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SPATIO-TEMPORAL BOUNDARY DYNAMICS IN AN EAST CENTRAL INDIANA TALLGRASS PRAIRIE RECONSTRUCTION

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ABSTRACT. The spatial and temporal dynamics of ecological boundaries reveal insight into interspecific competition, species responses to anthropogenic and natural factors, and ecological function. During a fifteen year study, spatial analysis of species composition was conducted across a plant community boundary in a tallgrass prairie reconstruction in East Central Indiana (USA). Boundary formation appeared to have been influenced by short-term flooding that inundated lower portions of the study site shortly after initial seeding in spring 1993. During the first growing season, a plant boundary was perceived to be located along the flood line. In general, the flood zone was dominated by weedy unsown-species, whereas the adjacent upland area, located above the flood line, was dominated by sown-species. The purpose of the current study was to track boundary movement and analyze spatial change by assessing the associated changes in species composition along an elevation gradient. Permanent monitoring transects and a topographic grid were positioned over the apparent boundary and sampled periodically from 1993 to 2010. Sampling included estimated percent areal cover and density for all plant species. Ordinations of topographic grid data sets indicate that the boundary has shifted and become more diffuse, in a way that was interpreted as a directional transition. The association of changes in species composition with changes in elevation appeared to weaken over time. Overall, the results indicate that sown-species expanded down-slope into areas previously dominated by weedy unsown-species, thus suggesting a possible competitive advantage by sown-species under the current management regime.

Keywords: flood impacts, ordination, gradient analysis, tallgrass prairie restoration, ecological boundary, Indiana.

Across landscapes, vegetation exhibits discrete patches that are created by various natural and anthropogenic factors (Kent et al. 2006). In the past, a primary focus in ecology was to describe uniform portions of terrestrial systems, while transition areas that form boundaries between them were neglected. Recently, literature in ecology, biogeography, and conservation biology has broadened a once narrow view of plant communities to include boundaries (Hufkens et al. 2009). Boundary studies are beneficial for understanding links between ecological structure and function, such as biological responses to disturbance (Wiens et al. 1985), feedback mechanisms (Malanson 1997), and species-environment relationships (Stohlgren & Bachand 1997). These dynamics operate at multiple scales including ecotone between biomes, communities, and vegetation patches (Kark & van Rensburg 2006). It is clear that a thorough understanding of boundary dynamics is important as the portion of global landscapes comprised of boundaries has increased due to anthropogenic modifications with increase in agricultural and urban development (Kent et al. 2006).

Analysis of ecological boundaries provides insight into vegetation trends in space and time. Of particular interest are temporal trends in vegetation that indicate the potential for boundary movement and spatial change. Such dynamics indicate the expansion or contraction of individual species or plant assemblages, where the position, and often the spatial structure (Hufkens et al. 2009), of an ecological boundary changes (Peters et al. 2006). As a result, transition zones may represent areas of tension between dominant vegetation types (Odum 1953). Shifting boundaries have been studied in various settings including forest expansion into meadow (Norman & Taylor 2005; Halpern et al. 2010) and heath/grassy balds (Crawford & Kennedy 2009), shrub encroachment into perennial grasslands (Peters et al. 2006), and retreating vegetation due to desertification (Schlesinger et al. 1990). Such vegetation dynamics may reveal

underlying ecological processes. For example, shifting boundaries may indicate biological responses to disturbance (Hardt & Forman 1989; Sankey et al. 2006) or changing climatic regimes that govern species distribution (Foody & Boyd 1999; Wearne & Morgan 2001).

Although the temporal trends of shifting boundaries are well documented, the related spatial dynamics are not fully understood (Peters et al. 2006a). A review of several studies that mentioned the spatial dynamics of shifting boundaries revealed that the pattern of expansion may differ according to the ecosystem studied, whether in pine forests (Norman & Taylor 2005; Halpern et al. 2010), larch forests (Sankey et al. 2006), broadleaf deciduous forests (Hardt & Forman 1989), or shrubland (Peters et al. 2006b). The disparate outcomes of these studies may be explained, to some degree, by the different biological and environmental factors present in these ecosystems. For example, anthropogenic disturbances (e.g., land cover change, fire suppression, and grazing) may create selective pressures on certain species (Hardt & Forman 1989; Norman & Taylor 2005; Sankey et al. 2006). In addition, changing climatic regimes may favor certain species and initiate "pulses" of plant population or community expansion (Norman & Taylor 2005). Finally, boundary form (whether straight, concave, or convex) can influence spatial dynamics of biotic expansion (Hardt & Forman 1989). As of yet, the spatial dynamics of expanding tallgrass prairie are not well documented in literature.

Despite differences in the specific spatial pattern of shifting boundaries, a general pattern of "leap and infill" of expanding species is commonly observed (Norman & Taylor 2005 ; Peters et al. 2006b; Romme et al. 2009; Halpern et al. 2010). Basically, the infilling pattern can be explained by adventitious propagules that establish patches proximal to a source population (Peters et al. 2006a). Over time, patches serve as a seed source for newer seedlings to establish in the spaces between patches. Eventually, patches coalesce to form an intact stand. Thus, seed rain

is often referenced as the primary explanation for positive feedbacks associated with shifting boundaries (Malanson 1997).

An understanding of the factors that influence the location of ecological boundaries is important for the analysis of their migration over time. One category of factors that influence boundary formation is extrinsic and includes disturbance. Plant community boundaries resulting from human or natural disturbance answer specific questions regarding biological response patterns, secondary succession, and spatial and temporal patterns. At the local scale, disturbance-generated boundaries between plant communities are often sharp, especially anthropogenic boundaries, such as field edges, urban spaces, or roads (Kent, 1997). Examples of natural disturbances that cause ecological boundaries include flooding, fire, and grazing at local scales (Boughton 2006), and climate change at larger scales (Norman & Taylor 2005).

In the absence of disturbance or other extrinsic factors, vegetation changes may be associated with intrinsic factors. Site-specific variation in environmental factors such as soil type and moisture (i.e. edaphic variables), aspect, or elevation can be measured as different environmental gradients (Gosz 1992). Environmental variation produces site-specific conditions to which biota respond (Ries & Sisk 2004). Gradient analysis allows researchers to search for underlying processes that govern biological responses and that associate with vegetation patterns (Ter Braak & Prentice 1988). Gradient analysis can be performed *a priori* with variables directly measured, or *a posteriori* with gradients inferred from data structure. Either approach allows one to associate ecological boundaries with environmental gradients. The use of gradient analysis for detecting ecological boundaries is validated by the fact that transects directed along gradients are more effective at detecting vegetation patches (Gillison 1985). Ecological boundaries associated with several environmental gradients have been studied in various settings including alpine tree-

lines (Gosz 1992), temperate wetlands (Hoagland & Collins 1997), coastal vegetation (Walker et al. 2003), and Carolina bays (Laliberte et al. 2007). All these studies measured elevation, among other environmental variables. Several other similar studies measured elevation only. These include boundary studies along elevation gradients in California coastal sage-scrub (Hobbs 1986), North Wales grasslands (Zhang & Oxley 1994), a Ohio fen margin (Choesin & Boerner 2002), Ivory Coast forest-savannah (Hennenberg et al. 2005), New Mexico desert vegetation (Orloci & Orloci 1990), Florida scrubland (Boughton et al. 2006), and Eastern Europe alkaline grasslands (Zalatnai & Kormoczi 2004).

There are various methods and techniques for detecting and characterizing ecological boundaries. One common approach consists of detecting ecological boundaries uses line transects perpendicular to and passing through a transition area (van der Maarel 1976). Where plots are contiguous along transects, the moving split-window technique has gained attention in recent years (Kent et al. 2006). This technique, which locates discontinuities in data from a linear series of plots, often is limited to one dimension and applied only for boundary detection purposes, as the multiple transects typically cannot be related in any meaningful manner (Hufkens et al. 2009; Risser 1995). Spatial analysis in transition areas requires multiple transects, providing a multidimensional data set that is often best analyzed using multivariate statistics.

Ordination methods, a subset of multivariate analysis, are used in various ecological research designs to summarize data and reveal ecological trends where other, more traditional, statistics are less adequate (Anderson 1971). Of particular interest is the application of ordination methods to studies involving species-environment relationships, especially along environmental gradients (Ter Braak & Prentice 1988; Zhang & Oxley 1994). As of yet, there is no standard statistical analysis for detecting plant boundaries because appropriate methods depend on the

nature of measured variables and research goals (Hufkens et al. 2009). Disagreement over methods is reflected by the numerous definitions assigned to ecological boundaries (Strayer et al. 2003). Ordination methods using simulated data have been tested and discussed by a number of authors (Kessel & Whittaker 1976; Gauch & Whittaker 1972). As suggested by several recent reviews of ecological boundaries (Riser 1995; Kent 1997; Kark & van Rensburg 2006; Kent et al. 2006; Hufken et al. 2009), there appears to be great potential in the use of ordination methods for the detection and characterization of plant boundaries.

Ordination methods provide several benefits for boundary studies, including their ability to assess differences in species abundance across transition areas. If gradient analysis is employed, then underlying species-environment relationships, whether directly measured or indirectly inferred, can be revealed. Ordination methods have been applied to plant community boundaries for delineating wetlands (Carter 1994; Kirkman 1998; Choesin 2002; Laliberte et al. 2007), examining species interactions along a New Zealand coastal gradient (Walker et al. 2003; Lloyd et al. 2000), analyzing species-environment relationships along an elevation gradient in Venezuela (Baruch 1984), characterizing California coastal scrub vegetation (Hobbs 1986) and Southern Appalachian Mountain vegetation (Whittaker 1967), and locating the distribution limit of a high elevation conifer in Colorado (Stohlgren & Bachand 1997). However, most studies analyze trends for single transects and are unable to make any meaningful spatial conclusions. The only study capable of spatial analysis was limited to a single year and unable to observe temporal trends (Stohlgren & Bachand 1997). The analysis of plant boundary dynamics using a multidimensional data set over multiple years is not well documented in literature.

An increasing amount of literature involves the comparison of different ordination methods (see reviews – Kent & Ballard 1988; Kent et al. 2006). Thus, it is common for studies

that employ multivariate statistics to compare several ordination methods instead of using a single one (Gauch & Whittaker 1972; Gauch et al. 1977; Minchin 1987; Whittaker 1987). One ordination method in particular, principal components analysis (PCA), seldom is applied to spatial analysis of ecological boundaries, but theoretically is sound for some studies (Nichols 1977). PCA has been abandoned for gradient analysis and typically is not applied to boundary detection due to data distortions (Nichols 1977, van der Maarel 1980). The most noted distortion, the "horseshoe effect," occurs where the ends of a series of ordination points are curved towards each other. This distortion is attributed to unimodal species response curves in communities with high beta diversity, a trend often apparent along environmental gradients (Kessel & Whittaker 1976). In response, a newer ordination method, Detrended Correspondence Analysis, was developed to allow the normalization of the segments on the primary ordination axis (Hill & Gauch 1980). However, PCA still appears to be appropriate for gradient analysis in certain instances especially where the segments of the sampled environmental gradient are short and the species exhibit a linear response curve (Nichols 1977; Oksanen 1983). In this paper, PCA is used to detect a plant community boundary. Unlike other studies that compare ordination methods by assessing the nuances of each (Minchin 1987; Whittaker 1987), the primary goal of the current study was to assess the data structure by using PCA to separate the sampling units that are dissimilar in species composition.

