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Patterns of community structure during succession in tallgrass prairie

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ABSTRACT

COLLINS, S. L. (Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019). Patterns of community structure during succession in tallgrass prairie. *Bull. Torrey Bot. Club* 117: 397–408. 1990.—Patterns of species diversity are a product of many complex interactions that change during succession. The purpose of this study was to measure components of community diversity during succession in six experimental treatments: protected prairie, grazed prairie, once-plowed prairie, annually plowed prairie, abandoned field, and a re-plowed field. Phase-space analysis of ordination data is introduced as a means of assessing successional dynamics in communities. The phase-space analysis of DCA ordination revealed similar successional trajectories for the protected, once-plowed and annually plowed treatments and divergent patterns in the other plots. The degree and rate of change during succession varied among treatments long after experimental plowing ceased.

Patterns of species density, species diversity, mosaic diversity, community heterogeneity, and dominance changed among treatments over time. Heterogeneity decreased on four of five successional plots, but it increased on the grazed treatment. Mosaic diversity showed no clear pattern among the treatments during succession. When data from the successional treatments were combined, the overall patterns were more complex. Heterogeneity fluctuated during succession in response to changes in species density. As species density increased, species diversity increased, whereas heterogeneity and dominance decreased. Because of the temporal fluctuations in heterogeneity and the different components of community diversity, no simple monotonic model will adequately represent patterns of community structure during succession. By analyzing the complex components of structure at different spatial and temporal scales, it will be possible to more clearly understand patterns and mechanisms controlling diversity in plant communities.

Key words: heterogeneity, mosaic diversity, Oklahoma, species density, species diversity, succession, tallgrass prairie.

Community diversity is a product of numerous biotic and abiotic factors occurring at a variety of spatial and temporal scales (Delcourt *et al.* 1983; Hengeveld 1987). Traditionally, studies of diversity have focused on patterns of dominance, richness and evenness within communities (Peet 1974; Magurran 1989). However, a number of scale-related factors can influence temporal and spatial patterns in species diversity (Shmida and Wilson 1985; Ricklefs 1987). Thus, additional measures of community diversity such as heterogeneity, species density and mosaic diversity (Grime 1979; Istock and Scheiner 1987) may have important implications for understanding broad-scale patterns in plant community structure.

In grassland communities, topography, edaphic factors, and disturbances produce regional variation in composition and structure of vegetation (McNaughton 1983; Gibson and Hulbert 1987; Collins and Barber 1985; White and Glenn-Lewin 1984; Belsky 1988). These same factors increase diversity and heterogeneity within communities as well (Belsky 1986; Schimel *et al.* 1985; Milchunas *et al.* 1988). For example, spatial variation in grazing intensity creates heterogeneity within a grassland by altering dominance relationships and species composition among patches of vegetation (Senft *et al.* 1985; Collins 1987). Additional causes of small-scale patterns in grasslands include soil disturbances by small-mammals, fecal deposition by grazers, and microvariation in soil nutrient supply (Wiens 1976; Collins and Barber 1985; Inouye *et al.* 1987; Gibson 1988; Tilman 1988). This combination of large- and small-scale processes in grasslands produces a dynamic mosaic of species assemblages within and between communities (White and Glenn-Lewin 1984; Belsky 1988) which enhances both local and regional diversity (Collins and Glenn 1988).

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Individual disturbances in grasslands may induce vegetation dynamics either as small-scale gap-filling processes (Rapp and Rabinowitz 1985; Collins 1989) or as large-scale species replacement sequences during secondary succession (Collins and Adams 1983). At any spatial scale, succession is a function of three general causes: i) the nature of the disturbance, ii) species availability, and iii) the differential performances of species that eventually occupy the disturbed area (Pickett *et al.* 1987). Despite a plethora of studies on secondary succession (Finegan 1984; Pickett *et al.* 1987; Walker and Chapin 1987), few generalizations exist concerning patterns of diversity and heterogeneity during succession in grasslands. In fact, Muraoka *et al.* (1984) noted the lack of studies quantifying factors affecting heterogeneity in successional communities in general. In this context, heterogeneity refers to point-to-point similarity in species composition (Inouye *et al.* 1987) where high values of heterogeneity represent low mean similarity among samples.

The overall objective of this study was to identify patterns of diversity and heterogeneity during succession following different experimental disturbances in native tallgrass prairie vegetation. Specific questions addressed in this study are:

- (1) Do different initial conditions alter the rate and pattern of succession in grasslands?
- (2) How does spatial heterogeneity change during succession in grasslands?
- (3) What is the relationship between heterogeneity, species richness, species diversity and dominance during succession in grasslands?

Methods. **FIELD METHODS.** The study area is located at the University of Oklahoma Grassland Research Area in McClain County, central Oklahoma. In 1949, as part of a series of experimental field studies on vegetation dynamics in tallgrass prairie (Kelting 1954, 1957; Penfound and Rice 1957a, 1957b; Collins and Adams 1983), several small grassland plots (ca. 0.1 ha) were subjected to different disturbance treatments including 1) five years of annual plowing of previously grazed prairie (annually plowed prairie), 2) one year of plowing of previously grazed prairie (once-plowed prairie), 3) abandoned field, 4) one year of plowing previously abandoned cropland (replowed field), 5) continuous grazing by cattle of unplowed prairie (grazed prairie), and 6) ungrazed, unplowed prairie (protected prairie). Changes in

species composition during succession were previously described for the annually plowed, once-plowed and protected prairies by Collins and Adams (1983). In the absence of fire on coarse-textured soils, invasion by woody species may rapidly convert tallgrass prairie to shrubland and woodland (Collins and Adams 1983).

