Ecology, 73(6), 1992, pp. 2001–2006

FIRE FREQUENCY AND COMMUNITY HETEROGENEITY IN TALLGRASS PRAIRIE VEGETATION[1]

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Abstract. Few studies have directly addressed the effects of disturbance on spatial and temporal heterogeneity. Spatial heterogeneity is the degree of dissimilarity in species composition from one point to another in a community, whereas temporal heterogeneity is compositional change within a site over time. The purposes of this study were to determine (1) if a quadratic relationship exists between within-site heterogeneity and disturbance frequency as predicted by the intermediate disturbance hypothesis (IDH), (2) if disturbed and undisturbed sites have similar heterogeneity as implied by the disturbance heterogeneity hypothesis (DHM), and whether or not these results differed with scale, and (3) if there is a relationship between spatial and temporal heterogeneity as implied by the DHM. Analyses were based on plant species composition data collected over 9 yr in quadrats permanently located in experimental management units subjected to different burning frequencies at Konza Prairie Research Natural Area, Kansas, USA.

The relationship between disturbance frequency and within-site heterogeneity was opposite that predicted by the IDH. Heterogeneity was lowest at intermediate disturbance frequencies. Heterogeneity in annually burned prairie was lower than in unburned prairie and prairies burned once every 4 yr in contrast to predictions of the DHM. However, this relationship did not hold at larger spatial scales. There was a positive relationship between within-site spatial and temporal heterogeneity on annually burned sites, sites burned once every 4 yr, and nearly so on sites burned every other year. Within-site heterogeneity was negatively correlated with cover of *Andropogon gerardii,* and positively correlated with total richness and species diversity. Studies of variation, in addition to averages, will increase our ability to predict patterns of species distribution and abundance within and between communities in response to disturbance.

Key words: Andropogon gerardii; *fire; grassland vegetation; intermediate disturbance hypothesis; Konza Prairie; spatial heterogeneity; species density; species diversity.*

INTRODUCTION

Pattern in plant communities is a function of many biotic and abiotic factors and these factors operate on different species at different spatial scales (Pielou 1960, Greig-Smith 1979, Legendre and Fortin 1989). One product of the nonrandom distribution of species at different spatial scales is community heterogeneity. In this paper, spatial heterogeneity is the mean degree of dissimilarity in species composition from one point to another in a community (Inouye et al. 1987, Collins 1990). Heterogeneity differs from pattern analysis in that the latter is a measure of the degree of spatial autocorrelation, or distance decay in the case of gradients, in a community (Palmer 1988, Legendre and Fortin 1989). Like the measurement of pattern, the measurement of spatial heterogeneity is scale dependent; larger samples are likely to include a larger subset of species in a community, and thus, increase the degree of similarity among plots, than are smaller samples.

One common mechanism producing spatial heterogeneity in communities is disturbance (e.g., Collins 1989, Chaneton and Facelli 1991, Glenn et al. 1992). Studies of disturbance effects on heterogeneity, however, are often confounded by scale problems. Two theoretical models, the disturbance heterogeneity model (DHM, Kolasa and Rollo 1991), and the intermediate disturbance hypothesis (IDH, Connell 1978) are relevant. These models make contrasting predictions concerning the relationship between heterogeneity and disturbance.

The DHM (Kolasa and Rollo 1991) is a between-patch heterogeneity model based on analyses that combine measurements from both disturbed and undisturbed patches. In this case, disturbance increases community heterogeneity in areas where the size of the disturbance is small relative to the size of the community (e.g., the effects of gaps in forests). As size of the disturbed area increases relative to the total area of interest, the DHM predicts a quadratic relationship in which heterogeneity is highest in communities where 50% of the area is disturbed (Kolasa and Rollo 1991). One important assumption of the DHM providing the basis of the quadratic relationship is that spatial heterogeneity within disturbed patches is similar to heterogeneity within undisturbed patches.