In the current study, gradient analysis was employed to detect changes in species composition that appeared to be associated with topography and a short-term flood event that, just weeks after seeding, inundated the lower portions of the tallgrass prairie reconstruction under study. This may have prevented the establishment of sown-species by washing seeds off-site, burying seeds in sediment, or causing seed death. The flood zone was dominated by weedy

unsown-species, whereas the adjacent upland area, located above the flood line, was dominated by sown-species. Differences in species composition associated with elevation were perceived to occur along the flood line and could be attributed to the combination of site modification followed by flood disturbance. Direct gradient analysis was repeated three years and fifteen years after site establishment, which provided an indirect method to examine any effects of flood disturbance on long-term vegetation structure. The primary goal of the current study was to examine the impact of the short-term flood event on long-term vegetation structure during the first 17 years after the establishment of a tallgrass prairie reconstruction in East Central Indiana.

The objectives of the current study were to: 1) describe the vegetation of a portion of the Avis Prairie field site encompassing an area that was susceptible to flooding and an adjacent area above the apparent flood pool, 2) test for spatial and temporal changes in the plant community structure across the perceived elevation gradient, 3) assess whether the perceived flood-induced boundary can be identified by changes in the plant community structure across the elevation gradient, and 4) assess shifts of the flood induced boundary (if found to exist) up or down the elevation gradient. The *a priori* questions asked whether the perceived boundary initially existed and whether the boundary had moved during the timeframe of the study. If the boundary had indeed shifted, then we asked whether the spatial pattern of the boundary changed. The null hypothesis is stated as, "No spatial changes in plant community structure have occurred across an elevation gradient during fifteen years of the current study."

METHODS

Study site.—The Avis Prairie, located in Grant County, Indiana (N40°27.2', W85°0), is a 10 ha (25 acre) tallgrass prairie reconstruction (Fig. 1), on land currently owned by Avis

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Industrial Corporation and managed by the Earth and Environmental Science Department of Taylor University. Before the restoration project, the site was planted in row crops and used for pasture. Prior to seeding in late June 1993, the site was treated with Round-up[®] herbicide (glyphosate – produced by Monsanto Co.) in April and tilled in early June. The seed mix comprised 43 species of the regional prairie ecotype (see Appendix). A border approximately 30 m wide was planted with a forb-rich seed mix (>20% prairie forbs) surrounding a grass-rich interior with < 10% forbs. This study was conducted in the grass-rich area in the southern edge of the site. This "mosaic" planting pattern was designed and implemented by Peter Schramm of "Prairie Restorations," Galesburg, IL. Site management has included spring burns from 1994 to 2008, except for a fall burn in 2005, and periodic selective glyphosate treatments on field thistle (*Cirsium arvense* (L.) Scop.) in areas of the site not used for this study (McIndoe et al. 2008).

Heavy rains in July 1993 caused flooding that inundated the lower portions of the eastern edge and southeastern corner of the study site that was contained by an east-facing slope. Local precipitation reports from Marion (Station 2 N), IN, < 20 mi away, recorded a total of 170 cm of precipitation in July 1993, several days exceeding 15 mm, and one day exceeding 50 mm (Indiana State Climate Office 2010). This flood zone has been prone to intermittent flooding, but not to the extent of the 1993 growing season. Mean annual precipitation is 991 mm and mean annual temperature is 10.2 ° C for the local area. Annual precipitation ranged from 728 mm to 1,389 mm during the course of the current study from 1993 to 2010 (Indiana State Climate Office 2010).

Initially, species composition in the flood zone was typical of old-fields in the local area (Squiers 1989). Several prairie sown-species established successfully in areas above the flood line (Rothrock and Squiers 2003), whereas areas of the study site affected by intermittent

flooding resembled a wet meadow where unsown-species were dominant (McIndoe et al. 2008). Within the flood zone, the substrate of the topographic gradient transitions from heavily eroded Morley Series clay subsoil in higher areas to Bono series silty clay in lower areas (Jensen et al. 1983). Initial differences in species composition did not appear to be associated with soil type.

Permanent monitoring transects.—In 1995, three pairs of transects were arranged along the east-facing slope that contained flood waters in order to monitor vegetation change as a result of flood disturbance. All transects were positioned parallel to the perceived flood boundary. One pair of transects was positioned in the flood zone (transects 1 & 2), another in the upland zone (transects 5 & 6), and a third in the transition zone (transects 3 & 4) (Fig. 1). Pairs of transects were positioned approximately twenty meters apart and separated from other transect pairs by approximately sixty meters. All transects were fifteen meters in length.

Topographic grids.—In 1995, five transects, ranging from 9 m to 16 m in length, were positioned perpendicular to the apparent flood boundary with either end extending into adjacent plant assemblages (Fig. 2). This sampling method was utilized in order to test for spatial changes in the plant community structure across the perceived elevation gradient. Transects were aligned down-slope along the elevation gradient of which the apparent flood line was associated. The east ends of transects were uniformly spaced at approximately five meters apart. All transects gradually converged down-slope in order to remain perpendicular to the natural topography of the east facing slope. Six sampling points were located uniformly at 0.12 m elevation intervals along each transect, forming a topographic grid. Elevation changes were located using basic land surveying techniques with an optical theodolite (David White® Meridian LT6-900 Level-Transit) and measuring rod.

In 2010, the original 1995 topographic grid was reestablished (Fig. 3) and three additional transects were added to the south side of the grid in order to expand the analysis along the slope. All transects were lengthened by an additional fifteen sampling points in order to extend past the perceived new plant community boundary that had appeared to shift down-slope since 1995. This sampling method was utilized in order to test for temporal changes to plant community structure and shifts of the flood induced boundary. The first thirteen sampling points down-slope were located at 0.12 m elevation intervals mirroring 1995 grid design. Sampling points fourteen to eighteen were located at 0.06 m elevation intervals in order to restrict the distance between each sampling point to < 10 m. Sampling points nineteen to twenty-one were located either at 0.06 m elevation intervals or at 10 m from the previous sampling point where a 0.06 m elevation change did not occur within 10 m from the previous sampling point. The extended topographic grid contained twenty-one sampling points (twenty elevation intervals) and eight transects. For both years, sampling points included paired quadrats (1 m × 1 m) spaced one meter apart.

Sampling.—Data were collected along each of the permanent monitoring transects from fifteen randomly selected 0.25 m × 0.25 m quadrats. The original quadrats were sampled annually from 1995 to 1998. For the 2000, 2003, 2005, and 2010 data collection, three additional quadrats were added to each transect for a total of eighteen. The topographic grid quadrats (1 m × 1 m) were sampled in 1995 and 2010. Sampling was conducted in late July or early August and included estimated percent cover and density for all plant species for both the monitoring transects and the topographic grid according to methods described by Kent & Coker (1992). Percent cover was estimated and rounded to the nearest ten percent for values ranging from ten to one hundred and to the nearest whole percent for values ranging from one to nine. Values

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between 0.0% and <0.5% were rounded to 0.5%. For the topographic grids, density values of

graminoids were collected according to "clumps" in 1995 and according to tillers in 2010 due to

differences in plant size related with plant age. The variable and relatively large size of

graminoid "clumps" prevented an accurate assessment of density according to data collection

methods in 1995, which limited the comparison of graminoid density between sampling years.

Nomenclature follows the US Department of Agriculture Plants Database (USDA 2010).

     Data analysis.—Descriptive statistics of the data from permanent monitoring transects

were used to assess the temporal trends across the upland and flood zones. Species present in the

initial seed mix (sown-species) were grouped separately from species not present in the initial

seed mix (unsown-species). Groupings allowed long term monitoring at the interface of prairie

sown-species adjacent to an area dominated by unsown weedy species. Species cover values

were relativized to allow the comparison of data between sampling dates and adjust for

differences in plant sizes. Original cover values were used for analysis of individual years.

     Data from paired quadrats were totaled for each sampling point on the topographic grids.

Hereafter, paired quadrats are referred to as "plots," and "sampling point" refers to the point

along transects where paired quadrats were located. The variation between quadrat pairs and that

of sampling points was compared using two-way analysis of variance General Linear Model in

Minitab statistical software (Minitab Incorporated 1988, version 15). The two factor analysis

included cover values of paired quadrat data and elevation intervals.

     Plot ordinations of species cover values from the topographic grid data were performed

with principal components analysis (PCA) using PC-ORD™ Version 5 (McCune and Mefford

2006). PCA uses eigenanalysis to project a set of points with respect to plot dissimilarity.

Ordination points were calculated from a variance/covariance matrix of species scores based

upon weighted averages (McCune and Grace 2002). The main matrix for PCA was comprised of cover values from the topographic transects, and a second data matrix included the elevation of position for each sampling point. The utilization of both PCA matrices allowed us to test for a flood-induced boundary across an elevation gradient by separating dissimilar plots with respect to species composition. Plot ordinations were performed on four data sets in order to attempt to detect boundaries and to examine changes in species composition by comparing data from 1995 and 2010. The four data sets were: 1) 1995 species cover values, 2) 1995 and 2010 combined relative species cover values, 3) 2010 species cover values for the first six elevation intervals similar to the 1995 data set, and 4) 2010 species cover values for all elevation intervals from the extended transects. PCA reduced data to two principal dimensions allowing the detection of patterns in species composition between elevation intervals and across transects. In addition to PCA, two other ordination methods, detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMS), were explored. Groups of similar sample plots were determined from hierarchical cluster analysis using Ward's method with a Relative Euclidean distance measure in PC-ORD™ (McCune and Mefford 2006).

RESULTS

Vegetation Description.—Mean relative cover for sown and unsown-species revealed striking temporal trends when groups of species were plotted as a function of time (Figs. 4–9). First, sown-species cover increased, overall, for all transects during the fifteen years of the current study (Figs. 4–9). For most years, sown-species cover was highest in the upland zone and lowest in the flood zone (Figs. 4, 8). Because these results were relativized, unsown-species cover consistently revealed an opposing trend and unsown-species cover was lowest in the

upland zone and highest in the flood zone (Fig. 5, 9). The transition zone was intermediate in terms of sown-species cover (Fig. 6, 7). An exception to this trend was observed in the upland zone for years 1996 and 1997. During this two year period, prairie species appeared to be establishing themselves and cover values for unsown-species remained similar to or higher than cover values for sown-species. After this initial decline, sown-species cover increased above 90% by year 2003 and remained relatively unchanged during the following seven years of the study. The increase in sown-species cover for the flood and transition zones was more gradual than that of the upland zone. Sown-species cover of the transition and flood zones was very low during the initial years, and since has steadily increased.

Second, the experimental zones exhibited different levels of between-plot heterogeneity. The variation in species cover was greater in the upland zone compared to the transition and flood zone from 1995 to 1997 (Figs. 4–9). This pattern changed after the year 2000 when the variation in species cover was greater in the transition and flood zones than in the upland zone. During the remaining ten years of the current study, between-plot heterogeneity remained higher in the transition and flood zones than in the upland zone.