All treatments were located on level to gently sloping sandy to sandy-loam soils. The annually plowed, once-plowed, grazed, and protected prairie treatments had been lightly to moderately grazed until 1949, had never been plowed prior to the study, and had not been burned during the study period. The two abandoned field treatments were eight years old at the beginning of the study. Except where noted, each treatment was sampled with 25 32-cm × 32-cm quadrats evenly spaced along two randomly located transect lines. This quadrat size is large enough to contain several different species per sample, yet small enough to reflect potential small-scale neighborhood interactions (e.g., competition, allelopathy) that may drive succession. Because the analyses are based on quantitative values, they are biased towards the common species which are adequately sampled. See Kelting (1954) for a justification of this sampling scheme. Aerial cover of all species was estimated within each quadrat. Treatments were sampled in several years from 1949 until 1982. Many of the treatments were abandoned or destroyed during the early 1960's, and all treatments were destroyed by 1984. The various treatments and years during which they were sampled are listed in Table 1. Collins and Adams (1983) include a list of species in the different successional stages.

DATA ANALYSIS. Analysis of community structure was performed at two levels. Broad-scale changes in community structure during succession were measured by analyzing changes in average cover values within a treatment over time. More detailed changes in community structure were determined by analyzing variation among the 25 quadrats within a sample period. In this case, a community is defined as the species occurring together at a sample date within a treatment.

Detrended correspondence analysis (DCA, Hill and Gauch 1980) was used to assess broad-scale patterns of community dynamics within treatments over time. To do so, average cover values were calculated for all species in a treatment at each sample date ($N = 25$ quadrats except where indicated in Table 1). The 34 sample (late sum-

Table 1. Treatments and years during which each treatment was sampled. s = spring, all other samples were in late July–early August.

Treatment	Year											
	49	50s	50	51	52	54	56	58	59	62	63	81/2
Protected prairie	X	X	X		X				X	X		X
Grazed prairie	X	X							X	X		
Once-plowed prairie			X						X	X		X
Annual plowed prairie			X	X	X	X	X	X	X	X	X	X
Abandoned field				X	X	X			X	X		
Replowed field		X	X	X	X	X				X		

mer samples only) by 94 species matrix was subjected to DCA with downweighting of rare species. A phase-space plot (Schaffer 1985) was constructed to determine successional trajectories among communities within each of the experimental treatments. Phase-space analysis is derived from chaos theory and permits the analysis of successional trajectories, measurement of rate of change, and assessment of domains of attraction during succession. As developed here, phase-space analysis allows the simultaneous combination of several ordination axes, weighted by their importance, to measure patterns and rates of successional change. For this study, phase-space plots were constructed with two DCA axes (additional axes added little information). First, the scores for a stand along DCA axes I and II were multiplied by their respective eigenvalues for each axis. The weighted DCA axes I and II scores were then summed. The phase-space plot is constructed by plotting the weighted, summed DCA score for a sample at time t versus the weighted, summed DCA score for time $t + 1$. This provides a time trajectory of compositional change along the two ordination axes that is weighted by the importance of each axis. Temporal heterogeneity is a function of changes in species composition between sample dates and is reflected in the length of the vector connecting two samples. Temporal heterogeneity may also be a function of the time interval between samples. Spearman's rank correlation coefficient was used to determine if vector length (a measure of heterogeneity) is related to the time interval (years) between samples.

Affinity analysis was used to derive measures of spatial heterogeneity among the quadrat samples from within communities (Istock and Scheiner 1987; Scheiner and Istock 1987). This analysis provides two independent measures of community structure, community heterogeneity and mosaic diversity. *Heterogeneity* is the mean similarity in species composition among sam-

ples. In this study, Jaccard's coefficient modified for species cover values (Gleason 1920) was calculated for all possible combinations of quadrats in a treatment. For a treatment sampled with 25 quadrats, this resulted in a similarity matrix of 300 values. Community *heterogeneity* (h), a measure of variation among samples, is the obverse of mean similarity. Thus, a high h would indicate a high degree of compositional variation among samples within a community. *Mosaic diversity* is a measure of the amount of variation around the mean similarity value for a set of samples (Istock and Scheiner 1987). This index is derived by calculating the mean similarity of each sample i (\bar{S}_i) and then determining how different this sample is compared to the \bar{S} 's for every other sample using the Wilcoxon T statistic. \bar{S}_i is then plotted against the mean Wilcoxon T statistic (\bar{T}_i) for sample i . Mosaic diversity of a community is the slope of the regression of \bar{S} vs. \bar{T} for all samples. Thus, mosaic diversity measures variance and pattern in the similarity values. The greater the amount of structure in the data set, the greater is the mosaic diversity of a community. Heterogeneity and mosaic diversity are statistically independent measures ($r = -0.24$, $P = 0.15$) of community structure. The reliability of mosaic diversity increases with sample size (Scheiner and Istock 1987). Because 25 quadrats is below the recommended minimum of 30, mosaic diversity is used here in a comparative manner because all communities were sampled with the same intensity with only a few exceptions (Table 1).