The IDH is a within-patch model that predicts a

[1] Manuscript received 11 March 1991; revised 6 January 1992; accepted 13 January 1992.

quadratic relationship between disturbance frequency and species diversity. Given that diversity is positively correlated with heterogeneity (Whittaker and Levin 1977), this model predicts that within-patch heterogeneity will be highest at intermediate frequencies of disturbance.

Whereas spatial heterogeneity is measured over a number of points in space at a single point in time, temporal heterogeneity is measured over several points in time at a single point in space (Kolasa and Rollo 1991). A linkage between space and time is an important component of many models of landscape dynamics (Delcourt et al. 1983, Urban et al. 1987, Turner et al. 1989), yet few studies have documented a statistical space–time relationship between community variables in terrestrial systems. Kolasa and Rollo (1991) state, however, that there is a positive relationship between spatial and temporal heterogeneity in an area over time.

In this study, I used community composition data collected over a 9-yr period in quadrats permanently located in experimental management units to test hypotheses derived from the IDH and DHM models. First, I determined if within-patch heterogeneity showed a quadratic relationship with disturbance frequency as predicted by the IDH. Secondly, I determined if burned and unburned grasslands exhibited similar degrees of spatial heterogeneity as assumed by the DHM. The relationship between disturbance and heterogeneity may differ at larger spatial scales (Glenn et al. 1992). As noted above, the DHM predicts a quadratic relationship between among-site heterogeneity and number of sites disturbed in a region. Thirdly, I determined if there was a positive relationship between spatial and temporal heterogeneity as suggested by Kolasa and Rollo (1991).

METHODS

Study site.—The study was conducted at Konza Prairie Research Natural Area (KPRNA), a 3487-ha tallgrass prairie located in Riley and Geary counties, northeastern Kansas, USA. The climate is continental with hot summers, cold winters, strong winds, and low humidities. Mean annual temperature is ≈13°C, and mean annual precipitation, which varies drastically from year to year, is 835 mm (1951–1980), most of which occurs in May–June and September. From 1981 to 1990, growing season precipitation (April–September) ranged from a low of 434 mm in 1988 to a high of 849 mm in 1986. As part of the Long-term Ecological Research Program (LTER), KPRNA is divided into a series of replicated management units subjected to different frequencies of spring (mid-April) burning (Hulbert 1985).

Data collection.—Vegetation data have been collected on eight study sites since 1981. In 1983, an additional six sites were added, and five more sites were added in 1984 for a total of 19 sites in 12 management units. In each of the 19 study sites, species composition was measured in permanently located 10-m^2 circular quadrats. Five quadrats were evenly spaced (12.5 m) along each of four 50-m long transects within a study site (total = 20 quadrats per site). Because each site is subjected to a controlled disturbance regime, a site as used here represents a disturbed (burned) or undisturbed (unburned) patch. In each year, cover of species in each quadrat was estimated in May, July, and September using a modified Daubenmire scale (1 = 0–1% cover, 2 = 2–5% cover, 3 = 6–25% cover, 4 = 26–50% cover, 5 = 51–75% cover, 6 = 76–95% cover, 7 = 96–100% cover). Although this cover scale yields relatively coarse estimates of cover in a single quadrat, it is a highly repeatable method for rapidly sampling a large number of quadrats over a short period of time (total = 380 quadrats). For each species, Daubenmire scale values were converted to the midpoint value per quadrat for analysis.

Data analysis.—As noted above, spatial heterogeneity is measured as the mean dissimilarity in species composition among samples at a site within a year (Inouye et al. 1987, Collins 1989, Scheiner 1990). In this study, percent dissimilarity (PD) was defined as:

$$PD = 1 - PS$$

$$PS = 1 - 0.5 \sum_{i=1}^{s} |p_a - p_b|,$$

where PS is percent similarity, p_a is the proportional cover of species p in quadrat a, p_b is the proportional cover of species p in quadrat b, and s is the total number of species (Whittaker 1975). As the degree of difference in composition among quadrats increases, spatial heterogeneity, as measured by PD, increases. Percent dissimilarity was calculated for all possible two-way combinations of quadrats at a site, resulting in a matrix of 190 values. Within-site heterogeneity is the average of the 190 values.