Finally, results from pairs of transects were not always consistent (Figs. 4–9). In the upland zone, species cover of transect pairs (transects 5 and 6) initially were different and converged over time (Figs. 4, 5). For the initial ten years, transect 6 had higher sown-species cover than transect 5, except for year two where mean values were relatively comparable. Conversely, species cover of transect pairs in the transition zone (transects 3 and 4) initially were similar and diverged over time (Figs. 6, 7). After year three, sown-species cover of transect 4 remained higher than transect 3. Species cover of transect pairs in the flood zone (transect 1 and

2) were not meaningfully different for consecutive years, although sown-species cover of transect 2 was slightly higher than transect 1 for most sampling years (Figs. 8, 9).

Summary statistics for both sampling years of topographic grid data (Table 1) provide an overview of species cover and density values for all sampled quadrats. In 1995, mean percent cover of four dominant species comprised 54% of the total percent cover for all quadrats. In descending order, these species were *Rudbeckia hirta*, *Andropogon gerardii*, *Setaria faberi*, and *Sorghastrum nutans*. By 2010, two dominant species, *A. gerardii* and *Solidago altissima*, accounted for 85% of the total percent cover for all quadrats, and one, or both of these species were observed in all quadrats.

Vegetation Dynamics.—For all analyses using ordination, reducing the data to the first two axes was sufficient for the determination of plot dissimilarity and its association with an elevation gradient. The summation of cover values from quadrat pairs for use in ordinations was appropriate based upon the General Linear Model that indicated the cover values of paired quadrats were not significantly different for any species and there was no interaction (quadrat pair × elevation) between paired quadrants and sampling intervals. In addition, no obvious "horseshoe effect" was observed for any ordination graph. Data distortion, if it occurred at all, did not hinder the interpretation of plot dissimilarity according to the separation of plots in ordination space. All species exhibited a linear response curve, which met the assumptions of PCA, as determined by repeated analyses of individual species abundance plotted as a function of elevation. As a result, beta diversity remained relatively low because a short segment, not the entirety, of the environmental gradient was sampled.

Plot ordination and cluster analysis of 1995 data demonstrated that plots were not evenly distributed along an elevation gradient in terms of species composition. The principal

components analysis (PCA) of cover values revealed an abrupt change in species composition between elevation intervals 3 and 5 (Fig. 10). PCA extracted 62.9% of the variation in the data in the first two axes, which separates to 50.3% for axis 1 and 12.6% for axis 2. Elevation intervals 1 to 3 were consistently grouped together for all transects, and elevation intervals 5 and 6 were separated and scattered from this group. Elevation interval 4 was not grouped consistently with intervals 1 to 3 or 5 and 6, and represented the transition between the two groups of plots. Elevation data were included in a second data matrix and provided a single elevation vector shown in the PCA biplot. By aligning parallel to PCA axis 1, the elevation vector was strongly associated with the majority of variation in the data set.

The separation of plots along PCA axis 1 was associated with variable cover values for three dominant sown-species, *R. hirta*, *A. gerardii*, and *S. nutans*, and two dominant unsown-species, *S. faberi* and *Trifolium repens* (Fig. 10). Cover values for the three sown-species were consistently high for elevation intervals 1 to 4 for all transects. *Rudbeckia hirta* was most influential of the three dominant sown-species. Cover values for *R. hirta* were highest in two points farthest on the left side of PCA axis 1 (3f and 1f). Cover values for the two unsown-species, *S. faberi* and *T. repens*, were consistently high in elevation intervals 5 and 6. Cover values for *S. faberii* were especially high in plots on the right side of PCA axis 1. In general, the further a point was toward the right side of the plot, the higher the cover value for *S. faberii*. The separation of plots along PCA axis 2 was associated with the presence of several scattered and relatively large patches of *Setaria glauca*. The large separation of two points, 5h and 5g, from all other points on PCA axis 2 was associated with very high cover values for *S. glauca*. Cover values for *S. glauca* were highly variable and the species was absent from the majority of plots. The remaining separation of plots along PCA axis 2 was associated with the variable cover

values of a single dominant sown-species, *S. nutans*, and two dominant unsown-species,

Ambrosia artemisiifolia and *Symphyotrichum pilosum*. Cover values for *S. nutans* and *S. pilosum*

were high for points low on PCA axis 2. Cover values for *A. artemisiifolia* were high for points

in the middle of PCA axis 2, and separated from groupings lower on PCA axis 2.

In addition to the patterns associated with dominant species, several subdominant species

also exhibited a unique pattern. Three subdominant unsown-species, *A. artemisiifolia*, *S.*

pilosum, *Oenothera biennis*, had moderately high cover values in plots from the first four

elevation intervals, but were either absent or had very low cover values in plots from elevation

intervals five and six. *Ambrosia trifida* also contributed to this trend, but was absent from the

majority of plots. Thus, groupings of plots were associated, for the most part, with a separation

of dominant sown and unsown-species, but several subdominant unsown-species associated with

sown-species also contributed to this pattern.

The species composition of plots changed considerably during the fifteen years of the

current study. The PCA of combined data from both sampling years of the original topographic

grid revealed marked differences in species composition between sampling years (Fig. 11). PCA

extracted 89.9% of the variation in the data along the first two axes, which separates to 76.9% for

axis 1 and 13.1% for axis 2. Two trends were observed in regards to temporal vegetation

dynamics in this area of the topographic grid. First, between plot heterogeneity decreased and

vegetation became more uniform over time, as depicted by the tight cluster of points for 2010

plots (Fig. 11). Also, 2010 plots exhibited a much greater similarity in terms of species

composition than plots from 1995. Plots initially comprised a greater diversity of sown-species

and cover values of unsown-species of most plots were > 10. Over time, sown-species became

dominant with *Andropogon gerardii* comprising the vast majority of sown-species cover.

Second, changes in species composition along an elevation gradient detected in 1995 were no longer persistent in 2010 for the same plots. In sum, species composition differed in association with elevation in 1995, but not in 2010.

The separation of plots along PCA axis 1 was associated with variable cover values of one sown dominant species, *A. gerardii*. In 2010, the species composition of all plots was dominated by *A. gerardii* (> 75% per 1m^2). In 1995, cover values for *A. gerardii* were highly variable, ranging from 0 to 70%. As a result, plots from 2010 were very closely grouped on the right of PCA axis 1, and plots from 1995 were grouped on the left of PCA axis 1. The separation in the 1995 plots was associated with variable cover values for *A. gerardii* within 1995 data. Plot 3e has the highest cover value for *A. gerardii,* and was furthest to the right of the 1995 plots. In contrast, plot 1g has the lowest cover value *A. gerardii* for elevation intervals 1 to 3*,* and was the furthest left of the primary group of 1995 points. The separation of plots along PCA axis 2 seemed to be associated with the variable cover values in the 1995 data. The pattern of 1995 plots, when plotted with the 2010 data, was similar to the 1995 data plotted by itself (Fig. 10). Elevation intervals 1 to 3 are grouped together in the lower portion of PCA axis 2. Elevation intervals 5 and 6 are separated towards the top of PCA axis 2. The elevation vector was nearly parallel to PCA axis 2, which suggests that plots spread along PCA axis 2 were associated with an elevation gradient. 1995 data account for the separation of plots of PCA axis 2 and therefore are strongly associated with an elevation gradient. Conversely, the 2010 plots show no consistent variation related to elevation in species composition or cover values along PCA axis 2.

The tight cluster of points for 2010 data, when plotted with 1995 data (Fig. 11), prevents easy analysis of species composition. Thus, cover values from the 2010 sample of the original topographic grid were plotted without 1995 data (Fig. 12) in order to more effectively examine

this tight cluster of data points. PCA extracted 85.6% of the variation in the data along the first two axes, which separates to 66.2% for axis 1, and 19.4% for axis 2. The species composition of all plots was dominated by *A. gerardii* ($> 75\%$ per $1m^2$). The remaining variation in species composition created no pattern between plots of similar elevation. In addition, the elevation vector was absent from the graph even though the data were still included in the analysis. This indicates that plots were not sorted along an elevation gradient for this subset of plots. The separation of plots along PCA axis 1 was associated with varying cover values for *Silphium integrifolium*, and the plot most separated from all others (1d) had the highest cover value for this species. The remaining variation of PCA axis 1 was associated with variable cover values for *A. gerardii*. The separation of plots on PCA axis 2 was associated with variable cover values for *S. altissima* and the single plot with a relatively moderate cover value (20%) for *S. integrifolium* (1d).

Boundary Detection.—In order to assess whether the perceived flood-induced boundary can be identified by changes in the plant community structure across the elevation gradient, plots were grouped using cluster analysis. Cluster analysis distinguished two groups of plots from the 1995 data (percent chaining = 5.06) according to similarities in species composition and provided a dividing line for the separation of plots observed from the ordination. The separation of data into two groups along elevation interval four was presumed to represent the boundary associated with short-term flooding. The group of plots dominated by sown-species was presumed to indicate an area above the flood line. The other group of plots dominated by weedy unsown-species was presumed to indicate the portion of the Avis Prairie study site affected by flooding.

Descriptive statistics for both groups revealed specific differences in species cover and density (Table 2). Of the four dominant species determined from summary statistics of all quadrats (Table 1), three had much higher cover and density values in the first group of plots. All three were sown-species including *R. hirta*, *A.gerardii*, and *S. nutans*. The forth dominant species, *S. faberii*, was almost entirely located in the second group, and was the only dominant unsown-species. In addition to these four dominant species, two subdominant unsown-species were also responsible for the separation of plots into two groups. *A. artemisiifolia* had much higher mean cover and density values in the first group. In contrast *T. repens*, had much higher mean cover and density values in the second group, similar to *S. faberii*.

The detection of the boundary in 2010 was more complex and involved the use of cluster analysis as well as an interpretation of the PCA of the data from the extended topographic grid (Fig. 13). The separation of plots along PCA axis 1 was associated with variable cover values for one dominant sown-species, *A. gerardii*, and three dominant unsown-species, *S. altissima*, *Persicaria pensylvanica*, and *Phalaris arundinacea*. Plots with high cover values for *A. gerardii* were grouped towards the left of PCA axis 1. Plots with high cover values for *S. altissima*, *P. pensylvanica*, and *P. arundinacea*, and low cover values for *A. gerardii* were scattered towards the right of PCA axis 1. The separation of plots along PCA axis 2 was associated with variable cover values for one sown-species, *Silphium laciniatum*, and one unsown-species, *Cirsium arvense*. Cover values for *S. laciniatum* and *C. arvense* were greatest in plots located high on PCA axis 2. The elevation vector was parallel to PCA axis 1, which suggests the majority of the variation in the data set was strongly associated with an elevation gradient. Four groups were used from cluster analysis (percent chaining = 1.58) instead of two because the division between the two plant assemblages was wider. The second and third groups from the cluster analysis were

more similar to each other than either the first or fourth group in terms of species cover for the

six most dominant species. The second and third groups were combined and presented as a single

group (group 2) in order to simplify the interpretation of the plant boundary and identify the

boundary in 2010. The fourth group derived from cluster analysis was therefore presented as the

third group.

Descriptive statistics for three groups of plots from 2010 data (Table 3) reveal the key

species that account for the plot separation observed from the ordination. The two most abundant

species, determined from summary statistics for all plots (Table 1), were not equally distributed.