The Shannon-Weaver index, $H' = -\sum p_i \ln p_i$, was used as a measure of *species diversity*, where p_i is the relative cover of species i . *Dominance* was measured with the inverse of Simpson's index, $1/\sum p_i^2$. *Species richness* is the total number of species found among the 25 quadrats per site, and *species density* is the average number of species per quadrat. Kwiatkowska and Symonides (1986) have demonstrated that Shannon-Weaver diversity and associated measures

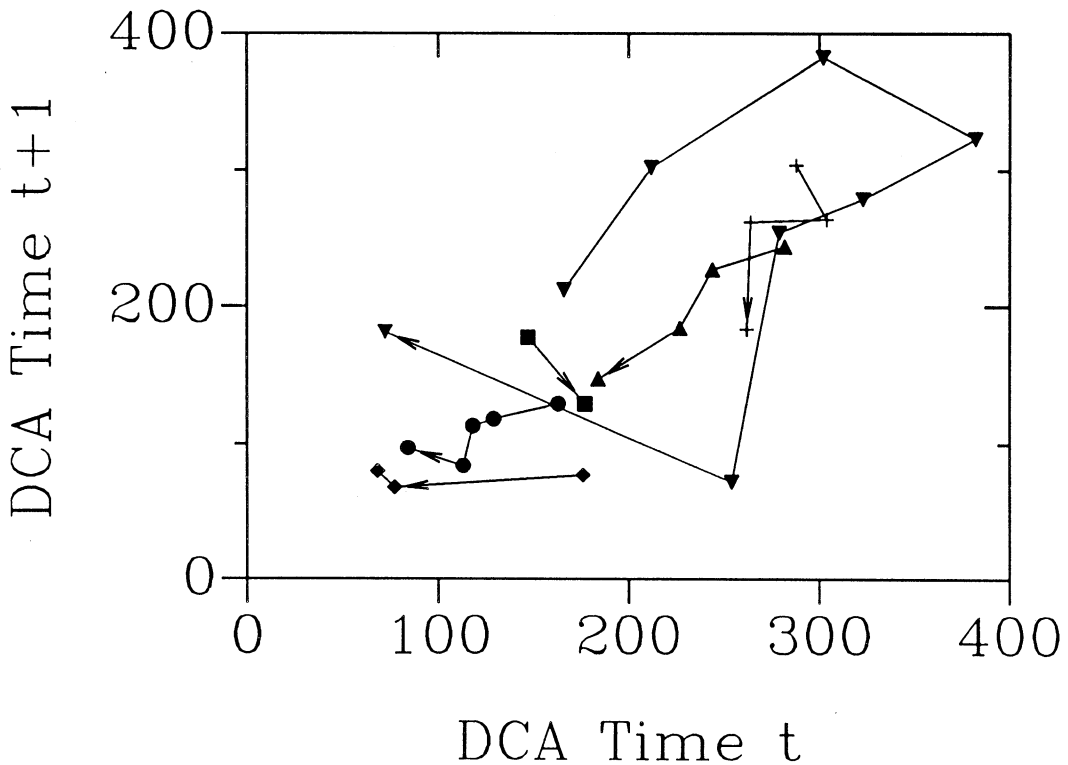


Fig. 1. Phase-space analysis of successional dynamics in six experimental grassland treatments in central Oklahoma. Arrows indicate direction of change. ▼ = Annually plowed prairie, ◆ = once-plowed prairie, ▲ = abandoned field, + = replowed field, ■ = grazed prairie, ● = protected prairie.

are non-linearly related to quadrat size and that variation in these values increases with decreasing quadrat size. Thus, it is important to recognize that the results reported in this study are influenced by, but nonetheless relevant to, a small spatial scale of measurement. In total, these measurements of community structure address structure at two distinct spatial scales. Species density is measured at the scale of a quadrat (m^2), whereas all others are community level measurements.

Growing season precipitation may affect the degree and rate of change during succession in grasslands (Risser *et al.* 1981). For the combined data sets, correlation analysis was used to determine the relationship between the various measures of diversity and precipitation, as well as diversity and successional age. Additionally, correlation analysis was used to determine if there were any significant changes in diversity measures within a treatment during succession. In all comparisons, $P \leq 0.05$ was considered to be significant.

Results. BROAD-SCALE PATTERNS. Axis I of the detrended correspondence analysis of the

treatment plots was a successional axis with a gradient length of 4.2 standard deviation units and an eigenvalue of 0.68. This corresponds to a nearly complete turnover of species along the ordination axis (Hill and Gauch 1980). The gradient along the second axis was 2.2 SD units with an eigenvalue of 0.29. Together the two axes form a successional plane ranging from communities dominated by short-lived grasses and forbs, to communities in which woody vegetation occurs in the absence of fire. The complete successional sequence in the data set ranges from old-field annuals to dominance by perennial grasses which are eventually replaced by shrubs and trees.

