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Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in the Northern Mixed Prairie, USA

Mario E. Biondini[1], Allen A. Steuter[2] & Carolyn E. Grygiel[2]
[1] *Department of Animal and Range Sciences, North Dakota State University, Fargo, ND 58105, USA;*
[2] *The Nature Conservancy, Niobrara Valley Preserve, Route 1, Johnstown, NE 69214, USA*

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Abstract

The effects of fire season on forb diversity patterns, density, and composition were determined for a northern Mixed Prairie site, USA. Repeated spring burns (dormant season), summer burns, fall burns (dormant season), and unburned treatments were compared over a 3-yr period characterized by wet and dry moisture conditions. Alpha and beta diversity were highest on unburned and summer burn treatments, while landscape mosaic diversity was highest on fall burns. Forb density was highest on fall and spring burn sites. Nine forb species comprised 82% of total densities and were significantly affected by fire season and year to year variations in moisture. Forb composition for unburned and spring burn treatments was similar, but both treatments were different from the summer burn and fall burn treatments which were similar to each other. Fire alone did not appear to be an intense enough disturbance to initiate drastic changes in the forb component of vegetation patches. Specific fire seasons did appear to either mask or enhance forb structure arising from other disturbance(s). Fire season also affected the scales of forb organization in the landscape. Contrasting spatial characteristics of the forb component of prairie plant communities may provide a diagnostic technique for exposing the interaction of disturbances at different temporal and spatial scales.

Nomenclature: Great Plains Flora Association, 1986. Flora of the Great Plains. University Press of Kansas.

Introduction

The forb component of central North American grassland communities has been characterized as a dynamic set of species originating within disturbed patches (Loucks *et al.* 1985). The initial composition of these patches is broadly determined by the impact of disturbance size and intensity on resource availability (Collins *et al.* 1985; McConnaughay & Bazzaz 1987; Coffin & Lauenroth 1988). Forb composition within disturbed patches generally changes with time from a community dominated by annual/biennial species to one with a preponderance of perennial (often rhizomatous) species (Platt 1975; Miller 1982; Gibson 1988). The patches eventually become dominated by perennial grasses, while forbs become less dominant. Community structure thus becomes a function of both the size and frequency of the disturbance events (Miller 1982; Bakker *et al.* 1983), and the interactions between disturbance types (Collins 1987; Gibson & Hulbert 1987).

The role of fire disturbance in the evolution of North American grasslands has been widely discussed (Wells 1965, 1970; Vogel 1974, Wright & Bailey 1982; Anderson 1982). Historical accounts dramatize the relatively high frequency and large scale nature of fire disturbance (Nelson & England 1971; Moore 1972; Higgins 1986). An intrinsic characteristic of fires in the prairie landscape is the season in which they occur (Anderson *et al.* 1970; Henderson 1981; Lovell *et al.* 1982). Recent studies by Gibson & Hulbert (1987), Collins (1987), and Gibson (1988) have emphasized the interactions between fire periodicity and disturbances of different scales on the structure of the Tallgrass Prairie. Perennial grasses have been the primary focus of fire ecology in these grasslands.

Prairie plant species are variously adapted to recurrent fires (Lovell *et al.* 1982) but their response is dependent upon fire intensity, fire frequency, and weather patterns (Kruger 1984; Gibson & Hulbert 1987). Collins (1987) proposes that one of the main effects of fire disturbance in grasslands is the alteration of patch structure and dynamics, and thus, the invariant vegetation structure. The invariant structure of a grassland (*sensu* Collins 1987 consists of matrix species (mostly perennial grasses) which consume the majority of the resources and non-matrix species which occupy areas between matrix-forming dominants and thus may be more sensitive indicators of the frequency and intensity of a particular disturbance. Forbs are a major component of the non-matrix component in North American grasslands. The central focus of this paper is the impact of repeated fires at different seasons (spring, summer, and fall) on the: (1) number of species (richness) and density of forbs; (2) diversity patterns of the forb community at different scales (alpha, beta, mosaic diversity); (3) forb community composition; and (4) individual response of dominant forbs. We hypothesize that the seasonality of fire events (a temporal scale) is reflected in the diversity, composition, and density patterns (spatial scales) of the forb community.