Linear and polynomial regressions were used to test the hypothesis from the IDH that there was a quadratic relationship between disturbance frequency and heterogeneity. For this analysis within-site heterogeneity was measured as the heterogeneity of a site (n = 19) in 1990, the most recent year of sampling. Disturbance frequency was measured as the number of times the site had been burned since the experimental protocol was established in 1972 (max = 19 times).

To test the assumption of the DHM that heterogeneity within undisturbed sites is similar to heterogeneity within disturbed sites, within-site heterogeneity of management units burned annually, every other year, every 4 yr, and unburned were compared using Kruskal-Wallis one-way nonparametric analysis of variance and Dunn's multiple-comparison test (Neave and Worthington 1988). Statistical comparisons were made for all years from 1983 to 1990 (too few sites for comparison in 1981).

Spearman rank correlation was used to test the hypothesis that a relationship existed between the within-site heterogeneity at time t, and the temporal change in species composition at a site from time t to time $t + 1$. That is, does the degree of within-site heterogeneity in one year affect the amount of change in composition from one year to the next at that site? Again, within-site heterogeneity is measured as average dissimilarity among the 20 quadrats at a site. Temporal variation in composition is dissimilarity in species composition at a site from one year to the next. In this case, temporal variation is a single PD value based on average cover values ($n = 20$) for all species at a site at time t and time $t + 1$. Data for these analyses were segregated by burning frequency.

Because measurement of heterogeneity may be scale dependent, I analyzed the larger scale effects of fire frequency on heterogeneity among different sites, as well. To do so, I calculated the mean cover value for each species among the 20 quadrats at each site. Percent dissimilarity then was calculated for all pairwise comparisons among all sites at Konza, resulting in matrices of 28 values for 8 sites in 1981, 91 values for 14 sits in 1983, and 171 values for 19 sites in 1984 to 1990. Regional heterogeneity is the mean percent dissimilarity for all pairwise comparisons in each year. Spearman rank correlation and polynomial regression were then used to determine if there as a linear or quadratic relationship, respectively, between regional heterogeneity and the proportion of sites burned each year.

Results

Heterogeneity in 1990 was significantly negatively related to burning frequency (Fig. 1). The quadratic relationship ($r^2 = 0.42$, $F = 5.9$, df $= 16$, $P = .02$) had a higher r^2 but lower P value than the linear relationship ($r^2 = 0.39$, $F = 10.9$, df $= 16$, $P = .004$). More importantly, the quadratic relationship was opposite that predicted by the IDH. That is, heterogeneity was lowest at an intermediate frequency of disturbance. This result is important given the significant positive relationship between heterogeneity and species diversity (measured as the Shannon-Wiener index, H'; $r_s = 0.90$, df $= 17$, $P < .0001$) and total species richness ($r_s = 0.78$, df $= 19$, $P < .01$).

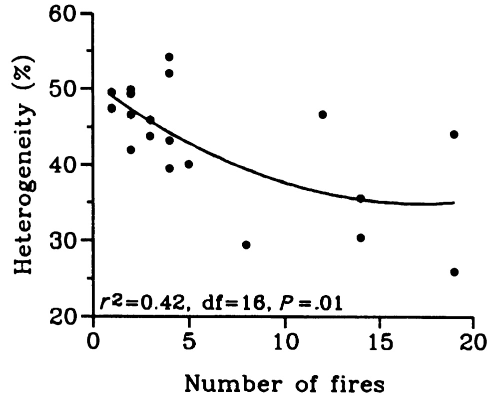

FIG. 1. Relationship between number of times a site has been burned between 1972 and 1990 and site heterogeneity (= 1 − percent similarity) in species composition, as measured in 1990.