The phase-space plot based on this ordination provides a clear indication of the degree of heterogeneity between sample dates within a treatment (Fig. 1). This heterogeneity is a function of successional change. The successional trajectories for the once-plowed and protected prairies are similar in length and direction, indicating a degree of successional convergence and a moderate degree of compositional change over time. The trajectories for the abandoned field and replowed field also indicate directional change. The

single vector for the grazed prairie is divergent from the general direction of the trajectories of the other treatments. Finally, the trajectory for the annually plowed prairie is initially opposite that of the other treatments. The annual plowing treatment reversed succession. However, once plowing stopped, this field rapidly recovered its successional trajectory but it did not converge with the once-plowed and protected prairies (Fig. 1). Changes in the trajectories of the annually plowed, once-plowed, and protected prairies reflected increasing dominance by woody shrubs such as *Rhus copallina*, *R. glabra*, and *Symphoricarpos orbiculatus*.

The degree of heterogeneity between sample dates is indicated by the length of the vectors connecting two samples. The length of these vectors was not correlated with the number of years between sample dates ($r_s = -0.11$, $P > 0.2$), thus compositional change occurred rapidly on some treatments, and slowly on others. This clearly indicates the variable rate of change during a successional sequence. Additionally, the largest vectors were for the annually plowed prairie (Fig. 1). This disturbance had dramatic effects on rate of change that lasted well after the plowing had ceased.

WITHIN-COMMUNITY PATTERNS. Heterogeneity and mosaic diversity tended to fluctuate during succession on each of the six study areas (Fig. 2). Despite these fluctuations, heterogeneity decreased significantly over time on the grazed treatment ($r = -0.75$, $P < 0.05$) and increased significantly during succession on the annually plowed ($r = 0.65$, $P < 0.05$), once-plowed ($r = 0.68$, $P < 0.05$), replowed field ($r = 0.61$, $P < 0.05$) and protected prairie ($r = 0.62$, $P < 0.05$) treatments. Mosaic diversity appeared more variable over time than heterogeneity (Fig. 2). Nevertheless, mosaic diversity increased significantly over time in the abandoned field ($r = 0.66$, $P < 0.05$) and grazed prairie ($r = 0.86$, $P < 0.01$).

When data from all treatments are combined, heterogeneity was not significantly related to growing season precipitation ($r = 0.02$, fall samples only) or species richness ($r = -0.14$). Heterogeneity was positively correlated with species diversity ($r = 0.45$, $P = 0.008$, Fig. 3a). As species diversity increased, the mean similarity among samples decreased. Community structure in grasslands is often controlled by dominant species, such as *Andropogon gerardii*, that form a competitive matrix. However, neither hetero-

geneity nor mosaic diversity were related to combined cover of the matrix-forming grasses ($r = -0.08$ and 0.13 , respectively). Instead, heterogeneity was significantly negatively related to dominance ($r = -0.54$, $P = 0.0005$, Fig. 3b). As dominance increased, the degree of similarity among samples increased. Thus, regardless of the type of species, heterogeneity will be a function of the degree to which a few species dominate a treatment. Finally, heterogeneity was also significantly negatively related to species density ($r = -0.48$, $P = 0.003$, Fig. 3c) indicating that the degree of variation among samples decreased as the average number of species per quadrat increased.

Mosaic diversity was not significantly related to species diversity, although with the removal of one outlier the relationship was significant ($r = -0.37$, $P = 0.03$). Mosaic diversity was significantly negatively related to species density ($r = -0.44$, $P = 0.006$, Fig. 4). Thus, the fewer species per sample, the greater the overall variance in the data structure. Species diversity was positively correlated with species density ($r = 0.36$, $P = 0.04$). Therefore, as species density increases, diversity increases and the samples become more similar reducing the overall variance in the data structure.

The limited relationships between mosaic diversity and other measures of diversity could be the result of combining treatments in which successional change is rapid with other treatments in which the vegetation is less dynamic. When the data set is divided into two subsets, successional samples from vegetation ≤ 20 years and those > 20 years old, the relationships between heterogeneity, mosaic diversity and environmental factors changed. Mosaic diversity was still unrelated to precipitation, dominance, and species diversity in vegetation ≤ 20 years of age. However, mosaic diversity was again significantly negatively related to species density ($r = -0.55$, $P = 0.006$). In the early successional plots, if the two most recent samples from the plowed prairie treatments are included, heterogeneity had a significant but complex relationship with time since abandonment ($r^2 = 0.35$, $P = 0.03$, Fig. 5). This complex function reflected a sequential pattern of increasing and decreasing heterogeneity during the early stages of grassland succession. As in the analysis of the complete data set, heterogeneity of successional communities was negatively related to dominance ($r = -0.54$, $P = 0.008$) and species density ($r = -0.41$, $P = 0.05$).