Methods

Site description and experimental design

The study was located on the Samuel H. Ordway, Jr. Memorial Prairie in north-central South Dakota, USA. Ordway Prairie is a 3160 ha native northern Mixed Prairie preserve owned and managed by The Nature Conservancy. Plant community descriptions for the preserve have been reported by Barnes *et al.* (1983) and the geology of the glaciated prairie pothole landscape has been described by Christensen (1977). This region has a continental climate which is typified by long cold winters and short warm summers. Precipitation data for the site from 1982 tot 1985 are shown in Table 1.

The study was initiated in 1982 and organized as a completely randomized design with 4 treatments and 3 replications. The 12 30 m by 30 m plots were located within a 97 ha enclosure. The vegetation in the study plots was characterized by mid-prairie and high-prairie plant communities (Barnes *et al.* 1983). Soils on the site were classified as Vida and Williams fine-loamy soils, mixed Typic Argiborolls. The vegetation in the enclosure had been lightly to moderately grazed by bison (*Bison bison*) prior to the beginning of the study and unburned for at least 10 yr. The treatments consisted of annual spring burns, alternate year summer burns, annual fall burns and unburned controls. Spring burns were applied between April 19–26, summer burns between August 3–5 and fall burns between October 5–17. The summer burn treatment plots were ignited annually but carried a fire only in 1982 and 1984. A description of the fire behaviour and weather conditions has been reported by Steuter (1986).

Data were collected from each of the study plots during mid-July through early August with

Table 1. Actual cool season (9/1 to 5/31) and warm season (6/1 to 8/31) precipitation (cm) during the study period and deviation (cm) from the long-term average.

	9/1/82 to 5/31/83	6/1/83 to 8/31/83	9/1/83 to 5/31/84	6/1/84 to 8/31/84	9/1/84 to 5/31/85	6/1/85 to 8/31/85	Total
Study period[1]	25.4	29.2	24.9	15.7	20.8	11.6	127.6
Deviation from long-term average[2]	−3.3	8.3	−3.7	−5.2	−7.9	−9.2	−21.0

[1] Recorded at gauge 0.75 km from study plots.
[2] Recorded at U.S. Weather Station (18 yr) Leola, South Dakota 16 km east of study site.

the use of nested quadrats (0.25 m^2 and 0.50 m^2). Ten quadrats were randomly located in each study plot within each of the three replications on the study site. Plot size and numbers were derived from the analysis of data from 40 samples of various plot sizes collected before treatment application. The 0.25 m^2 was selected so no individual forb would have a frequency higher than 86%. The 0.50 m^2 was selected so as to detect rare forbs when estimating species composition. The data collected consisted of forb densities by species. Data from the 0.25 m^2 quadrats were used for analysis requiring presence and absence (P/A) information while the 0.50 m^2 quadrat data were used in analysis involving actual forb densities and composition.

Data analysis

Number of species (species richness) and densities of forbs (both total and individual species) were analyzed with analysis of variance (AOV). Data were square root ($\sqrt{y} + 0.5$) transformed to reduce heteroscedasity that results from counts of rare events (Snedecor & Cochran 1967).

Alpha diversity was estimated with the Shannon-Wiener index (Shannon & Weaver 1973) using a ratio of the relative density of forbs. One of the results of disturbances like fire is the creation of niches for rare forbs. We selected the Shannon-Wiener index of diversity for its sensitivity to detect them (Barbour *et al.* 1980). Beta-diversity was calculated as mean dissimilarity (1 – mean similarity) among quadrats within a plot and mosaic diversity was calculated as the variation (range of similarity values) and degree of structuring around the mean similarity (departure from the central tendency of the landscape) as proposed by Istock & Scheiner (1987). Beta and mosaic diversity were estimated from the P/A data with the use of affinity analysis (Scheiner & Istock 1987). Alpha and beta diversity were analyzed with the use of the Kruskall-Wallis test (Mosteller & Rourke 1973). Mosaic diversity values were standardized and analyzed with the use of the bootstrap technique outlined by Scheiner & Istock (1987). Because of the skewness that characterizes the empirical distribution of the mosaic diversity index MU, three standard deviations (as suggested by Scheiner & Istock 1987) were used as a conservative test to determine whether the forb mosaic diversity of the landscape (defined here as each individual plot), was different from the random expectation.