Mean heterogeneity on annually burned grasslands was always less than on unburned grasslands (Table 1). Sites burned every other year were often less heterogeneous than unburned sites and both were sometimes less heterogeneous than 4-yr burn sites (Table 1). The decrease in heterogeneity with burning results from increased cover of C_4 grasses following fire. Cover of the dominant C_4 grass *Andropogon gerardii* was significantly negatively related to heterogeneity ($r_s = -0.48$, df $= 19$, $P = .05$).

The relationship between heterogeneity in a site at time t (spatial heterogeneity) and change in species composition from time t to time $t + 1$ (temporal heterogeneity) was significant and positive on annually burned sites ($r_s = 0.44$, df $= 30$, $P < .01$), and on sites burned every 4 yr ($r_s = 0.65$, df $= 40$, $P < .01$) (Fig. 2). A similar trend occurred on sites burned every other year ($r_s = 0.33$, df $= 10$, $.05 < P < .10$). There was no relationship between spatial heterogeneity and temporal variation on unburned sites.

At the regional level, there was no linear ($r_s = 0.03$,

TABLE 1. Average heterogeneity in species composition (=1 − percent similarity) of vegetation on management units with different burning frequencies. Values in the same rows with similar superscripts were not significantly different based on Kruskal-Wallis (K-W) one-way analysis of variance and Dunn's multiple-comparisons test.

	Burn frequency									
	Annual		2-yr		4-yr		Unburned			
Year	%	n	%	n	%	n	%	n	K-W	P
1981	30.6	2	...		44.2	4	42.1	2	2.0	
1983	25.3[a]	4	...		33.1[ab]	4	40.2[b]	6	11.0	<.01
1984	24.4[a]	4	26.6[a]	2	34.8[b]	7	40.8[b]	6	12.9	<.01
1985	22.6[a]	4	19.8[a]	2	33.6[b]	7	37.9[b]	6	14.2	<.01
1986	26.9[a]	4	27.5[a]	2	37.8[b]	7	45.4[b]	6	13.8	<.01
1987	29.5[a]	4	30.4[a]	2	39.2[ab]	7	48.0[b]	6	10.8	<.02
1988	33.1[a]	4	25.9[a]	2	44.8[ab]	7	51.6[b]	6	11.5	<.01
1989	33.7[a]	4	38.5[ab]	2	42.4[ab]	7	46.6[b]	6	10.0	<.02
1990	38.9[a]	4	38.0[ab]	2	44.6[ab]	7	48.4[b]	6	4.4	.05

df = 7, $P > .70$) or quadratic ($r^2 = 0.09$, $F = 0.3$, df = 7, $P = .75$) relationship between heterogeneity and the proportion of sites burned in a year.

Discussion

Results from this study indicate that for tallgrass prairie (1) heterogeneity was lowest on sites with intermediate burning frequencies, (2) heterogeneity on burned grassland was significantly lower than on unburned grassland at a small but not at a larger scale, (3) there was a positive relationship between spatial and temporal heterogeneity in two of the four burning treatments, and (4) heterogeneity was positively correlated with species richness and diversity. Patterns of heterogeneity at Konza are consistent with other analyses of disturbance effects on prairie heterogeneity. For example, small-scale heterogeneity (0.25 m^2) in a grassland burned one time was significantly lower than in unburned grassland in Oklahoma (Collins 1989). However, at a larger scale, there were no significant differences in among-site heterogeneity between burned and unburned sites in the region of Konza Prairie on sites with an unknown disturbance history (Glenn et al. 1992). Thus, at larger spatial scales, factors including site history, regional climate, edaphic factors, and topography may have a greater impact on heterogeneity than fire frequency.