The most abundant species overall, *A. gerardii*, had much higher mean cover and density in the

first and second group compared to the third group. Mean cover and density values for *A.*

gerardii were highest in the first group (95.1% and 429.8, respectively), intermediate in the

second group (61.8% and 244.4, respectively), and lowest in the third group (11.5% and 46.1,

respectively). The second most abundant species, *S. altissima*, exhibited an opposite spatial

sorting pattern. Mean cover and density values for *S. altissima* were lowest in the first group

(0.8% and 1.1, respectively), intermediate in the second group (20.2% and 24.5, respectively),

and highest in the third group (56.5% and 73.3, respectively). The third most abundant species,

P. pensylvanica, behaved similarly to *S. altissima*, and was mostly located in the third group.

Boundary Shift.—The boundary detected in 1995 was not detected at the same sampling

location in 2010. The plant boundary was perceived to have shifted down-slope. Transects were

extended down-slope until a different plant community was reached in order to detect a shift in

the plant community boundary since 1995. Ordination of the extended topographic grid revealed

a different pattern of plot separation in ordination space (Fig. 13) than that observed in 1995

(Fig. 10). PCA extracted 92.9% of the variation in the data along the first two axes, which

separates to 87.9% for axis 1 and 5% for axis 2 (Fig. 13). A boundary shift was confirmed by the tight cluster of plots from most elevation intervals from one to twelve on the left of PCA axis 1. The species composition of these plots was very similar, whereas the species composition of elevation intervals five and six were very different in the 1995 ordination (Fig. 10). The 2010 boundary, as described in the previous subsection (i.e. Boundary Detection), moved downslope approximately twenty meters.

Synthesis of the analyses described above reveals the spatial trends between sampling years. In 1995, changes in species composition along an elevation gradient were abrupt and were more or less consistent for individual elevation intervals. This sharp boundary was detected at a finer scale and was limited to an elevation change of 0.24 meters (i.e. two elevation intervals), which required only sixteen meters in transect length to detect. Cluster analysis determined two distinct plant assemblages from plot ordinations. The 2010 boundary was more diffuse than the 1995 boundary and required approximately eighty meters in additional transect length in order to detect. Changes in species composition occurred more gradually along an elevation gradient which was less consistent across individual elevation intervals than those in 1995 data. Three general groups were determined based upon the cluster analysis (percent chaining = 1.58). Groups 1 and 3 were the most dissimilar groups of plots and were separated by approximately fifty meters in transect length. *Andropogon gerardii* was dominant in the group of plots located in an upland setting and *S. alitissma* was dominant in the other group of plots in the flood zone. Group 2 plots comprised a heterogeneous mix of *A. gerardii* and *S. altissima* and other subdominant sown or unsown-species which may best define the wide and diffuse boundary in 2010. Indeed, species cover of *A. gerardii* in group 2 plots increased slightly the closer a plot was to group 1, and species cover of *S. altissima* increased the closer a plot was to group 4.

Moreover, this interspace between group 1 and 4 comprised, to slightly differing degrees, a heterogeneous mix of similar species which separated one homogeneous group from the other.

DISCUSSION

Overall, the results indicate that a flood-induced boundary shifted and changed spatially during the fifteen years of the current study. Three years after site establishment, a sharp plant boundary was detected and species composition changed abruptly along an elevation gradient. The boundary divided two distinct plant communities along the flood line between a flood zone and an adjacent upland area. Changes in species composition were strongly associated with elevation, which suggests the boundary was a result of flood disturbance soon after site preparation and initial seeding. After fifteen years, this artificially created boundary became more diffuse and resembled a gradual transition with numerous patches of expanding species scattered in space along the boundary front. The association between species composition and elevation weakened, but was still detected. In general, prairie sown-species have expanded down-slope into an area previously dominated by weedy unsown-species, revealing a competitive advantage of sown-species over unsown-species. Despite this trend, the distinct plant communities of upland and flood zones have persisted since site modification. Flooding, just weeks after initial seeding, has had lasting effects, although the initial effects have diminished.

A change in boundary location was evident based upon the analysis of data from both the monitoring transects and the topographic grid. Along all monitoring transects, sown-species cover increased, while unsown-species cover decreased. More importantly, sown-species cover gradually increased in the flood zone where these species were nearly absent during the initial

sampling years. This trend suggests that a directional migration of the boundary between sown and unsown-species has occurred. This conclusion is further supported by results from topographic grid data that provide more specific details concerning the distance of boundary migration. In order to detect the 2010 boundary, topographic transects from 1995 were extended approximately eighty meters. This distance effectively passed through the community boundary based upon the fact that species composition of plots at both ends of transects were most dissimilar.

Boundary migration did not occur as a uniform front moving through space. Instead, the boundary changed from a sharp boundary to a gradual transition, with numerous patches of the expanding sown-species. Most topographic transects exhibited "gaps" in sown species cover where plots dominated by unsown-species separated individual plots dominated by sown-species. Plots dominated by sown-species are scattered and did not uniformly progress down-slope. Also, the distribution of sown-species was patchy in the flood and transition zones when compared to the uniform cover of sown-species in the upland zone. This was apparent from visual observation during field sampling and was supported by greater variation in sown-species cover in the transition and flood zones compared to the upland zone.

The spatial change from a sharp boundary to a gradual transition resulted in increased boundary width. Direct gradient analysis of topographic transects provided a means to assess the association of changes in species composition with elevation. Within this framework, the spatial differences over time were used to determine effects of short-term flooding on long-term prairie establishment. The results from the topographic grid in 2010 demonstrated that plots of the same elevation did not exhibit similar species composition, unlike those sampled fifteen years earlier. As a result, the association between species composition and elevation diminished over time. In

addition, elevation intervals showed a progressive pattern along the first ordination axis where the majority of the variation in the data is represented. The results from the monitoring transects also demonstrated this weakened association between species composition and elevation over time. Transect pairs in the upland and flood zones were relatively similar in terms of sown-species cover. By contrast, the pair of transects in the transition zone showed clear differences in sown-species cover. The initial placement of this transect pair in both distinct plant communities, with the flood boundary between the transect pair, likely caused this pattern. These observations suggest that the transition zone represented a continuum of species compositions along the slope, which may have implications for debates regarding biological responses along gradients (Austin 1985; Hoaglands & Collins 1997).

A critical question to ask is how the boundary in the current study fits with previous models that explain spatio-temporal boundary dynamics. Several studies that propose a predictive model for boundary dynamics discuss the potential role of disturbance such as fire, flooding, grazing, windfall, animal burrows, or climate change (Wiens et al. 1985; Risser 1995; Peters et al. 2006a). In addition, they suggest that the severity, nature, and duration of disturbance can cause variable vegetation patterns. In the current study, there was a disturbance due to site modification (i.e., tilling and herbicide treatment) and due to flooding that resulted in variable seeding density across the study site. Additional variability in species distribution and community expansion may be influenced by the edaphic conditions present in Avis Prairie study site and the fire management regime. Peters et al. (2006a) predicted that boundary dynamics were controlled, to a degree, by site-specific abiotic constraints and biotic factors following disturbance. Furthermore, if a human-induced disturbance modifies the boundary, then secondary succession will eventually restore the original boundary. If this is the case, then the

boundary in the current study most closely follows the description by Kent et al. (1997) that reads, "Human-created boundaries…tend to be the sharpest, with a 'softening' of the boundary occurring where past activity has now been abandoned and the vegetation of the transitional area is returning towards a more semi-natural state (p 326)." Although flooding is a natural event, the ecological boundary in the current study can be described as human-induced in that the anthropogenic site modifications made prior to flooding were the principal factors that influenced vegetation patterns.

The pattern of community expansion observed in the current study is similar to that described in the literature for studies of shifting boundaries. Norman and Taylor (2005) characterized pine forest expansion into an adjacent meadow as a complex "leap and infill (p 56)" process, distinctly different from a uniform shift. In their study, trees encroached as isolated units and the space between them gradually filled over time. Similar accounts of infilling by expanding species have been recorded and explained in several other ecosystems. Romme et al. (2009) characterized shrub expansion into grassland in the Desert Southwest as expansion followed by infilling. Halpern et al. (2010) found that the spatial structure of infilling differed for two species of conifers expanding into alpine meadow. Basically, a shade intolerant species performed the expansion step, while a shade tolerant species performed the subsequent infilling. In the Chihuahuan Desert, Peters et al. (2006b) provided an explanation for the pattern of shrub expansion and infilling that they observed. Contrary to previous theories of plant population expansion, they found that the size of patches did not decrease with distance from the boundary front. Instead, large patches were separated from the boundary front by smaller patches. This pattern was explained by different processes that govern plant population expansion. They suspected that infrequent, long distance seed dispersal events created patches under favorable

conditions. Then, a more typical infilling process between patches followed. The results from the current study indicate an early stage of infilling based upon greater between-plot heterogeneity in the flood zone compared to the adjacent area that was not affected by flooding.

There are different types of migrating boundaries. Peters et al. (2006a) distinguishes between directional and shifting transitions based upon the strength of abiotic and biotic factors that influence the boundary. Shifting transitions are primarily controlled by inherent abiotic constraints. Any vegetation shift likely is in direct response to shifts in abiotic factors. Conversely, directional transitions are governed by biotic drivers such as invasive species. Once established, these species further expand through site modifications and positive feedback mechanisms. Thus, strong abiotic factors control shifting transitions, whereas biotic feedbacks are key factors controlling directional transitions. Within this framework, the boundary detected in the current study most closely resembles a directional boundary. Individual species characteristics most likely played a stronger role in boundary dynamics than edaphic site conditions. Consequently, several prairie sown-species, especially *A. gerardii*, appeared to fulfill the role of expanding species within this tallgrass system.

The primary mechanism responsible for prairie community expansion likely was dispersion of propagules via seed rain or propagules in runoff waters. Since the study site historically did not support tallgrass prairie vegetation, one can rule out a persistent soil seed bank as an explanation for sown-species recruitment into the flood zone. Peart (1989) found seed rain to be crucial in species recruitment during grassland succession, and it was predominantly comprised of species dominant in nearby vegetation patches. Likewise, in the current study, the most dominant species in the upland zone (i.e. *A. gerardii*) was recruited in the flood zone far more than any other sown-species established in the upland zone. This observation may suggest

the existence and potential role of positive feedback mechanisms in species recruitment. If expanding species establish in adjacent habitat, then further expansion is possible due to additional new seed sources (Malanson 1997). If this process occurred in the current study, then it was initiated soon after seeding, as indicated by increased sown-species cover in the flood zone a few years after sampling began. However, there is a possibility that patches of sown-species in the flood zone occurred as a result of postponed germination after initial seed burial.

Community expansion can be influenced by anthropogenic factors such as land cover change, (Hardt & Forman 1989), human-controlled grazing (Sankey et al. 2006), and fire suppression (Halpern et al. 2010). In some instances, a combination of the aforementioned environmental and anthropogenic drivers may interact (Norman & Taylor 2005). The principal anthropogenic factor that may explain the temporal pattern observed in the current study is fire management. Most prairie species are adapted to fire management where canopy gaps are opened, which favors their colonization. In absence of fire, colonization of new species decreases over time as a continuous canopy of perennial species prevents new species recruitment (Bartha et al. 2003). Due to this ecological trend, we speculate the boundary would not have expanded to its present extent had the Avis Prairie study site not been annually burned. Frequent burning may have prevented unsown perennial establishment and reduced canopy cover, favoring the colonization of sown-species into adjacent habitat. Fire management likely is the most influential human-induced change to the system that resulted in prairie community expansion (Towne & Owensby 1984).