Detrended correspondence analysis (Hill 1979; Hill & Gauch 1980) was used to analyze forb plant community structure and detect composition gradients. Data from ordination axes 1 and 2 were analyzed with the use of multiresponse permutation procedures (MRPP) and its randomized block design counterpart (MRBP) (Biondini *et al.* 1988) to determine the impact of season of fire and year to year climatic variations on the forb community structure. The relationship of dominant forbs to the ordination axes were analyzed with the use of least absolute deviation regression (Bloomfield & Steiger 1980). This procedure was used (as opposed to least square regression) to reduce the impact of outliers. This was particularly necessary because with some species while most of the quadrats had relatively low (high) densities a few (due to natural patchiness) had very large (or very small) densities. In summary there was a large difference between the median and the mean density values. The correlation (and p-values) between the regression line and the actual data was calculated using the Spearman rank correlation coefficient (Mosteller & Rourke 1973).

Results

Forb diversity patterns

The season of burning had a significant impact on the diversity patterns of the forb community. Significant differences among treatments ($p < 0.05$) in species richness were found only in 1983 (following a year of above normal summer precipitation (Table 1). In that first year, unburned and summer burns had a higher number of species than the spring and fall burns (an average of 51 vs 38 species, Fig. 1a). No significant differences among treatments were found in subsequent years (Fig. 1a), but the average number of species across treatments dropped from 45 in 1983 to 33 in the 1984–1985 period (rainfall in these two years was 26% below the long term average).

Alpha and beta diversity had a similar response to the season of burning. The fall and the spring burn treatments had lower ($p < 0.05$) alpha and beta diversity (Fig. 2a and 2b) than the unburned and summer burn in both 1984 and 1985. Landscape mosaic diversity had a response pattern distinctively different from the one observed at the alpha and beta level (Fig. 2c). Throughout the three years of the study the mosaic diversity of the unburned plots was not significantly different from the one expected from a random distribution of species across the landscape (Fig. 2c). The fall treatment had a mosaic diversity that was consistently higher than the one expected from a random distribution model (Fig. 2c). Spring and summer treatments showed mosaic diversity patterns consistent with a random distribution model 2 out of the 3 years (Fig. 2c).

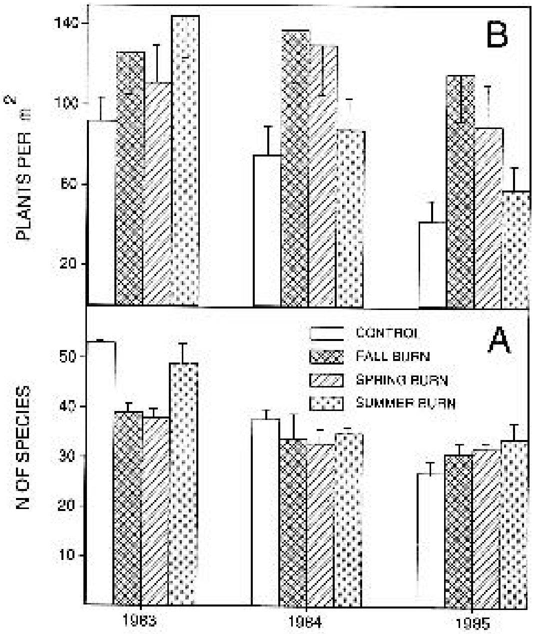

Fig. 1. (A) Number of forb species (species richness); (B) Density of forbs. Standard error bars are given for each value.

Forb community patterns

Forb density was significantly higher ($p < 0.05$) on both fall and spring burns when compared with the unburned and summer burn treatments in both 1984 and 1985 (dry years) (Fig. 1b). In 1983 (following a year of above normal precipitation (Table 1) there was no difference in forb density among the burn treatments but they had higher forb densities than the unburned control (Fig. 1b). In addition to lower densities both the unburned and the summer burn treatments showed large declines (54% and 60% respectively) in forb densities from 1983 to 1985 while the fall and spring burns resulted in more constant forb densities (declines amounted to 9% and 19% respectively).

