

# Disturbances in tallgrass prairie: local and regional effects on community heterogeneity

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## Abstract

Community heterogeneity in tallgrass prairie was analyzed at regional and local levels to assess the effects of disturbances on community structure at different spatial scales. The sites were part of NASA's First ISLSCP Field Experiment (FIFE) in Kansas, and were located on grassland treatments that were undisturbed, and burned-only on Konze Prairie Research Natural Area, and grazed-only and grazed +burned on adjacent ranch land. Sites in grazed-only or grazed +burned treatments were less similar to each other, on a regional scale (15 x 15 km), than were burned-only or undisturbed sites. Grazing reduced the cover of dominant species, making space available for the establishment of immigrants from the region. Each site was different because of establishment by different species from the large regional species pool. At the local scale (0.1 ha), the most homogeneous treatments were those that were most heterogeneous at the regional scale. Undisturbed treatments at the local scale were the most heterogeneous compared to sites under other treatments. Therefore, regional responses to disturbances were more variable than local responses, and were not predictable from within-site analyses.

## 1. Introduction

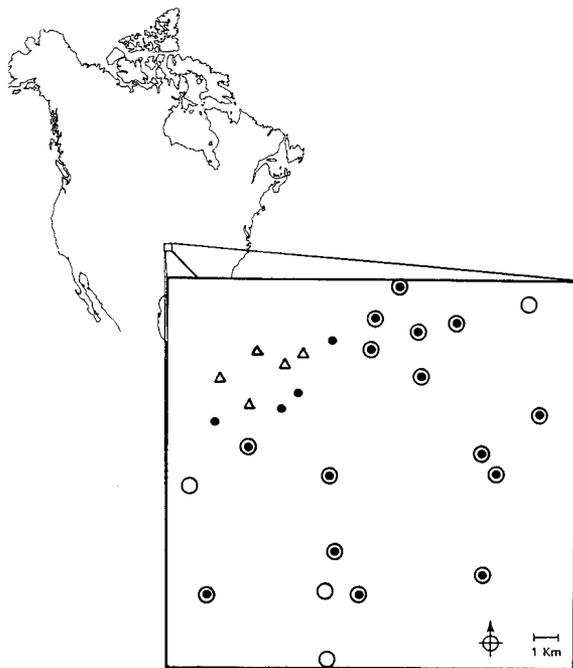
The interpretation of patterns in natural communities is clearly scale dependent because processes may act differently when viewed from different spatial or temporal scales (Allen and Starr 1982). Local scale is defined as within a site or community and regional scale is between-sites or communities. Observed patterns may not always be consistent at different scales. Because the effects of scale may not always be predictable, an understanding of pattern and process at one hierarchical level may not provide useful information about pattern and process at other hierarchical levels (Hengeveld 1987).

Although there are an increasing number of studies on the effects of disturbance on community structure, logistic constraints often limit analysis of disturbance at different spatial scales. However, several studies have noted that the effects of disturbances on community structure are scale-dependent. For example, high levels of disturbances decreased diversity at local scales in tropical rocky intertidal communities, but the resultant local scale patchiness resulted in long-term increases in diversity at larger spatial scales (Menge *et al.* 1985). McGuinness (1987a,b) reported that the effects of disturbances in the rocky intertidal were confounded by the particular species present and interactions of other factors at different scales, such as substrate

heterogeneity. Other studies of disturbances have addressed effects on community heterogeneity. Community heterogeneity is defined as the dissimilarity in species composition between samples. Beatty (1988) noted that mass movement of soil in grasslands increased local heterogeneity, but soil movement had little effect on regional heterogeneity. In Arizona, ungrazed, semi-desert grassland was more heterogeneous than grazed grasslands (Bock *et al.* 1984), however, in Argentina, grazed grasslands were more diverse than ungrazed grasslands at local scales, but less diverse at regional scales (Facelli *et al.* 1989). North American mixed-grass prairie that was burned in the spring or fall was less heterogeneous at a local scale and more heterogeneous at a regional scale than unburned or summer burned prairie (Biondini *et al.* 1989). Therefore, disturbance effects on community heterogeneity may vary with the scale of analysis.

In North American grasslands, disturbances occur over a variety of spatial and temporal scales (Collins and Glenn 1988) and different kinds of disturbances often interact to affect community structure (Collins and Barber 1985; Collins 1987). Previous research indicated that tallgrass prairies in Oklahoma were more heterogeneous on small soil disturbances than on undisturbed sites, but undisturbed sites were more heterogeneous than burned sites (Collins 1989). However, fire had no effect on heterogeneity between the highly variable soil disturbances (Collins 1989). Two disturbances that commonly occur over broad spatial scales in grasslands are fire and grazing. However, there have been no studies that have considered the interactive effects of fire and grazing in grasslands at both the local scale (0.1 ha) and regional scale (15 × 15 km).