A related component of fire management as an explanation for boundary migration involves interspecific competition during ecological succession. Most of the sown-species that quickly established in the upland zone were late successional species. The competitive ability of

late successional species often increases during succession (Tilman 1988), and certain prairie species have been found to out-compete weedy species (Blumenthal et al. 2004). Based upon these observations, sown-species recruitment and expansion likely was due to a competitive advantage of sown-species over unsown-species. Changes in species composition of the upland zone were characteristic of areas of the study site where prairie reconstruction was successful (McIndoe et al. 2008). The flood zone and portions of the transition zone initially were dominated by weedy species, with seed sources presumably either from the soil seed bank or seed rain from the surrounding area. In these zones, sown-species cover remained lowest, which likely was due to an absence of propagules of sown-species. As a result, there was a lag time between sown-species establishment in the upland zone and their recruitment in the flood zone. The rate of expansion also may have been increased by initial tilling prior to seeding (Foster et al. 2007). However, the sampling design of the current study was not suited to determine the degree to which tilling or fire management influenced this possible competitive advantage.

In addition to extrinsic factors, such as tilling and fire, several natural intrinsic factors may have influenced the prairie community expansion that was observed in the current study. Wearne and Morgan (2001) found that abiotic and biotic factors controlling seedling recruitment across a shifting boundary may be site-specific. Specifically, the rate of boundary migration may be affected by intrinsic abiotic factors more than biotic factors. In their study, soil moisture was the most influential abiotic factor for explaining the variation in seedling recruitment. Conversely, variation in seedling recruitment was not affected by biotic factors including ground cover type, biomass, and seedling number. In the current study, soil moisture likely is the most influential abiotic factor controlling seedling recruitment down-slope, although it was not

measured directly. The flood zone has been prone to intermittent flooding, which could have further inhibited sown-species recruitment of certain species established in the upland zone.

The specific spatial variation in species composition observed in 1995 is notable, but of less direct relevance to overall temporal trends already discussed. The primary differences between the distinct plant communities on either side of the flood line involve between-plot heterogeneity and species sorting. The plant community affected by flooding had greater between-plot heterogeneity, which may indicate different initial seed sources that were influenced by variations in soil conditions and topography inherent in both areas. The upland zone received a uniform spread of species in the initial seed mix. Conversely, the seed source of the flood zone likely was the existing soil seed bank and other stochastic sources such as wind dispersion. The soil seed bank in particular has been found to be quite heterogeneous (Rothrock et al. 1993), which may have created greater between-plot heterogeneity than seeding methods of conventional prairie reconstruction. In addition, the weedy unsown-species sorted differently across the flood-induced boundary. Two common old-field species, *A. artemisiifolia* and *S. faberii*, were partially responsible for the observed boundary effect observed in 1995. These species may not have been affected by short-term flooding to the extent sown-species were because they can persist in the soil seed bank. However, their spatial pattern suggests that the timing of disturbance may have altered species establishment. *Setaria faberii* has been found to germinate after a disturbance through more of the growing season than *A. artemisiifolia* (Squiers 1989). The time of flooding may have prevented germination of *A. artemisiifolia* in low plots where *S. faberii* was dominant. In plots not apparently affected by flooding, *A. artemisiifolia* was subdominant in addition to several other sown-species, and *S. faberii* was nearly absent. One can

speculate that *S. faberii* would not have been dominant in low plots if flooding had not occurred or if it occurred later in the growing season after *A. artemisiifolia* would have germinated.

Ordination methods were effective for boundary detection by separating dissimilar plots according to species composition. In addition, plot ordinations depicted temporal changes in species composition across the shifting boundary. The measured elevation gradient was closely associated with the majority of the variation in the data when a boundary was detected. The application of PCA for direct gradient analysis in the current study affirms its use for similar research goals and expands the versatility of this ordination technique.

Alternative data manipulations performed by DCA and NMS seemed not to benefit data interpretation. The spatial pattern of plots was very similar to that of PCA. NMS did not change the overall pattern of plots in ordination space and it did not provide a direct link between ordination axes and the separation of plots. Slight shifts in groups of sampling points provided no advantage for analyzing patterns of species composition between sampling points or along an elevation gradient. Despite the different nuances that exist between these ordination techniques, their performance for the particular objectives of the current study, and those of other studies involving short coenoclines (Oksanen 1983; Kent & Ballard 1988), are comparable.

In a recent review of studies involving boundary dynamics and related methodologies, Hufkens et al. (2009) emphasized the importance of spatial and temporal analysis in combination. Boundary dynamics are multi-dimensional, and, as such, require a two-dimensional sampling method that is repeated in time. This approach, which can be applied to various studies examining vegetation dynamics, aided our analysis of a shifting boundary. Although this approach may require additional time for data collection, future research concerning boundary dynamics may find benefit from it when assessing spatial changes that influence temporal trends.

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Table 1. Mean percent cover and density values for all quadrats sampled in 1995 (n=60) and 2010 (n=336) for topographic grid. Values are x̄ ± standard error. Values of species with mean cover ≤0.1% and mean density ≤0.1 were totaled as "all others."

Species	% Cover		Density	
	1995	2010	1995	2010
Abutilon theophrasti Medic.	0.13 ± 0.08	–	0.50 ± 0.26	–
Acalypha rhomboidea Raf.	0.05 ± 0.03	0.07 ± 0.01	0.53 ± 0.33	0.11± 0.03
Ambrosia artemisiifolia L.	13.12 ± 2.42	0.11 ± 0.02	13.98 ± 2.78	0.22 ± 0.06
Ambrosia trifida L.	2.53 ± 0.97	1.55 ± 0.15	0.73 ± 0.24	2.59 ± 0.27
Andropogon gerardii Vitman. *	19.03 ± 2.69	69.96 ± 1.90	1.77 ± 0.21†	304.0 ± 10.0†
Asclepias syriaca L.	–	0.34 ± 0.05	–	0.26 ± 0.03
Cirsium arvense (L.) Scop.	0.58 ± 0.26	0.57 ± 0.17	0.42 ± 0.17	0.82 ± 0.27
Conyza canadensis (L.) Cronquist	0.57 ± 0.34	–	0.35 ± 0.12	–
Desmodium canadense (L.) DC. *	3.18 ± 0.84	0.40 ± 0.12	0.37 ± 0.08	0.28 ± 0.07
Echinochloa crus-galli (L.) P. Beauv.	0.37 ± 0.20	–	1.12 ± 0.49	–
Erigeron annuus (L.) Pers.	–	0.13 ± 0.02	–	0.29 ± 0.05
Euthamia graminifolia (L.) Nutt.	–	0.12 ± 0.09	–	0.11 ± 0.08
Hibiscus trionum L.	0.92 ± 0.24	0.13 ± 0.02	3.73 ± 1.05	0.24 ± 0.04
Lactuca serriola L.	0.40 ± 0.19	–	0.33 ± 0.15	–
Medicago sativa L.	0.17 ± 0.17	–	0.02 ± 0.02	–
Monarda fistulosa L. *	0.72 ± 0.47	–	0.22 ± 0.17	–
Oenothera biennis L.	2.68 ± 0.46	–	10.10 ± 1.76	–
Panicum virgatum L. *	0.35 ± 0.33	0.13 ± 0.07	0.07 ± 0.05†	0.30 ± 0.20†
Persicaria pensylvanica (L.) Small.	0.30 ± 0.14	5.26 ± 0.60	1.12 ± 0.68	7.65 ± 0.90
Phalaris arundinacea L.	2.27 ± 0.79	2.72 ± 0.40	0.30 ± 0.10†	17.67 ± 2.50†
Plantago lanceolata L.	0.38 ± 0.20	–	0.35 ± 0.15	–
Plantago rugelii Decne.	1.25 ± 0.40	–	1.70 ± 0.76	–
Ratibida pinnata (Vent.) Barnhart. *	0.02 ± 0.02	0.35 ± 0.07	0.02 ± 0.02	0.85 ± 0.18
Rudbeckia hirta L. *	23.17 ± 2.66	–	77.00 ± 10.9	–
Rumex crispus L.	0.35 ± 0.19	–	0.18 ± 0.08	–
Setaria faberi Herrm.	14.95 ± 3.85	–	99.68 ± 23.9	–
Setaria glauca (L.) P. Beauv.	8.83 ± 2.20	–	39.15 ± 6.86	–
Setaria viridus (L.) P. Beauv.	1.05 ± 0.85	–	4.45 ± 3.48	–
Sida spinosa L.	0.10 ± 0.08	–	0.55 ± 0.40	–
Silphium integrifolium Michx. *	–	1.01 ± 0.31	–	1.14 ± 0.35
Silphium laciniatum L. *	–	0.89 ± 0.30	–	0.19 ± 0.06
Silphium perfoliatum L. *	–	0.18 ± 0.14	–	0.09 ± 0.07
Silphium terebinthinaceum Jacq. *	–	0.10 ± 0.06	–	0.01 ± 0.01
Solidago altissima L.	–	16.65 ± 1.36	–	21.09 ± 1.81
Sorghastrum nutans (L.) Nash. *	14.58 ± 2.49	1.21 ± 0.29	1.63 ± 0.23†	4.55 ± 1.27†
Symphyotrichum novae-angliae (L.) G.L. Nesom. *	0.20 ± 0.10	0.24 ± 0.08	0.33 ± 0.19	0.29 ± 0.11
Symphyotrichum pilosum (Willd.) G.L. Nesom.	11.80 ± 2.36	–	6.73 ± 1.49	–
Symphyotrichum sp. *	2.55 ± 0.52	–	4.93 ± 0.97	–
Taraxacum officinale Weber.	0.22 ± 0.07	0.25 ± 0.02	0.47 ± 0.17	0.47 ± 0.05
Trifolium hybridum L.	1.52 ± 0.71	–	3.10 ± 1.23	–
Trifolium pratense L.	1.20 ± 0.41	–	3.40 ± 1.18	–
Trifolium repens L.	3.85 ± 0.84	–	14.03 ± 2.68	–
Veronica peregrine L.	–	0.05 ± 0.01	–	0.16 ± 0.04
All others	0.10	0.26	0.03	0.29
Total	133.38	102.42	293.37	363.34

* denotes sown species.

† Density values of grass species were collected according to "clumps" in 1995, and tillers in 2010.

Table 2. Mean percent cover and frequency values for all quadrats sampled in 1995 for topographic grid (Group 1, n=38; Group 2, n=22). Values are x̄ ± standard error. Values of species with mean cover ≤0.1% and mean density ≤0.1 were totaled and presented as "all others." Groups were determined using cluster analysis.