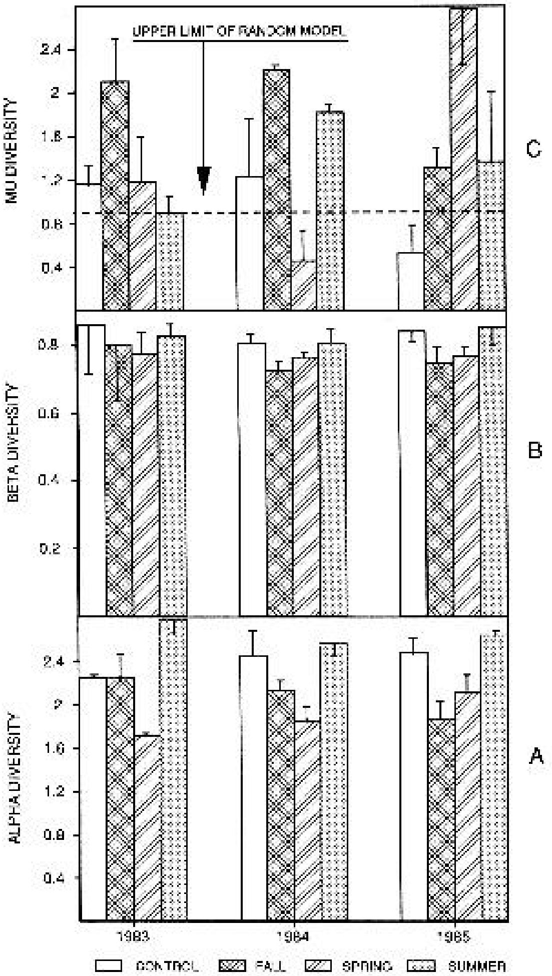

Fig. 2. (A) Alpha diversity (Shannon-Wiener index); (B) Beta diversity (estimated as average dissimilarity); (C) Mosaic diversity (MU). Standard error bars are given for each value. See Methods section for details about calculation procedures.

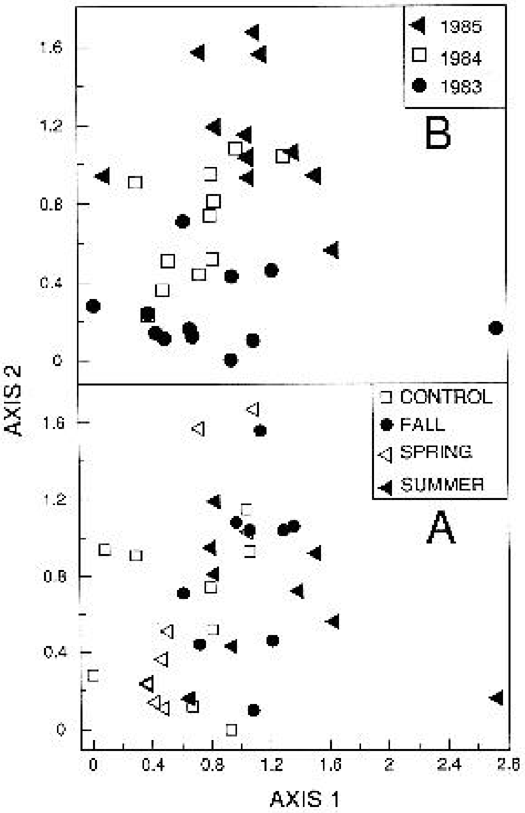

Fig. 3. Ordination axis values from the detrended correspondence analysis. (A) Stands are identified by treatment; (B) Stands are identified by year.

The ordination analysis showed another level of response of the forb community to the season of burn treatments (Fig. 3a and 3b). Two major axes of variation emerged from the ordination analysis: axis 1 ($\lambda = 0.35$) represents a treatment response axis while axis 2 ($\lambda = 0.15$) represents a year to year variation in species composition (which in practice represented a moisture gradient from a wet 1983 summer to a very dry 1985, Table 1). Before discussing the statistical analysis of the forb community responses along the two ordination axes, it is important to note a few general observation that readily emerge from Fig. 3a and 3b. First, with the exception of one data point (replication 3, summer burn treatment, 1983), ordination axis 1 and axis 2 have similar lengths (1.63 vs 1.67 standard deviation, sd) which indicates that the variability observed in species composition as a result of treatment effects (axis 1) is similar to that observed as a result of year to year (moisture gradient) variations (axis 2), and the species turnover from one end of the gradient to the other in both axes is very low, pointing to a high degree of species overlap among treatments and years. Second, along ordination axis 1 (the treatment axis) the summer burn and unburned treatments show a higher degree of variation in species composition