Although there was no relationship between

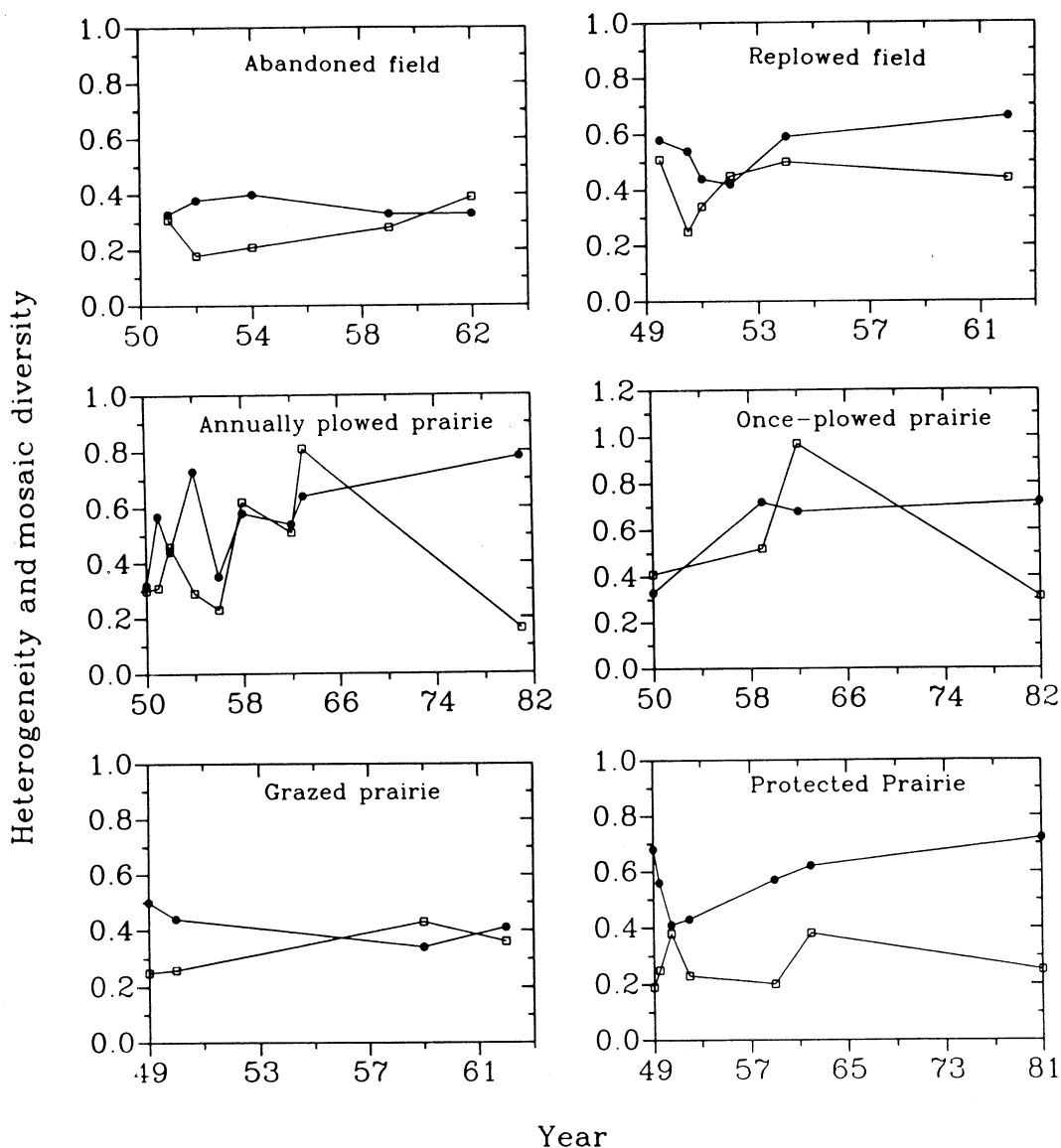


Fig. 2. Changes in heterogeneity (●) and mosaic diversity (□) over time on six successional grassland treatments. Mosaic diversity was multiplied by 100 to make the scales equivalent.

species diversity and heterogeneity in the successional plots, there was a strong positive correlation between species diversity and heterogeneity in the plots >20 years old ($r = 0.63$, $P = 0.007$, Fig. 6). Again, there was a significant positive relationship between heterogeneity and species density ($r = 0.69$, $P = 0.007$) and species density was positively related to species diversity ($r = 0.55$, $P = 0.01$). Mosaic diversity in older vegetation tended to be positively but not significantly related to dominance ($r = 0.48$, $P = 0.09$). Thus, in more stable vegetation, the degree

of variance among samples increased as dominance increased. No other factors were correlated with mosaic diversity.

Based on Kruskal-Wallis one-way analysis of variance, there were no significant differences in species diversity, density, richness, mosaic diversity, heterogeneity or dominance between early (vegetation <20 years old) and late successional samples.

Discussion. It is clear from these analyses that initial conditions have important and often long-

lasting consequences on successional dynamics in grasslands. For example, the annually plowed treatment showed rapid changes in species composition long after the plowing treatment stopped (Fig. 1). Similar initial treatment effects have been noted by Keever (1979), Squiers (1989), and Schafale and Christensen (1986) for changes in old-field communities in the eastern United States. In addition, the treatment subjected to continuous grazing had a successional trajectory different from the other treatments. Grazing is likely to counteract successional change because the dominant species that increase during succession in tallgrass prairie are the same species that are preferred by grazers (Voigt and Weaver 1951).