Species	% Cover Group 1	% Cover Group 2	Density Group 1	Density Group 2
Abutilon theophrasti Medic.	—	0.36 ± 0.20	—	1.36 ± 0.67
Ambrosia artemisiifolia L.	16.21 ± 2.95	7.77 ± 4.05	16.34 ± 2.72	9.91 ± 5.95
Ambrosia trifida L.	3.39 ± 1.42	1.05 ± 0.91	0.95 ± 0.35	0.36 ± 0.26
Andropogon gerardii Vitman. *	27.89 ± 3.45	3.73 ± 1.17	2.45 ± 0.27	0.59 ± 0.14
Baptisia leucantha Torr. & Gray. *	0.13 ± 0.13	—	0.03 ± 0.03	—
Cirsium arvense (L.) Scop.	0.92 ± 0.41	—	0.66 ± 0.26	—
Conyza canadensis (L.) Cronquist	0.61 ± 0.53	0.50 ± 0.22	0.21 ± 0.14	0.59 ± 0.23
Desmodium canadense (L.) DC. *	4.50 ± 1.21	0.91 ± 0.71	0.53 ± 0.12	0.09 ± 0.06
Echinochloa crus-galli (L.) P. Beauv.	—	1.00 ± 0.51	—	3.05 ± 1.26
Hibiscus trionum L.	0.21 ± 0.11	2.14 ± 0.54	1.21 ± 0.67	8.09 ± 2.38
Lactuca serriola L.	0.05 ± 0.05	1.00 ± 0.48	0.03 ± 0.03	0.86 ± 0.39
Medicago sativa L.	0.26 ± 0.26	—	0.03 ± 0.03	—
Monarda fistulosa L. *	1.13 ± 0.73	—	0.34 ± 0.26	—
Oenothera biennis L.	2.95 ± 0.62	2.23 ± 0.68	13.45 ± 2.43	4.32 ± 1.76
Panicum virgatum L. *	0.53 ± 0.53	0.05 ± 0.05	0.03 ± 0.03	0.14 ± 0.14
Persicaria pensylvanica (L.) Small.	0.13 ± 0.09	0.59 ± 0.33	0.32 ± 0.25	2.50 ± 1.78
Phalaris sp.	3.05 ± 1.12	0.91 ± 0.91	0.45 ± 0.16	0.05 ± 0.05
Plantago lanceolata L.	0.61 ± 0.31	—	0.55 ± 0.23	—
Plantago rugelii Decne.	1.42 ± 0.56	0.95 ± 0.52	2.50 ± 1.18	0.32 ± 0.22
Rudbeckia hirta L. *	30.63 ± 3.37	10.27 ± 2.66	109.26 ±14.68	21.27 ± 3.58
Rumex crispus L.	0.18 ± 0.14	0.64 ± 0.46	0.13 ± 0.09	0.27 ± 0.15
Setaria faberi Herrm.	0.13 ± 0.13	40.55 ± 8.03	0.95 ± 0.95	270.23 ±46.66
Setaria glauca (L.) P. Beauv.	6.32 ± 1.31	13.18 ± 5.51	38.61 ± 6.79	40.09 ±14.85
Setaria viridus (L.) P. Beauv.	—	2.86 ± 2.29	—	12.14 ± 9.39
Sida spinosa L.	0.13 ± 0.13	0.05 ± 0.05	0.55 ± 0.55	0.55 ± 0.55
Sorghastrum nutans (L.) Nash. *	22.34 ± 3.33	1.18 ± 0.51	2.37 ± 0.29	0.36 ± 0.12
Symphyotrichum novae-angliae (L.) G.L. Nesom. *	0.26 ± 0.15	0.09 ± 0.09	0.50 ± 0.29	0.05 ± 0.05
Symphyotrichum pilosum (Willd.) G.L. Nesom.	12.24 ± 2.34	11.05 ± 5.10	5.63 ± 1.19	8.64 ± 3.54
Symphyotrichum sp. *	1.84 ± 0.51	3.77 ± 1.08	4.55 ± 1.29	5.59 ± 1.47
Trifolium hybridum L.	1.47 ± 1.06	1.59 ± 0.69	2.76 ± 1.63	3.68 ± 1.83
Trifolium pratense L.	0.84 ± 0.43	1.82 ± 0.84	1.68 ± 0.80	6.36 ± 2.84
Trifolium repens L.	1.45 ± 0.49	8.00 ± 1.83	6.13 ± 1.98	27.68 ± 5.39
All others	0.42	0.09	1.55	0.14
Total	142.26	118.32	214.74	429.27

* Denotes sown species.

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Table 3. Mean percent cover and density values for all quadrats sampled in 2010 for topographic grid (Group 1, n=170; Group 2, n=108; Group 3, n=58). Values are $\bar{x}$ ± standard error. Values of species with mean cover ≤0.1% and mean density ≤0.1 were totaled and presented as "other species." Groups were determined using cluster analysis.

Species	% Cover			Density		
	Group 1	Group 2	Group 3	Group 1	Group 2	Group 3
Acalypha rhomboidea Raf.	0.09 ± 0.02	0.06 ± 0.02	0.02 ± 0.02	0.14 ± 0.04	0.13 ± 0.08	0.02 ± 0.02
Ambrosia artemisiifolia L.	0.04 ± 0.02	0.30 ± 0.07	–	0.04 ± 0.02	0.62 ± 0.19	–
Ambrosia trifida L.	0.06 ± 0.03	2.70 ± 0.30	3.78 ± 0.50	0.13 ± 0.08	5.07 ± 0.59	5.19 ± 0.69
Andropogon gerardii Vitman. *	95.09 ± 0.64	61.81 ± 2.39	11.52 ± 2.21	429.80 ± 9.20	244.40 ± 12.3	46.10 ± 8.40
Asclepias syriaca L.	0.26 ± 0.05	0.49 ± 0.11	0.28 ± 0.13	0.26 ± 0.05	0.33 ± 0.06	0.16 ± 0.07
Cirsium arvense (L.) Scop.	0.08 ± 0.03	0.19 ± 0.07	2.69 ± 0.95	0.09 ± 0.03	0.14 ± 0.06	4.19 ± 1.51
Desmodium canadense (L.) DC. *	0.59 ± 0.19	0.32 ± 0.20	–	0.46 ± 0.13	0.13 ± 0.08	–
Erigeron annuus (L.) Pers.	0.21 ± 0.03	0.08 ± 0.03	–	0.43 ± 0.08	0.23 ± 0.09	–
Euthamia graminifolia (L.) Nutt.	–	–	0.69 ± 0.50	–	–	0.62 ± 0.44
Hibiscus trionum L.	0.17 ± 0.03	0.15 ± 0.03	–	0.35 ± 0.07	0.19 ± 0.05	–
Panicum virgatum L. *	0.09 ± 0.07	0.28 ± 0.21	–	0.15 ± 0.11	0.69 ± 0.61	–
Persicaria pensylvanica (L.) Small.	0.08 ± 0.06	3.79 ± 0.58	23.17 ± 2.01	0.10 ± 0.07	5.39 ± 0.87	33.98 ± 3.11
Phalaris arundinacea L.	0.05 ± 0.02	3.41 ± 0.97	9.28 ± 0.96	0.14 ± 0.07	19.04 ± 4.84	66.52 ± 8.56
Ratibida pinnata (Vent.) Barnhart. *	0.51 ± 0.11	0.31 ± 0.13	–	1.28 ± 0.32	0.51 ± 0.20	0.24 ± 0.15
Rumex crispus L.	0.01 ± 0.01	0.13 ± 0.08	0.02 ± 0.02	0.01 ± 0.01	– –	– –
Silphium integrifolium Michx. *	0.34 ± 0.14	2.31 ± 0.93	0.59 ± 0.26	0.45 ± 0.18	2.49 ± 1.03	0.62 ± 0.23
Silphium laciniatum L. *	0.02 ± 0.01	2.67 ± 0.90	0.12 ± 0.07	0.01 ± 0.01	0.51 ± 0.17	0.12 ± 0.07
Silphium perfoliatum L. *	–	0.42 ± 0.42	0.26 ± 0.26	–	0.19 ± 0.19	0.17 ± 0.17
Silphium terebinthinaceum Jacq. *	0.01 ± 0.01	0.31 ± 0.20	–	0.01 ± 0.01	0.03 ± 0.02	–
Solidago altissima L.	0.80 ± 0.15	20.21 ± 1.96	56.47 ± 2.87	1.12 ± 0.23	24.49 ± 2.36	73.26 ± 4.76
Sorghastrum nutans (L.) Nash. *	0.21 ± 0.10	2.95 ± 0.83	0.91 ± 0.46	0.58 ± 0.35	11.86 ± 3.76	2.59 ± 1.24
Symphyotrichum novae-angliae (L.) G.L. Nesom. *	0.06 ± 0.02	0.29 ± 0.17	0.66 ± 0.32	0.08 ± 0.04	0.31 ± 0.24	0.83 ± 0.38
Taraxacum officinale Weber.	0.28 ± 0.03	0.26 ± 0.04	0.12 ± 0.05	0.56 ± 0.09	0.51 ± 0.09	0.12 ± 0.05
Veronica peregrine L.	0.09 ± 0.02	0.01 ± 0.01	–	0.28 ± 0.08	0.06 ± 0.06	–
All others	0.26	0.25	0.05	0.33	0.39	0.08
Total	99.14	103.45	110.58	436.47	317.32	234.73

* denotes sown species.

Figure 1. Map of the Avis Prairie showing topographic grid and permanent monitoring transect locations. The site is bordered by State Route 22 (SR 22) to the west and by State Route 26 (SR 26) to the south. Dark gray shaded area indicates topographic grid location in 1995 (Figure 2); Light gray shaded area indicates the expanded grid in 2010 (Figure 3); f = transects located in a flood zone; t = transects located at transition zone; u = upland transects located outside flood zone. Numbers on permanent monitoring transect pairs indicate specific identification.

Figure 2. Plot design and layout for topographic grid sampled in 1995. Sampling points are located at uniform 0.12 m elevation intervals and include two quadrats (1 m x 1 m) separated by one meter.

Figure 3. Plot layout for extended topographic grid sampled in 2010. Sampling points are located at uniform elevation intervals similar to topographic grid sampled in 1995 (Figure 2). After 1.44 m in elevation change, sampling points were located either at 0.06 m elevation intervals or at 10 m from the previous sampling point where a 0.06 m elevation change did not occur within 10 m from the previous sampling point. The area of the topographic grid sampled in 1995 (Figure 2) is bordered with a dotted line. Three additional transects (transects A to C) were added south and parallel to transect D of the topographic grid sampled in 1995.

Figure 4 - 9. Mean relative cover and standard error values of two groups of species plotted as a function of time of sampling year from permanent monitoring transects. Standard error bars are one standard error from mean.

Figure 10. PCA plot ordination of 1995 vegetation data (percent cover by species) based on 0.12m elevation intervals for five transects. Numerals indicate elevation and alpha characters indicate transect. Direction of elevation vector indicates elevation change down-slope. Circles enclose two groups of plots (Group 1, and Group 2) determined from cluster analysis that are further analyzed for differences in species composition.

Figure 11. PCA plot ordination of 1995 and 2010 vegetation data (relative cover by species) based on 0.12m elevation intervals for five transects. Numerals indicate elevation interval and alpha characters indicate transect. Direction of elevation vector indicates elevation change down-slope.

Figure 12. PCA plot ordination 2010 vegetation data (percent cover by species) based on 0.12m elevation intervals for five transects. Numerals indicate specific elevation interval along transects and alpha characters indicate transect identification. No elevation vector resulted from the spread of data along the measured elevation gradient, indicated by the cross symbol (+) and no associated arrow.