(2.08 and 1.06 sd) than the fall and spring burns (0.75 and 0.73 sd). This is consistent with the lower beta diversity of the fall and spring treatments when compared with the unburned and summer burn treatments (Fig. 2b). Conversely, the species composition of the summer burn and unburned treatments were less affected by year to year (moisture gradient) variability (axis 2) than the fall and spring burns (1.03 and 1.15 sd vs 1.46 and 1.56 sds, Fig. 3a).

In order to test differences in forb community structure resulting from differences in burning schedules we proceeded in the following way: a. MRBP analysis was run with the two ordination axes scores comprising the multivariate vector of responses and years representing blocks (to eliminate the year to year variability from the analysis); b. MRPP analysis was run with ordination scores from axis 1 only (for all three years) to test if our interpretation of axis 1 being a treatment response axis was correct (if this was so both analyses should give similar results). Both analyses gave similar results which confirmed the assumption that axis 1 was a treatment response axis. The unburned and the spring burn treatments were not significantly different in species composition ($p = 0.17$ for MRBP and $p = 0.29$ for MRPP), a similar result was found when the summer and fall burn treatments were compared ($p = 0.58$ for MRBP and $p = 0.36$ for MRPP). The unburned treatment, however, was significantly different in species composition from both the fall and summer burn treatments ($p = 0.013$ and $p = 0.04$ with MRBP, both axes used; $p = 0.009$ and $p = 0.04$ with MRPP, axis 1 only used). In a similar manner, the spring burn treatment was significantly different from both the fall and summer burn treatments ($p = 0.01$ and $p = 0.004$ for MRBP (both axes); $p = 0.006$ and $p = 0.003$ for MRPP, axis 1 only).

It is important to note that the response to the treatments at the forb community composition level was different from the one found at another level of organization, total forb densities. While analysis at a high level of organization (total forb densities) differentiated between fall and spring burns as a group and unburned and summer burns as a group, analysis at a lower level of organization (community composition) showed differences between unburned plus spring burns vs fall plus summer burns.

Similar analyses as those outlined above along ordination axis 2 (Fig. 3b) showed significant differences in species compositions among years ($p < 0.000005$) thus confirming the categorization of axis 2 as a year to year variation (moisture gradient) axis. It is important to note again that even though significant differences among treatments were found, turnover rates of species along both ordination axes was low. As a result the observed differences in species composition structure were the result of small shifts in the abundance of certain species rather than drastic alterations in the community structure. These results suggest that fire (even annual fires as in this experiment) and year to year variations in precipitation (including a drought 1985 (Table 1)) by themselves represent only mild disturbances to this ecosystem.

Forb species response patterns

To look more in detail at where the changes in species composition occurred we need to go to an even lower level of organization: the response of individual species. Nine species (comprising 82% of the total densities) showed significant responses to fire season, year to year variations in precipitation, or both. Four perennial rhizomatous species: *Galium boreale*, *Ambrosia psilostachya*, *Aster ericoides* and *Artemisia ludoviciana* were significantly affected by the fall burn treatment ($p < 0.05$) (Fig. 4a–d). *Aster ericoides* and *Artemisia ludoviciana* were positively correlated with ordination axis 1 ($y = 6.23 + 0.46x$, $r_s = 0.38$, $p < 0.02$; $y = 5.81 + 0.6x$, $r_s = 0.36$, $p < 0.03$) indicating an increase in densities along the unburned – fall burn gradient (from an average density of 6.8 and 8.2 plants m^{-2} respectively in the unburned treatment to 31.3 and 26 plants m^{-2}, respectively in the fall burn treatment). In addition, *Aster ericoides* was also positively correlated with axis 2 ($y = 3.65 + 2x$, $r_s = 0.56$,