The intermediate disturbance hypothesis predicts that diversity, and in turn, heterogeneity will be highest at intermediate disturbance frequencies. Just the opposite was found in this study. In general, frequent burning changes species composition (Gibson and Hulbert 1987) by eliminating fire-intolerant species and increasing productivity of fire-adapted matrix-forming species, such as the C_4-grass *Andropogon gerardii* (Knapp 1985, Collins 1987, Tester 1989). As productivity increases at Konza Prairie, species richness decreases (S. L. Collins and J. M. Briggs, *personal observation*), perhaps as a result of competitive exclusion (Wilson and Shay 1990). As production of a few species increases, heterogeneity decreases. Eventually, however, frequent burning results in chronic soil nitrogen deficiency (Seastedt and Ramundo 1990). Only species tolerant of burning and low nutrient conditions can exist on frequently burned sites. Assuming that N availability is patchily distributed (e.g., Tilman 1982) then compositional heterogeneity will increase as soil resource heterogeneity increases under long-term burning regimes.

The significant relationship between spatial and temporal heterogeneity on annually burned and 4-yr burning sites is intriguing. The pattern on 2-yr burn sites was nearly significant, as well (.05 < P < .10). All

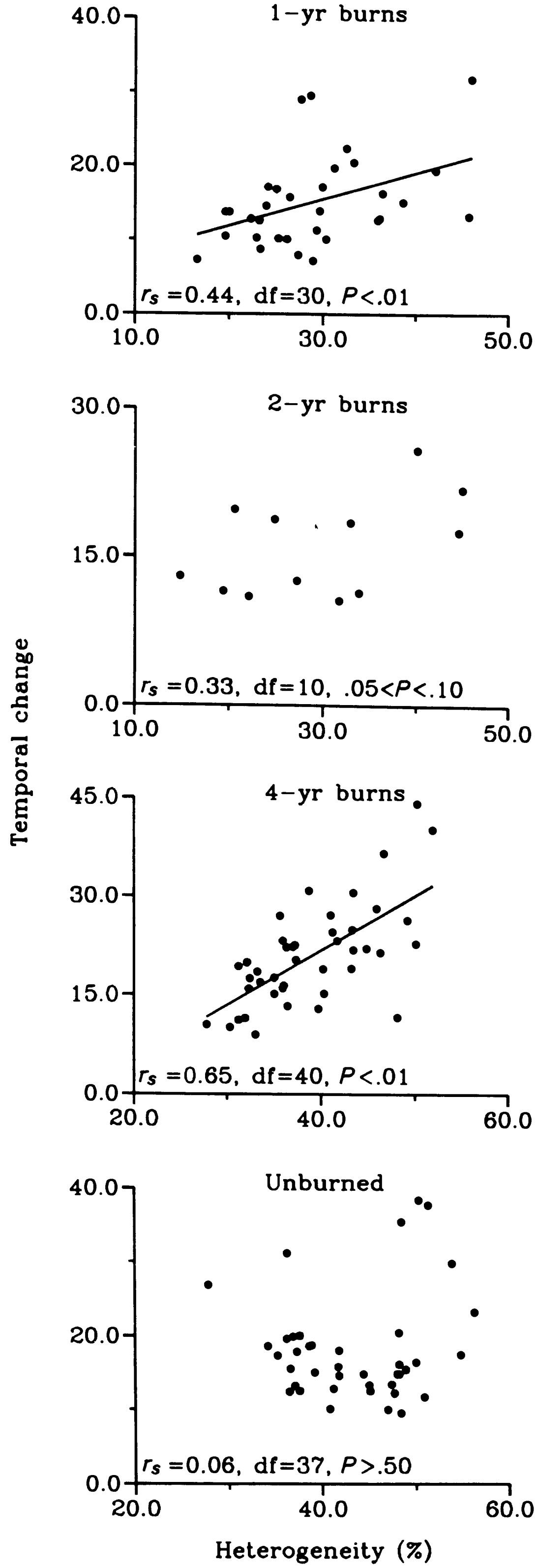

FIG. 2. Spearman rank correlation of within-site heterogeneity (=1 − percent similarity) in species composition in a given year and proportional change in species composition ← from one year to the next on sites that are annually burned, burned every 2 yr, burned every 4 yr, or unburned.