The phase-space analysis provided an effective means of representing vegetation dynamics and successional trajectories over time. It does appear that most changes were directional and they reflected an increase in cover of perennial grasses during succession (Collins and Adams 1983). The successional trajectories of the protected, once-plowed, and annually plowed prairies shifted away from the diagonal toward dominance by woody vegetation. This would represent a "basin of attraction" for mesic successional grasslands on coarse textured soils (Collins and Adams 1983). The grazed prairie and the two abandoned cropland plots are developing towards dominance by perennial grasses such as *Sorghum halepense* that are not characteristic of true prairie. Thus, previous land use has a long-lasting effect on grassland composition and dynamics.

Although few generalizations exist concerning successional dynamics (Drury and Nisbet 1972; Walker and Chapin 1987), it does appear that one characteristic of communities during succession is the sequential development and decay of the canopy as species composition changes over time (Bormann and Likens 1979; Peet and Christensen 1988). This pattern of canopy closure and decay would produce fluctuations in heterogeneity as noted in Fig. 5. Although the curve in this figure is strongly influenced by two data points, the general relationship is biologically meaningful because these two samples represent successional transition from grass-dominated to shrub-dominated vegetation in a manner similar to that reported by Archer *et al.* (1988). In addition, the temporal sequence of formation and breakdown of the plant canopy has important consequences for species diversity and community heterogeneity during succession. As canopy cover increases, dominance increases and

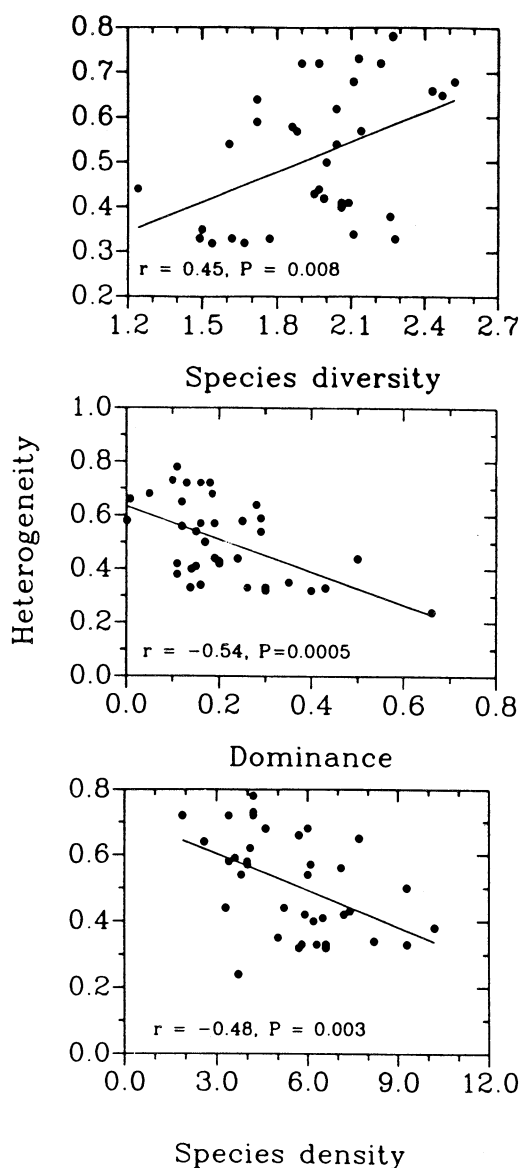


Fig. 3. The relationship of heterogeneity (average similarity among quadrats) to species diversity (H'), dominance (Simpson's index) and species density (average number of species per quadrat) for all samples.

diversity decreases. When dominance decreases, the number of species per quadrat (species density) increases. Density is positively related to species diversity. This pattern occurs several times during succession in Oklahoma old fields. Booth (1941) described four stages of vegetation that occupy a site for different lengths of time during succession in tallgrass prairie. In central Oklahoma, patterns of diversity and dominance have been shown to fluctuate in association with