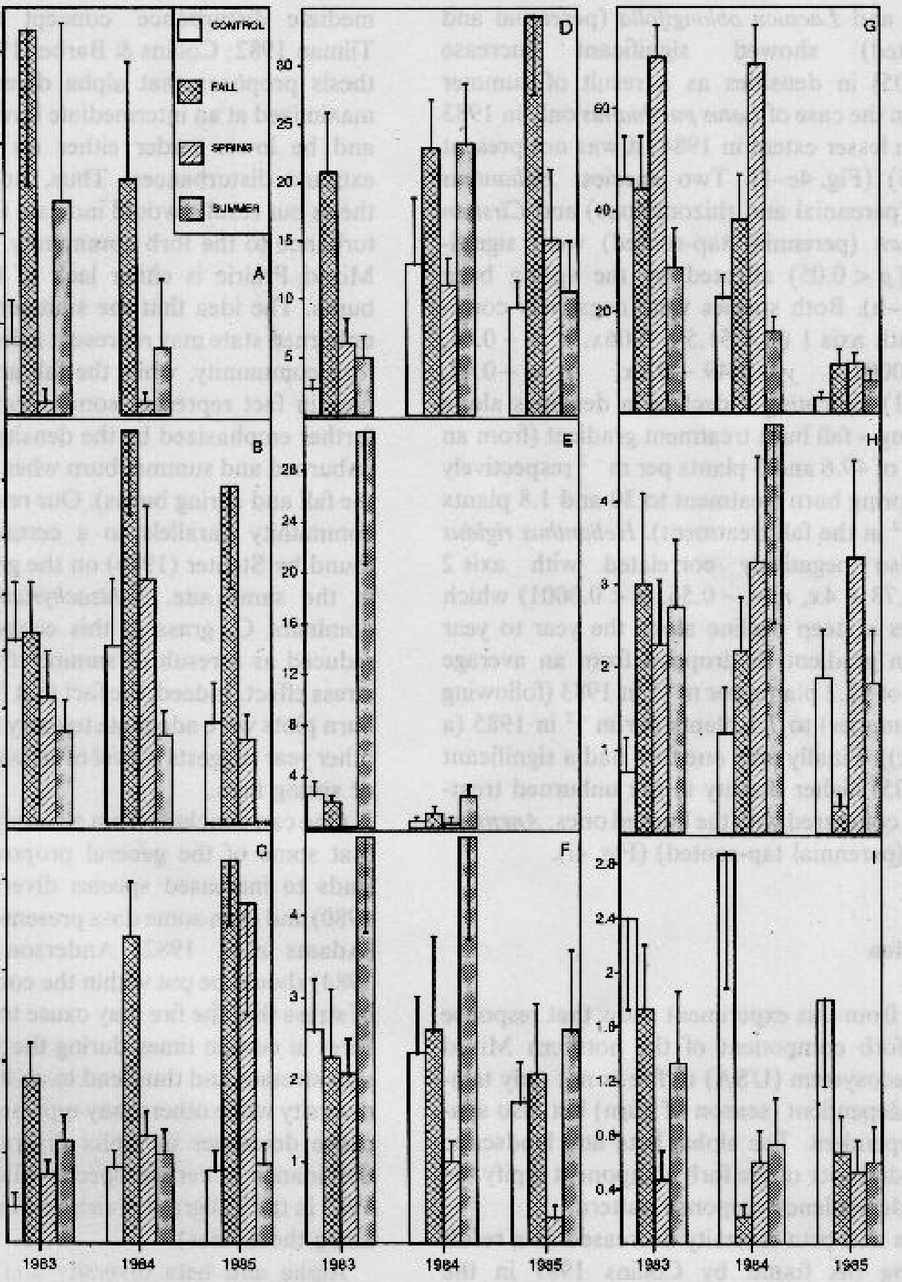

Fig. 4. Density data for: (A) *Galium boreale*; (B) *Ambrosia psilostachya*; (C) *Aster ericoides*; (D) *Artemisia ludoviciana*; (E) *Lotus purshianus*; (F) *Lactuca oblongifolia*; (G) *Helianthus rigidus*; (H) *Cirsium undulatum*; (I) *Anemone patens*. Standard error bars are given for each value.

$p < 0.001$) indicating an increase in densities along the year to year variation gradient (from an average of 10.25 plants m^{-2} in 1983 (following a wet summer) to 24.1 plants m^{-2} in 1985 (a dry year)).