Figure 13. PCA plot ordination 2010 vegetation data (percent cover by species) based on 0.12m, .6m or 0.0m (where no elevation change occurred within ten meters from previous plot) elevation intervals for eight transects. Numerals indicate elevation interval and alpha characters indicate transect. Direction of elevation vector indicates elevation change down-slope. Circles enclose two groups of plots (Group 1, Group 2 and Group 3) determined from cluster analysis that are further analyzed for differences in species composition.
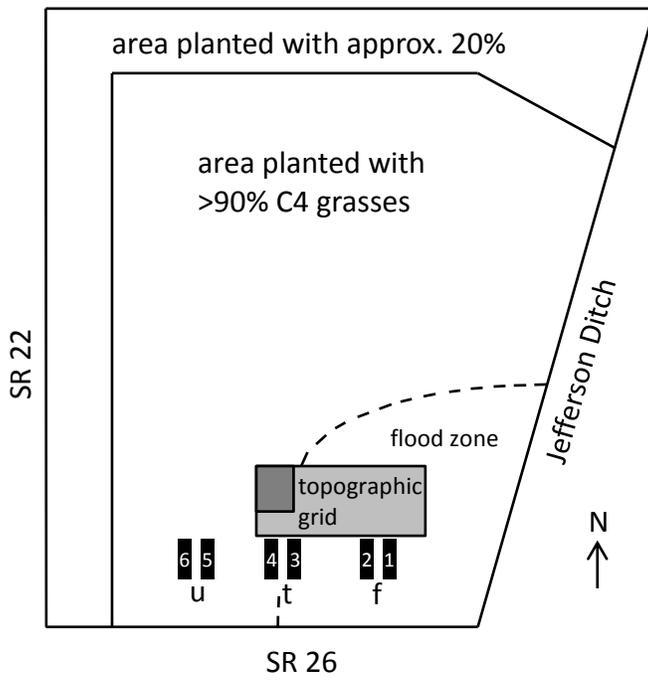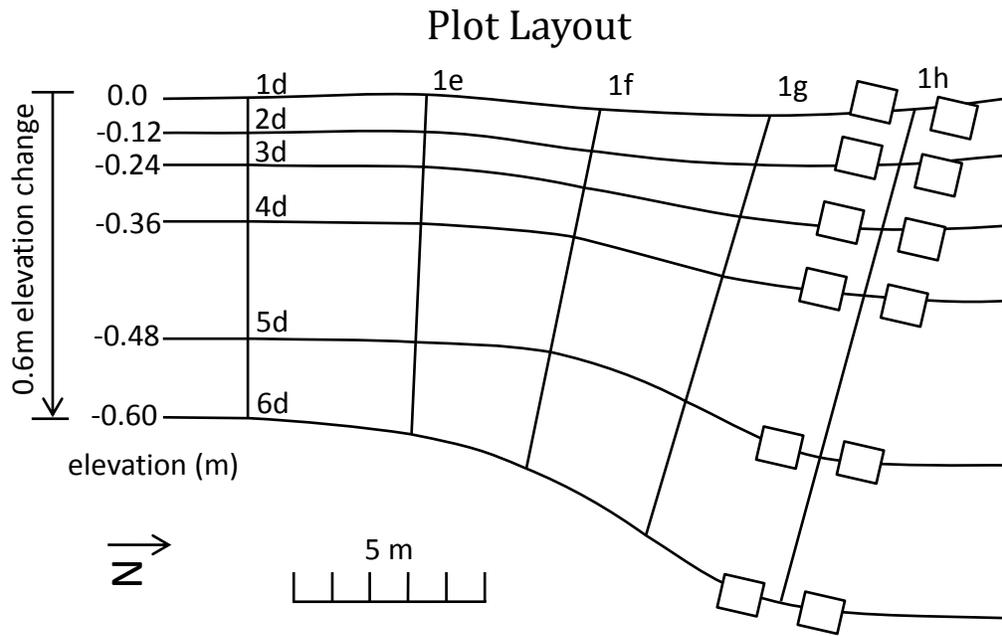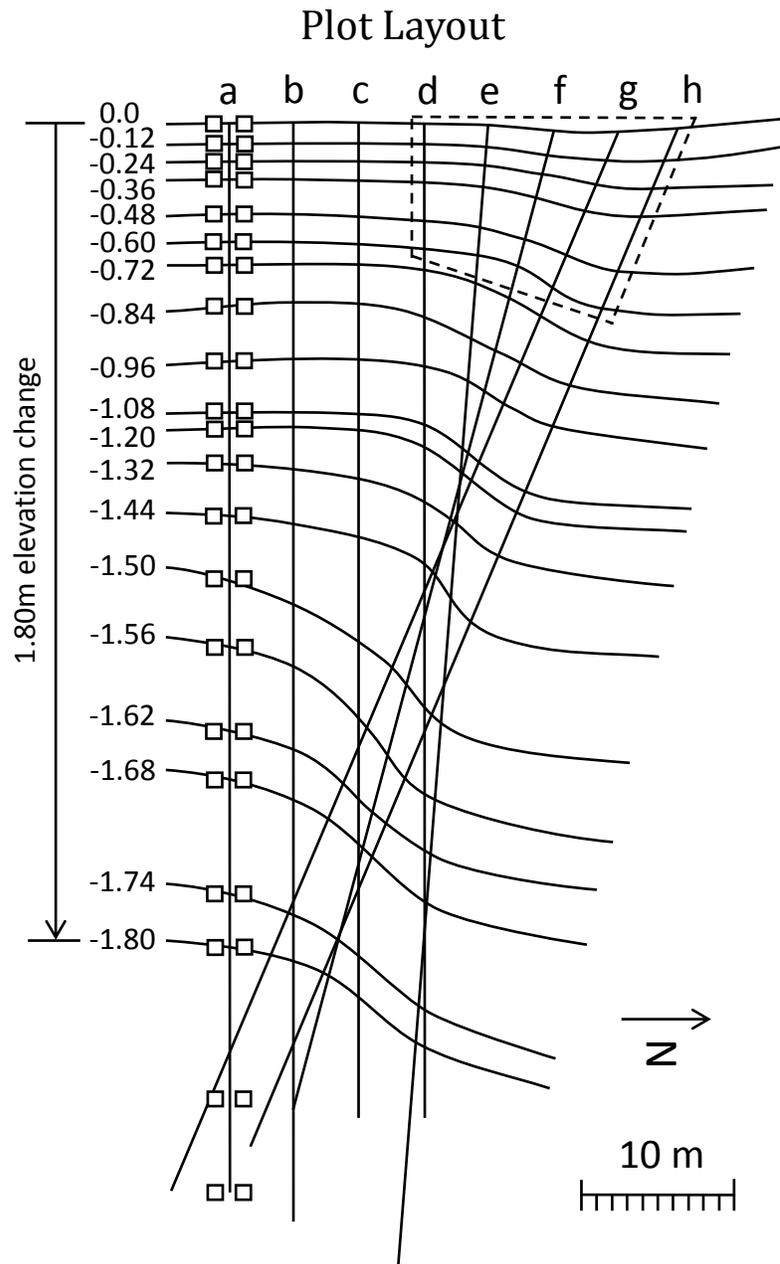
Figure 1

area planted with approx. 20%

area planted with
>90% C4 grasses

SR 22

Jefferson Ditch

flood zone

topographic grid

6 5   4 3   2 1

u   t   f

N

SR 26

Figure 2

Plot Layout

0.6m elevation change

0.0
-0.12
-0.24
-0.36
-0.48
-0.60

elevation (m)