relationships were positive, suggesting that high within-site heterogeneity yields high temporal heterogeneity at least under certain disturbance regimes. Indeed, previous analyses of community dynamics have demonstrated a high degree of spatial and temporal varibility in species distribution and abundance at Konza Prairie (Collins and Glenn 1990, 1991). Temporal variability is a measure of change in species composition over time (immigration plus extinction of species). Although immigration rates are constant on different sites at Konza (Collins and Glenn 1991), as species richness increases over time on a site, there is a significant increase in local rates of extinction (Glenn and Collins 1992). These patterns of immigration and extinction produce compositional change, which yields high temporal heterogeneity. The lack of a significant spatial-temporal relationship on unburned sites is probably a function of succession as these sites become dominated by long-lived woody perennials such as *Symphoricarpos orbiculatus, Rhus glabra, Rosa arkansana,* and *Ceanothus herbaceus.*

Other disturbances (e.g., grazing) are likely to have an effect on heterogeneity opposite that of fire (Gessaman and McMahon 1984). Grazing by ungulates, for example, may increase heterogeneity in grasslands by decreasing dominance and increasing diversity (Belsky 1983, Bakker et al. 1984, Collins 1990). This result would be system and scale dependent (Milchunas et al. 1988, Milchunas and Lauenroth 1989). For instance, Glenn et al. (1992) found that grazed sites had lower within-community but higher among-community heterogeneity compared to burned sites. Highest regional heterogeneity occurred among sites with a combination of burning and grazing.

Currently, generalities regarding heterogeneity are limited because of the small number of studies that have quantified patterns of heterogeneity or measured the mechanisms that create and maintain heterogeneity in communities (Legendre and Fortin 1989, Kolasa and Rollo 1991). Perhaps the relationship between disturbance and heterogeneity reflects a complex response of the system to climatic variation and evolutionary history of disturbance as suggested in the models of Denslow (1980) and Milchunas et al. (1988). Simple predictive models of heterogeneity in response to increasing size of disturbance (e.g., Connell 1978, Kolasa and Rollo 1991) provide a necessary first step for a predictive approach to scale-related questions on patterns of community heterogeneity. Such models are often based on the tenuous assumption that heterogeneity within a disturbance is equal to heterogeneity in adjacent undisturbed areas. Predicting community heterogeneity in response to disturbance will depend on community composition and productivity, evolutionary history, and the type and frequency of disturbance. As Kolasa and Rollo (1991) noted, there is indeed a heterogeneity of heterogeneity. A focus on variation, however, in addition to averages, will help to increase our understanding of factors that affect patterns of spatial heterogeneity and temporal variability in plant communities.

Acknowledgments

I thank Lynn Francis, Susan Glenn, Deborah Goldberg, Bruce Hoagland, Jurik Kolasa, Dan Milchunas, Ernie Steinauer, and two anonymous reviewers for many helpful comments on previous drafts of the manuscript. Earlier data sets were collected by Lloyd Hulbert, Ross Sherwood, Marc Abrams, David Gibson, and Gary Merrill. Data from Konza Prairie Research Natural Area were collected as part of the Konza Prairie LTER program (NSF grants DEB-8012166 and BSR-8514327), Division of Biology, Kansas State University. Data and supporting documentation are stored in data sets PVC01 and PVC02 in the Konza Prairie Research Natural Area data bank. Additional support for data analysis and manuscript preparation was provided by NSF grant BSR-9007450 to Scott Collins and Susan Glenn.

Literature Cited

Bakker, J. P., J. de Leeuw, and S. E. van Wieren. 1984. Micro-patterns in grassland vegetation created and sustained by sheep-grazing. Vegetatio **55**:153–161.

Belsky, A. J. 1983. Small-scale pattern in grassland communities in the Serengeti National Park, Tanzania. Vegetatio **55**:141–151.

Chaneton, E. J., and J. M. Facelli. 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. Vegetatio **93**:143–155.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology **68**:1243–1250.