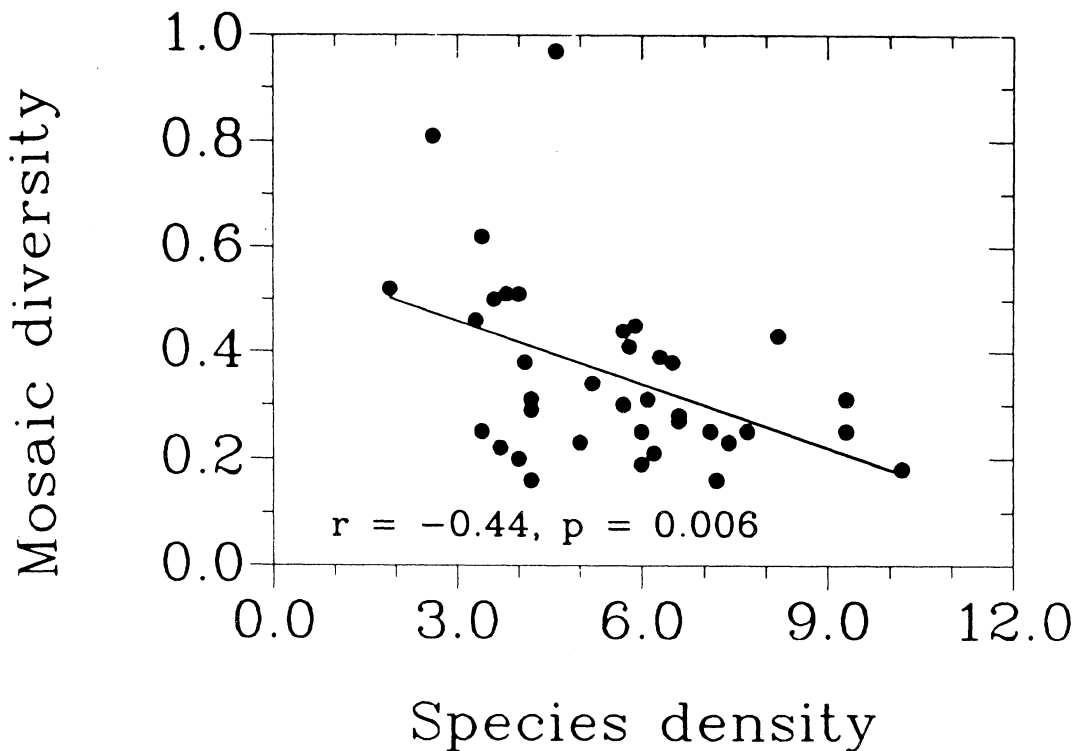


Fig. 4. Relationship of mosaic diversity (degree of variation among quadrats) to species density (average number of species per quadrat) for all samples.

these successional stages (Perino and Risser 1972; Kapustka and Moleski 1976). Although Collins and Adams (1983) reported that the sequence of vegetation change described by Booth (1941) did not occur at this site, they did report identifiable vegetation stages and rapid compositional changes during succession. As these stages change over time, diversity, dominance and heterogeneity fluctuate in response to changes in species composition.

Species density was the most important variable associated with species diversity, mosaic diversity and heterogeneity. Species density reflects patterns of dominance and diversity in a community. Hierarchy theory states that patterns at a specific focal level are the result of mechanistic processes at lower hierarchical levels and constraints imposed at higher levels (O'Neill 1989). Allen and Hoekstra (1986) suggested such an approach to unravel the complexity of grassland communities. In this study, patterns of mosaic diversity and heterogeneity, aspects of community structure, were a function of lower hierarchical interactions such as species density, a measure of species packing in a community. Mosaic diversity and heterogeneity, however, are con-

strained by higher level factors that limit species density such as the local species pool. The relationships between community structure and species density are clear cut. Density is limited by quadrat size and the number of species available in the community. At high species densities, a larger percentage of the local species pool is incorporated into each sample. Therefore, the degree of difference between samples decreases which decreases heterogeneity.

The limited number of correlations with mosaic diversity is not unexpected. This measure of community structure is a function of the degree of difference among samples in an area. There is no reason to expect this to correlate with environmental variables because any number of factors could cause a few samples within a community to be compositionally unusual. In fact, Glenn and Collins (1990) have shown that aspects of small-scale patch structure in tallgrass prairie may change randomly within and between growing seasons. Changes in mosaic diversity could also be a function of quadrat size because a small quadrat could be dominated by an uncommon but large plant. Mean similarity among samples, heterogeneity, fluctuated during

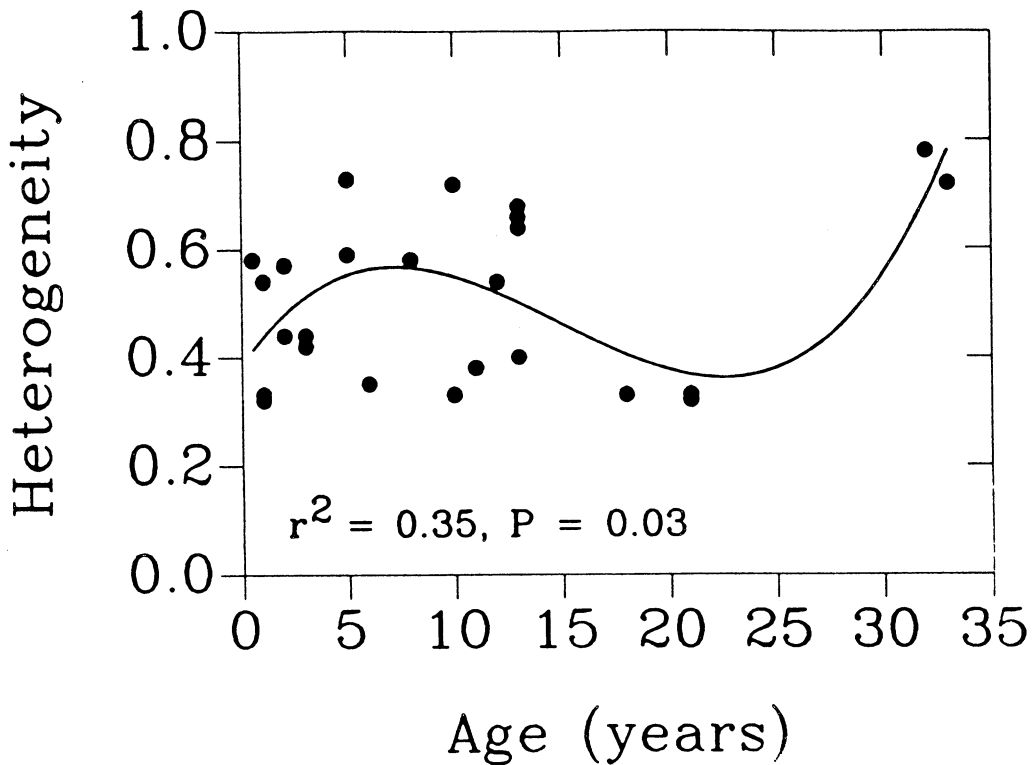


Fig. 5. Relationship of heterogeneity to age in successional vegetation ≤ 32 years old.

succession. When heterogeneity is low, a few outliers are likely to increase variance in the data structure, increasing mosaic diversity. Thus, as an index of variation at small spatial scales (quadrats within a treatment), mosaic diversity will often fluctuate within and between successional stages in response to many factors including vegetation pattern, dominance and disturbance (Biondini *et al.* 1989).