Two species: *Lotus purshianus* (annual and tap-rooted) and *Lactuca oblongifolia* (perennial and tap-rooted) showed significant increase ($p < 0.05$) in densities as a result of summer burns (in the case of *Lotus purshianus* only in 1983 and to a lesser extent in 1984; it was not present in 1985) (Fig. 4e–f). Two species: *Helianthus rigidus* (perennial and rhizomatous) and *Cirsium undulatum* (perennial tap-rooted) were significantly ($p < 0.05$) affected by the spring burn (Fig. 4g–h). Both species were negatively correlated with axis 1 ($y = 51.5 - 3.06x$, $r_s = -0.64$, $p < 0.00001$; $y = 2.49 - 0.1x$, $r_s = -0.42$, $p < 0.01$) indicating a decline in densities along the spring – fall burn treatment gradient (from an average of 49.6 and 3 plants per m^{-2} respectively in the spring burn treatment to 30 and 1.8 plants per m^{-2} in the fall treatment). *Helianthus rigidus* was also negatively correlated with axis 2 ($y = 59.73 - 4x$, $r_s = -0.56$, $p < 0.0001$) which indicates a steep decline along the year to year variation gradient (it dropped from an average density of 47.2 plants per m^{-2} in 1983 (following a wet summer) to 7.3 plants per m^{-2} in 1985 (a dry year)). Finally only one forb had a significant ($p < 0.05$) higher density in the unburned treatment as compared with the burned ones: *Anemone patens*, (perennial tap-rooted) (Fig. 4i).

Discussion

Results from this experiment show that response of the forb component of the northern Mixed Prairie ecosystem (USA) to fire is not only temporally dependent (season of burn) but also spatially dependent. The alpha, beta and landscape mosaic diversity of the forb component typify the spatial dependency response pattern.

Alpha and beta diversity decreased as a result of spring (as found by Collins 1987 in the Tallgrass prairie) and fall burns but remained unchanged in response to summer burns. These responses are probably directly tied to changes in forb density which followed an opposite pattern (higher in fall and spring burns and lower in the unburned and summer burns). Current theories relate diversity responses at this scale to the 'intermediate disturbance' concept (Huston 1979; Tilman 1982; Collins & Barber 1985). This hypothesis proposes that alpha diversity should be maximized at an intermediate level of disturbance and be lower under either no disturbance or extreme disturbances. Thus, under this hypothesis our results would indicate that the real disturbance to the forb community in the northern Mixed Prairie is either lack of fire or summer burns. The idea that the summer burns and the unburned state may represent a disturbance to the forb community, while the fall and spring burns may in fact represent some form of stimulus is further emphasized by the density data (lower in unburned and summer burn when compared with the fall and spring burns). Our results on the forb community parallels to a certain extent those found by Steuter (1986) on the grass component in the same site. *Schizachyrium scoparium*, a dominant C_4 grass in this ecosystem was also reduced as a result of summer fires indicating a stress effect. Indeed, the fact that fuels on summer burn plots were adequate to carry a fire only every other year suggests a level of stress higher than fall or spring fires.

One can conclude from an analysis at this scale that some of the general propositions that fire leads to increased species diversity (Ode *et al.* 1980) and even some data presented in this regard (Adams *et al.* 1982; Anderson 1982; Kruger 1984) should be put within the context of the level of stress that the fire may cause to the ecosystem. Fires at certain times during the year may represent stresses and thus lead to an increase in alpha diversity while others may represent stimulus and cause decreases in alpha diversity by favoring dominance of certain species (data from Collins 1987 in the Tallgrass prairie represent an example along these lines).