———. 1989. Experimental analysis of patch dynamics and community heterogeneity in tallgrass prairie. Vegetatio **85**: 57–66.

———. 1990. Patterns of community structure during succession in tallgrass prairie. Bulletin of the Torrey Botanical Club **117**:397–408.

Collins, S. L., and S. M. Glenn. 1990. A hierarchical analysis of species abundance patterns in grassland vegetation. American Naturalist **135**:633–648.

Collins, S. L., and S. M. Glenn. 1991. Importance of spatial and temporal variation in species regional abundance and distribution. Ecology **72**:654–664.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302–1310.

Delcourt, H. R., P. A. Delcourt, and T. Webb, III. 1983. Dynamic plant ecology: the spectrum of vegetational change in space and time. Quaternary Science Review **1**:153–175.

Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. Oecologia (Berlin) **46**:18–21.

Gessaman, J. A., and J. A. MacMahon. 1984. Mammals in ecosystems: their effects on the composition and production of vegetation. Acta Zoologica Fennici **172**:11–18.

Gibson, D. J., and L. C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio **72**:175–185.

Glenn, S. M., and S. L. Collins. 1992. Effects of scale and disturbance on rates of immigration and extinction of species in prairies. Oikos **63**:273–280.

Glenn, S. M., S. L. Collins, and D. J. Gibson. 1992. Disturbances in tallgrass prairie: local versus regional effects on community heterogeneity. Landscape Ecology, *in press.*

Greig-Smith, P. 1979. Pattern in vegetation. Journal of Ecology **67**:755–780.

Hulbert, L. C. 1985. History and use of Konza Prairie Research Natural Area. Prairie Scout **5**:63–93.

Inouye, R. S., N. J. Huntly, D. Tilman, J. R. Tester, M.

Stillwell, and C. Zinnel. 1987. Old-field succession on a Minnesota sand plain. Ecology **68**:12–26.

Knapp, A. K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. Ecology **66**:1309–1320.

Kolasa, J., and C. D. Rollo. 1991. Introduction: the heterogeneity of heterogeneity: a glossary. Pages 1-23 *in* J. Kolasa and S. T. A. Pickett, editors. Ecological heterogeneity. Springer-Verlag, New York, New York, USA.

Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio **80**:107–138.

Milchunas, D. G., and W. K. Lauenroth. 1989. Three-dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos **55**:82–86.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist **132**:87–106.

Neave, H. R., and P. L. Worthington. 1988. Distribution-free tests. Unwin Hyman, London, England.

Palmer, M. W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. Vegetatio **75**:91–102.

Pielou, E. C. 1960. A single mechanism to account for regular, random, and aggregated populations. Journal of Ecology **48**:575–584.

Scheiner, S. M. 1990. Affinity analysis: effects of sampling. Vegetatio **86**:175–181.

Seastedt, T. R., and R. A. Ramundo. 1990. The influence of fire on belowground processes of tallgrass prairie. Pages 99-117 *in* S. L. Collins and L. L. Wallace, editors. Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, Oklahoma, USA.

Tester, J. R. 1989. Effects of fire frequency on oak savanna in east-central Minnesota. Bulletin of the Torrey Botanical Club **116**:134–144.

Tilman, D. 1982. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

Turner, M. G., V. H. Dale, and R. H. Gardner. 1989. Predicting across scales: theory development and testing. Landscape Ecology **3**:245–252.

Urban, D. L., R. V. O'Neill, and H. H. Shugart. 1987. Landscape ecology. BioScience **37**:119–127.

Whittaker, R. H. 1975. Communities and ecosystems. Second edition. MacMillan, New York, New York, USA.

Whittaker, R. H., and S. A. Levin. 1977. The role of mosaic phenomena in natural communities. Theoretical Population Biology **12**:117–139.

Wilson, S. D., and J. M. Shay. 1990. Competition, fire, and nutrients in a mixed-grass prairie. Ecology **71**:1959–1967.