1d 1e 1f 1g 1h
2d
3d
4d
5d
6d

N

5 m

43

Figure 3

Plot Layout
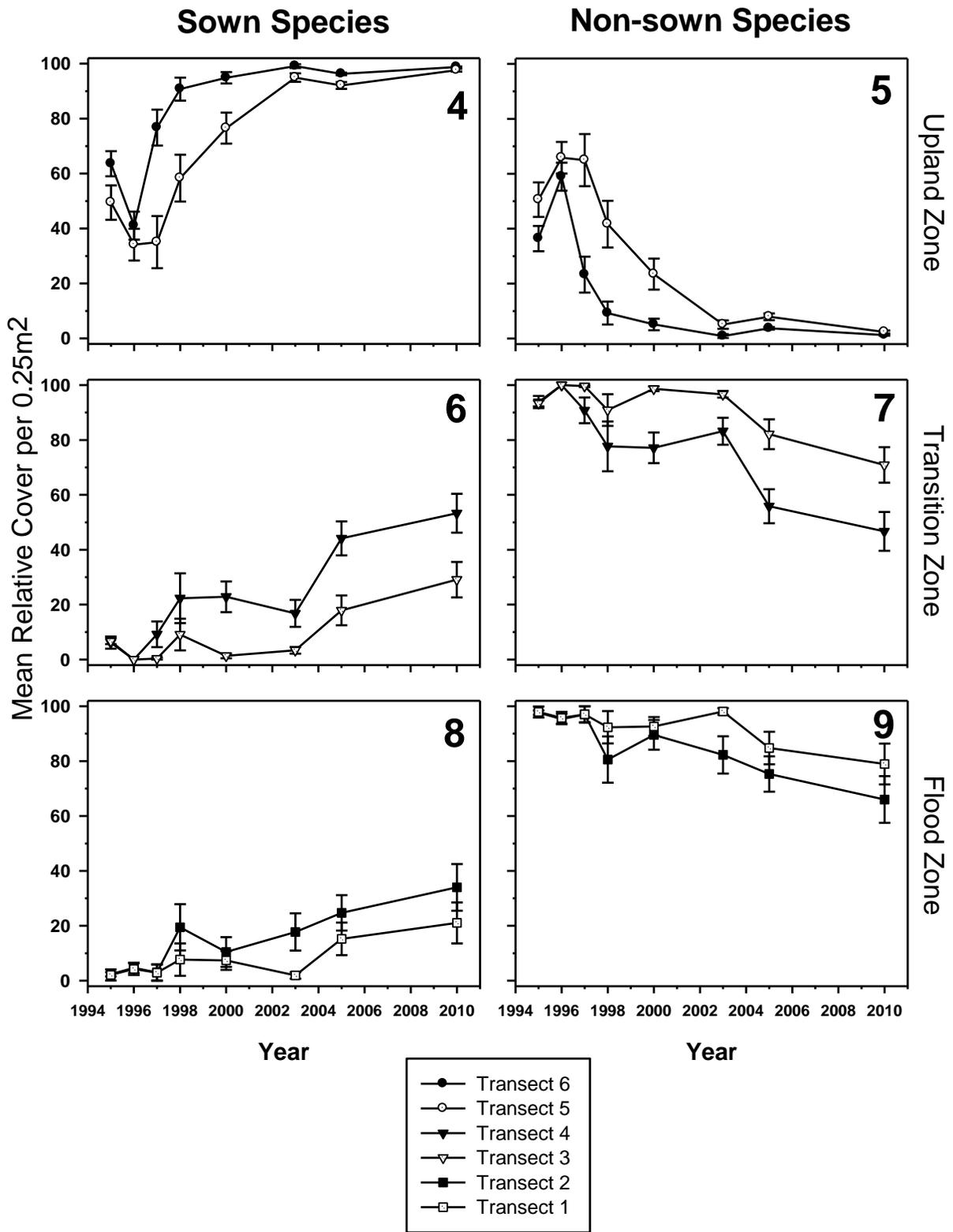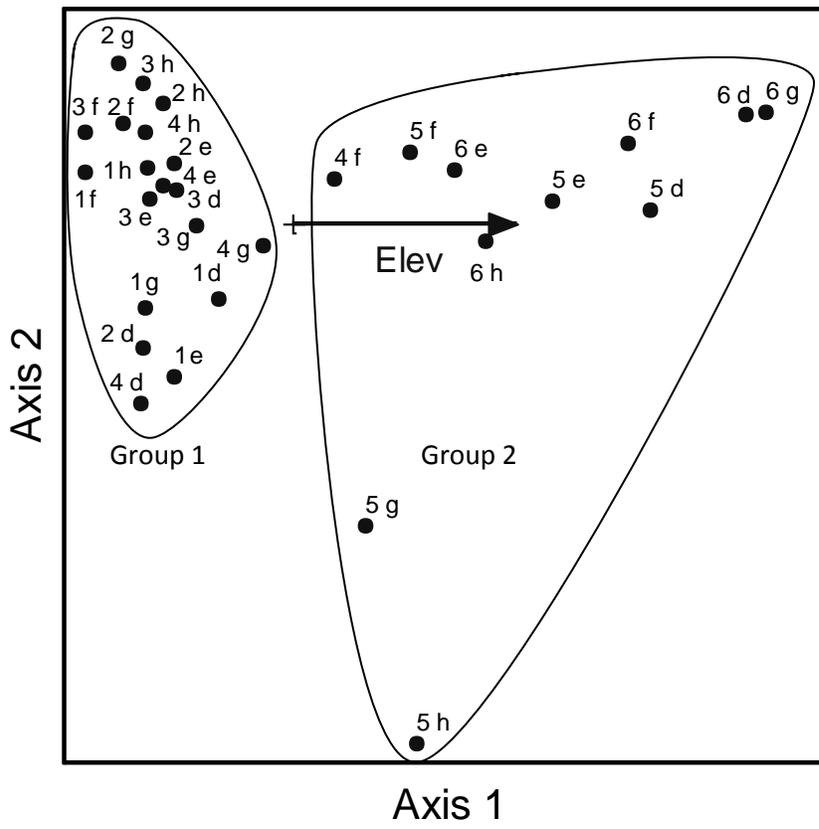
Figure 4-9
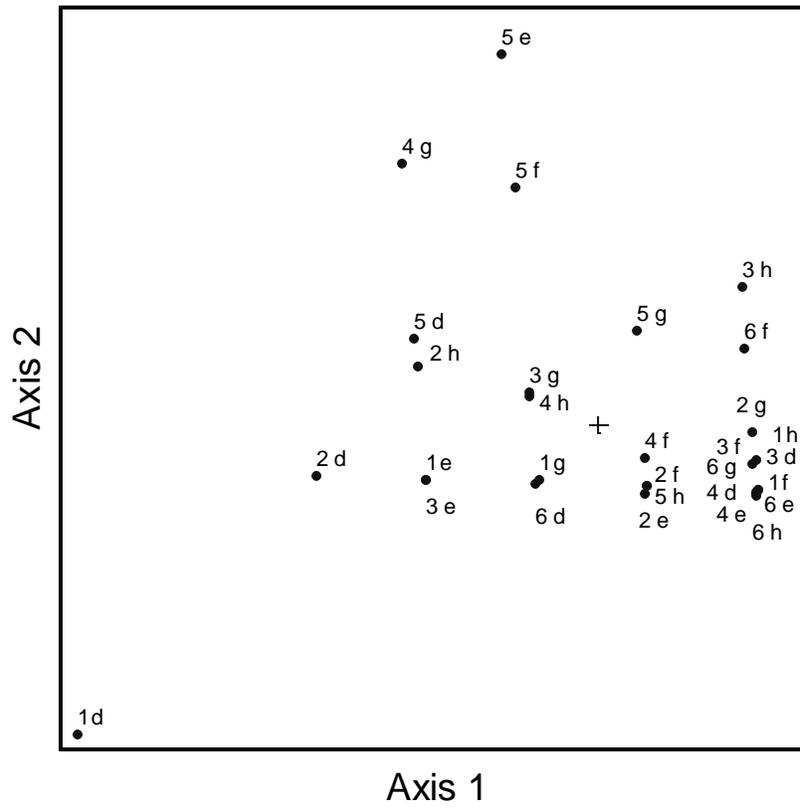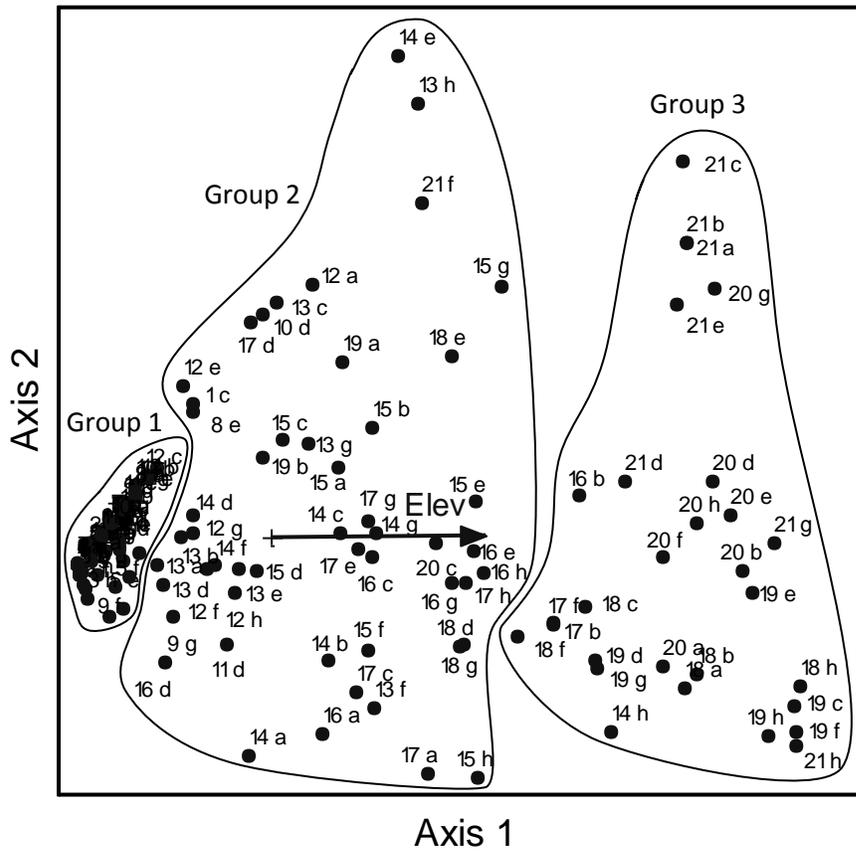
Figure 10

Figure 11
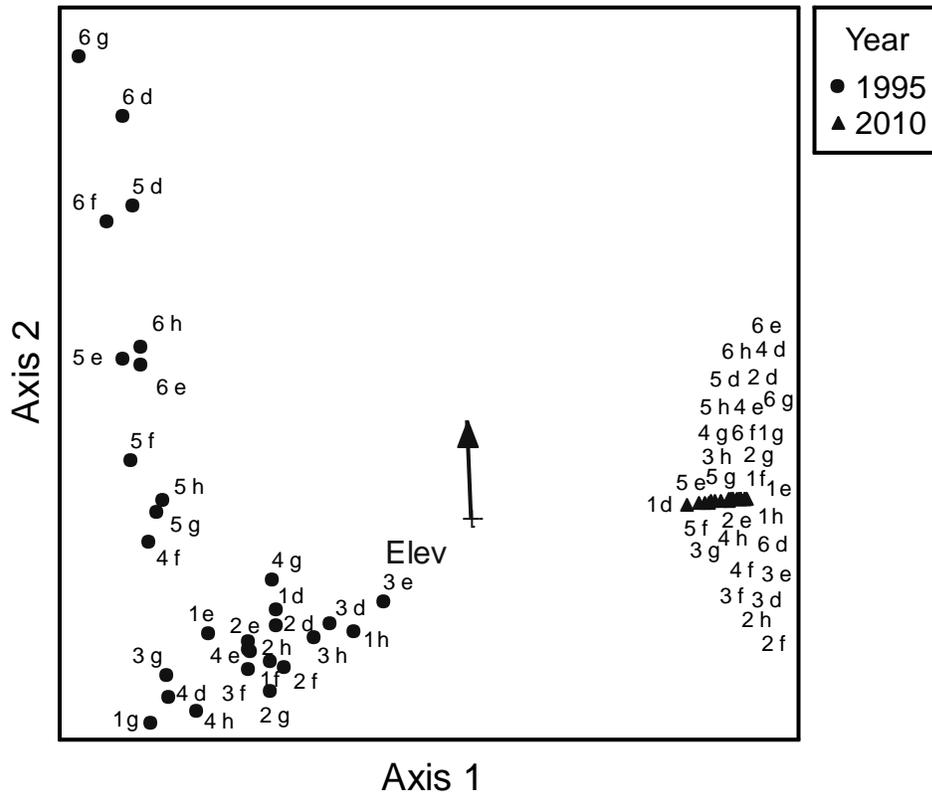
Figure 12

Figure 13

APPENDIX

Appendix A. List of species included in original seed mix for Avis Prairie. Seeding took place in late June 1993. Asterisks indicate values measured in pounds; all other values measured by the ounce.

Species	Quantity (lbs/ounce)
Amorpha canescens Pursh	6
Andropogon gerardii Vitman.	210 *
Asclepias tuberosa L.	8
Baptisia sp.	36
Ceanothus americanus L.	8
Coreopsis palmata Nutt.	6
Dalea candida Michx. ex Willd.	28
Dalea purpurea Vent.	64
Desmodium canadense (L.) DC.	6
Desmodium illinoense A. Gray	6
Echinacea pallida Nutt.	40
Echinacea purpurea (L.) Moench	24
Eryngium yuccifolium Michx.	64
Gentiana alba Muhl. ex Nutt.	6
Heliopsis helianthoides (L.) Sweet	40
Lespedeza capitata Michx.	40
Liatris aspera Michx.	24
Liatris pycnostachya Michx.	96
Monarda fistulosa L.	16
Oligoneuron rigidum (L.) Small	40
Panicum virgatum L.	6*
Parthenium integrifolium L.	64
Penstemon digitalis Nutt. ex Sims	8
Potentilla arguta Pursh	8
Pycnanthemum sp.	8
Ratibida pinnata (Vent.) Barnhart	40
Rosa carolina L.	4
Rudbeckia hirta L.	54
Schizachyrium scoparium (Michx.) Nash.	65 *
Silphium integrifolium Michx.	64
Silphium laciniatum L.	80
Silphium perfoliatum L.	10
Silphium terebinthinaceum Jacq.	64
Solidago nemoralis Aiton.	14
Solidago speciosa Nutt.	5
Sorghastrum nutans (L.) Nash.	210 *
Sporobolus heterolepis A. Gray.	10 *
Symphyotrichum laeve (L.) A. Löve & D. Löve	3
Symphyotrichum novae-angliae (L.) G.L. Nesom	32
Symphyotrichum oolentangiense (Riddell) G.L. Nesom	3
Tradescantia ohiensis Raf.	12
Veronicastrum virginicum (L.) Farw.	10
Zizia aurea (L.) W.D.J. Koch	4