The factors that contribute to community structure are clearly complex and variable. However, patterns at small spatial scales have significant non-random effects on large-scale plant community structure and vice versa (Collins and Glenn 1990). These patterns reflect processes in plant communities, such as competition and vegetative reproduction, which occur most often at relatively small spatial scales (Werner 1979; Cook 1980). These processes may reduce species density and community diversity by increasing dominance. Interspecific interactions, however, are constrained by higher level processes, such as disturbance and long-distance dispersal, which operate at larger spatial scales and tend to increase species density, community richness, and heterogeneity. The relative importance of these

factors probably changes with succession. That is, dispersal may provide a greater contribution to heterogeneity and community richness during earlier vs. later stages of succession (e.g., Egler 1954; Walker *et al.* 1986).

The patterns of species diversity and community heterogeneity described in this study are far more complex than many of the monotonic models used to describe the relationship between succession and diversity (e.g., Odum 1969; Connell 1978). Heterogeneity fluctuates during succession rather than simply increasing or decreasing over time. The changes in heterogeneity are a function of species density. Species diversity increases as density increases. Mosaic diversity and dominance decrease with increasing species density. As density decreases, dominance increases which reduces heterogeneity and diversity. By analyzing the various components of diversity at different spatial and temporal scales, it will be possible to more clearly understand patterns and mechanisms controlling species diversity in plant communities. It does appear, however, that factors associated with community-level structure are controlled by interactions that are directly associated with species density

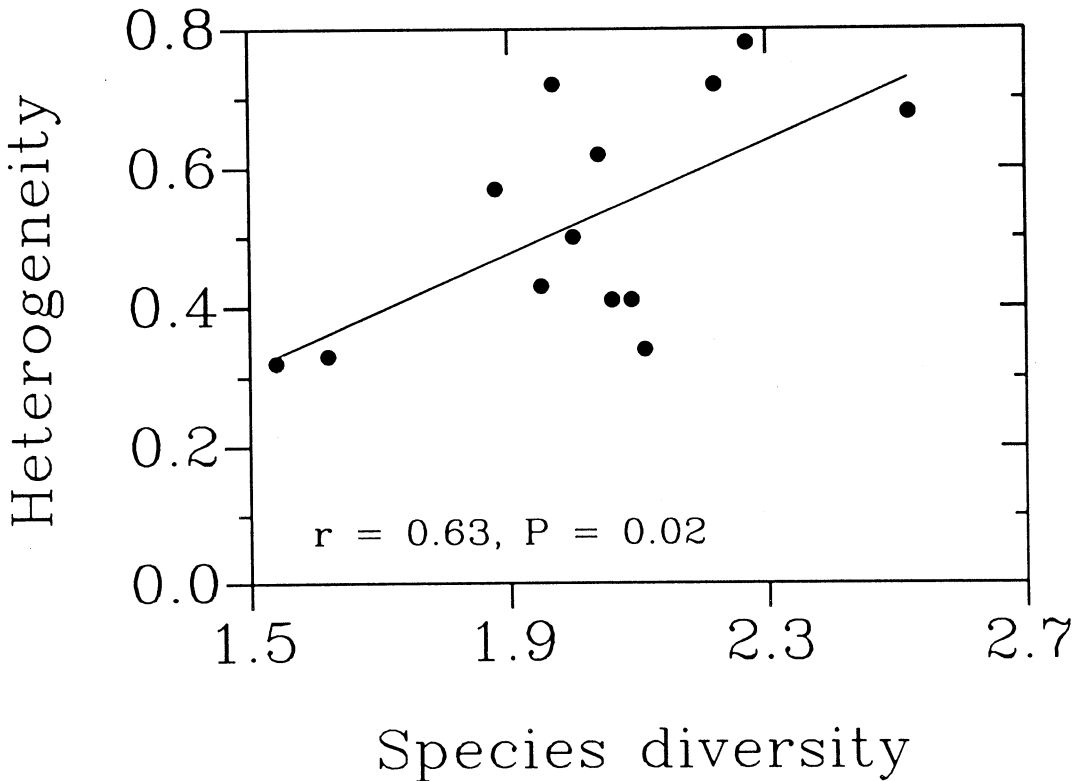


Fig. 6. Relationship of heterogeneity to species diversity (H') in mature vegetation >20 years old.

in these grasslands. The results presented here are based on a rather coarse temporal scale, and thus, more detailed successional data will be necessary to further test these predictions concerning changes in the structure of plant communities over time.

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