Alpha and beta diversity analyses deal with averages, at the point level or between two points, but not with the spatial aspects of the fire response, that is the distribution patterns of forbs across the landscape (landscape mosaic diversity). Results from our study show that while alpha and beta diversity were higher in the unburned vis-a-vis the fall burn, at the landscape level the results were reversed. The unburned treatment showed a random pattern of forb distribution across the landscape while the fall burn treatment showed a high degree of forb clustering (spring and summer burns showed random patterns 2 out of the 3 years). In order to understand the differences observed in landscape level response patterns in our study we need to look at the fire history of the region and the patterns of small scale disturbances. The works of Moore (1972) and Higgins (1986), provide a strong evidence that the Northern Mixed Prairie evolved in a primary matrix of dormant season fall (and to a less extent spring) fires. Within this matrix there would have occurred relatively small, irregular islands of vegetation that would burn periodically as a result of summer fires (Steuter 1986). To this matrix of fire events one has to add (as suggested by Collins & Barber, 1985) the impact of small scale disturbances to have a more clear picture of the potential mechanisms at work that may cause this dichotomy between point diversity (alpha) and landscape diversity. The presence of forb dominated patches in grasslands is almost always associated with the presence of intense small scale disturbances (Phillips 1936; Laycock 1958; Platt 1975; Hobbs & Mooney 1985). In grasslands one of the most common causes of small scale disturbances are small mammals (pocket gophers, prairie dogs, badgers etc.). In the case of pocket gophers there is evidence that the activity and distribution of mounds may be affected by fire events (Spencer *et al.* 1985). We hypothesize that fall fires (which are more in tune with the evolutionary history of the region) favor the growth of those perennial forbs that were established in small scale disturbances that occurred in the past and as such reinforces the inherent spatial patchiness of the forb community. The lack of fire in this ecosystem represents a form of stress (as we outlined before) in particular to nonmatrix species (*sensu* Collins 1987) like forbs. This stress condition led to higher alpha diversity but also to a more haphazard emergence of forbs across the landscape. In other words, the patterns of forb distribution in the landscape that are the consequences of small scale disturbances are lost. The result is a more random distribution of forbs across the landscape and thus lower landscape mosaic diversity. Summer and spring burns may represent a disturbance intensity continuum between unburned and fall burn levels. In summary, while the unburned and summer burns represent stressors that can alter competition patterns at the local level, preventing dominance and thus increasing alpha (and also beta) diversity, fall fires reinforce the inherent patchiness of forb distribution across the landscape which are the result of a different set of mechanisms that are spatial in nature: small scale disturbances (e.g. produced by small mammals) within the evolutionary matrix of predominantly fall fires.

We have contrasted the nature of the responses of forbs to fire season at two levels of organization: point and landscape diversity. At another level of organization, community composition, responses to fire season, even though discernible, was not as strong. At this scale, the dichotomy of unburned vs fall burn responses were maintained but summer and spring burn outcomes were interchanged (i.e. summer burn responses were closer to fall burns while spring burns resemble unburned). An important dimension that emerges at the community composition level, is that the variations due to year (in our case going from above normal precipitation to a drought) were as large as those caused by fire season. This may indicate that in fact fire alone is not an exceptional event but rather falls within the normal year to year climatic variations. This interpretation fits well with the fact that the observed changes in community composition due to both year and treatment, even though statistically significant, were in fact small. This seems to indicate that fire alone (even annual fires like in our experiment) is not a large enough disturbance to cause drastic changes in forb composition of northern Mixed Prairies (USA).

The strong and general response patterns to fire season observed at the diversity level and the less, but still measurable, general responses to both fire season and years (moisture levels) observed at the forb community composition level break down when one goes to even a lower scale: individual species. Individual species responses seem to follow the Gleasonian (Gleason 1926) individualistic model of each species responding independently to particular sets of circumstances. As an example *Lotus purshianus* (an annual) emerged and became established in 1983 as a result of a wet summer and a previous summer fire that damaged some of the dominant species. But this was not a systematic response to the summer burn treatment because it virtually disappeared in 1984 and 1985.

In summary, the impact of fire in diversity patterns and community structure of forbs in North American mixed prairie is scale dependent (spatial and temporal). The seasonality of fire determines the level of stress on, and relative size of the impacted vegetation and thus the differences in scale. Our analyses seem to suggest that the spatial characteristics of forbs within perennial grasslands are diagnostic of past disturbances. Although the effects of fire on the forb community composition fall within the range of year-to-year variation, differences in the seasonality of fire (or lack of it) may re-enforce or obscure vegetation patterns resulting from other disturbances. Thus, the patterns of forb diversity in the North American mixed prairie are a response to the various intensities and scales characteristic of the overall disturbance regime.

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