our results also indicate that there were both soil chemical and diversity gradients along the prairie-oak opening ecotone in the study area. Organic matter, pH, P, Ca, Mg, and total N decreased along the gradient from prairie to oak opening; plant diversity increased from prairie to oak opening. Given the importance of total N and available P to plant nutrition, the role and influence of OM in prairie soil development, and the impacts of Ca and Mg on plant distribution in calcareous and dolomitic soils, our results highlight the importance of soil gradients along the prairie oak opening transition in this study. However, the presence of *Phalaris* at the site may have had a strong influence on altering pre-*Phalaris*-invasion vegetation and soil patterns.

Integrating vegetation analyses with environmental and physiographic variables can provide a more robust basis for classification and characterization than vegetation analyses alone (Rowe 1984, Hix 1988, Palmer 1993). The soil gradient analysis and CCA results indicate that herbaceous species were influenced by soil gradients across the ecotonal landscape. The correlations between the soil variables and herbaceous species diversity indicate that plant diversity may also be influenced by soil chemical gradients. In the oak opening portion of the ecotone, lower nutrient availability may promote greater diversity compared to that of the prairie.

Ecotones may provide pathways for the invasion of exotic plants that can disrupt community dynamics (Risser 1990, Planty-Tabacchi et al. 1996). An important factor influencing the observed diversity patterns in our results was that *Phalaris* had a negative impact on herbaceous species diversity on the study site. *Phalaris* was a dominant species on the wetter soils on the prairie side of the ecotone but was not found in the oak

opening or the prairie-oak opening interface. *Phalaris* is an exotic species that grows in dense clumps, outcompetes local flora, and is highly resistant to flooding (Apfelbaum and Sams 1987, Chonchou and Fustec 1988). Seasonal flooding has occurred and continues to occur near and around an overflow ditch within the study area. *Phalaris arundinacea* was most dominant near the overflow ditch, and it follows that the ditch is quite possibly the vector by which seeds of *P. arundinacea* first entered the area.

Current management techniques (i.e., fire and selective brushing) may have influenced the ecotone under study. In addition, light (PAR) may have a long-term impact on the vegetation composition at the site depending on phenology, available wavelengths of light, and variation in herbaceous canopy composition. While the influence of these variables requires more investigation,

the results of the present study clearly demonstrate the potential influence of soil factors on the composition and distribution of herbaceous vegetation. We suggest that soil variables and gradients should be considered when studying characteristics of ecotones in restored habitats.

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Appendix A. A summary of all herbaceous species identified in the vegetation sampling.

Species	Total Biomass - g
<i>Agrostis alba</i> L.	21.3
<i>Allium cernuum</i> Roth.	11.7
<i>Andropogon gerardii</i> Vitm.	798.5
<i>Arctium minus</i> Bernh.	1.0
<i>Asclepias syriaca</i> L.	0.5
<i>Aster ericoides</i> L.	3.8
<i>Aster laevis</i> L.	5.6
<i>Aster lanceolatus</i> Willd.	9.8
<i>Aster novae-angliae</i> L.	148.9
<i>Aster oolentangiensis</i> Riddell	1.9
<i>Aster pilosus</i> Willd.	21.0
<i>Baptisia leucantha</i> T.&G.	47.9
<i>Blephilia ciliata</i> (L.) Raf.	1.1
<i>Brachelytrum</i> sp.	52.2
<i>Bromus inermis</i> Leyss.	18.2
<i>Carex</i> sp.	17.9
<i>Cirsium discolor</i> (Muhl.) Spreng.	3.3
<i>Cornus racemosa</i> Lam.	182.9
<i>Euphorbia corollata</i> L.	2.1
<i>Galium triflorum</i> Michx.	0.4
<i>Helianthus grosseserratus</i> Martens	602.4
<i>Hypericum perforatum</i> L.	14.7
<i>Lactuca canadensis</i> L.	36.0
<i>Lespedeza capitata</i> Michx.	100.3
<i>Liatris aspera</i> (L.) Willd.	14.0
<i>Lycopus americanus</i> Muhl.	4.2
<i>Monarda fistulosa</i> L.	658.0
<i>Oenothera biennis</i> L.	33.3
<i>Pastinaca sativa</i> L.	26.3
<i>Pedicularis canadensis</i> L.	2.2
<i>Phalaris arundinacea</i> L.	142.6
<i>Poa compressa</i> L.	21.8
<i>Poa pratensis</i> L.	52.2
<i>Polygonum pennsylvanicum</i> L.	85.2
<i>Pycnanthemum virginianum</i> (L.) Durand & Jackson	6.4
<i>Rosa</i> sp.	3.3
<i>Rubus occidentalis</i> L.	10.4
<i>Rudbeckia hirta</i> L.	0.3
<i>Silphium terebinthinaceum</i> Jacq.	42.1
<i>Solidago altissima</i> L.	732.7
<i>Solidago gigantea</i> Ait.	14.3
<i>Solidago nemoralis</i> Ait.	856.8
<i>Solidago ulmifolia</i> Muhl.	0.2
<i>Sorghastrum nutans</i> L.	504.8
<i>Toxicodendron radicans</i> (L.) Ktze.	0.6
Unknown	2.4
<i>Viola pedata</i> L.	0.1
<i>Vitis riparia</i> Michx.	0.0

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