The purpose of this study was to determine the effects of fire, grazing, and the two in combination on heterogeneity within and between communities in the tallgrass prairie landscape. Using tallgrass prairie in northeastern Kansas, we tested the hypothesis that regional (between-site) heterogeneity would be greater in grazed versus ungrazed sites and lower on burned versus unburned sites. We also tested the hypothesis that grazing alters fire effects such that heterogeneity will be highest between sites



**Fig. 1.** Map of relative positions of sample sites in northeastern Kansas. Triangles represent undisturbed sites (ungrazed and unburned), black circles represent burned sites, and open circles represent grazed sites.

that are both grazed + burned. Finally, we tested the hypothesis that regional patterns of heterogeneity would be similar to local patterns.

## 2. Methods

### 2.1. Field methods

Twenty-eight sites were sampled within a 15 by 15 km area on and to the south and east of Konza Prairie Research Natural Area, a Long Term Ecological Research Site in the Flint Hills of Kansas (Fig. 1). This area is within the largest expanse of unplowed tallgrass prairie remaining in the United States (Reichman 1987). Tallgrass prairie in this area is not a successional community, but is partially determined by climate, soils, and disturbance (Axelrod 1985). The sites were established as part of the First ISLSCP Field Experiment (FIFE) (Sellers *et al.* 1988). Experimental treatments included sites with different disturbance regimes: 4 sites grazed by

**Table 1.** Treatment, slope, aspect (N = north, S = south, E = east, W = west, TOP = crest of hill, BOTTOM = bottom of slope), elevation, and grazing pressure (0 = ungrazed on Konza Prairie, 1 = low grazing pressure with no sign of grazing or trampling, 2 = medium grazing pressure with chewed ends of leaves but grasses greater than 20 cm tall, and 3 = high grazing pressure with chewed leaves and grasses less than 20 cm tall) of each site in northeast Kansas.

Treatment	Slope (°)	Aspect	Elevation (m)	Grazing
Undisturbed	2	N	415	0
	1	TOP	405	0
	18	N	415	0
	11	NW	410	0
	5	E	405	0
Burned	1	TOP	445	0
	5	NE	430	0
	1	BOTTOM	410	0
	3	SW	385	0
Grazed	1	BOTTOM	385	1
	3	NE	390	2
	1	TOP	440	3
	2	N	350	3
Burned + grazed	4	E	415	1
	2	N	445	1
	2	N	385	1
	4	SW	410	1
	3	NE	440	3
	1	TOP	420	1
	18	W	350	3
	6	NE	415	3
	1	TOP	415	3
	1	TOP	420	1
	13	SE	420	2
	4	NE	365	3
	1	TOP	415	3
9	N	400	2	
10	S	405	3	

cattle, 4 burned sites, 15 sites both grazed and burned, and 5 undisturbed (not grazed and burned) sites. All burned sites had been burned in late March or early April 1987. Sites were placed on a variety of slopes (1–18°) and aspects in each grazing and burning treatment (Table 1, Sellers *et al.* 1988) in order to incorporate the variability of abiotic factors in each treatment. Ungrazed sites were confined to Konza Prairie because this was the only area released from cattle grazing in the region. The logistic constraint of accessibility was also a factor in site location.

Each site was sampled using 10 permanently located 2 m<sup>2</sup> circular plots arranged in a circle in a 0.1 ha area. Canopy cover of species was visually estimated in each plot using the Daubenmire (1959)

scale in May, June, August, and November, 1987. Only species responsible for greater than 5% live cover in a quadrat were sampled. Cover class values were converted to percent cover using class mid-points for analysis (Abrams and Hulbert 1987). One site was moved from a shrub dominated slope in May to a grass dominated upland in June, therefore, the May sample from this site was not used in this study. Therefore, 27 sites were sampled in May and 28 sites were sampled in June, August, and November. Tallgrass prairie is a variable community but all sites had at least 20% cover of *Andropogon gerardii*, a common tallgrass species. Over 100 additional species were sampled.

At each site, the grazing pressure in 1987 was estimated qualitatively and independent of composi-

tion (Table 1). Fire intensity was not measured but may be negatively correlated with grazing pressure because grazing reduces available fuel. Unfortunately, grazing and burning histories are not available for all sites, but it is likely that historically, all sites have experienced different management practices which include both periodic fire and grazing by cattle. Lack of similar historical landuse is a problem commonly encountered in field experiments at this spatial scale, and the between site variability is a real phenomenon in these communities. Therefore, there may be no true replicates in broad-scale ecological studies: a situation that would be consistent with middle number systems as opposed to statistical systems (Allen and Starr 1982).

## 2.2. Numerical analyses

### 2.2.1. Regional heterogeneity

Average cover of each species was determined for each site at each sampling time. Percent dissimilarity between pairs of sites was used as a measure of regional heterogeneity (McNaughton 1983; Belsky 1988) and was calculated based on average cover of all species at each site (Poole 1974). Average percent dissimilarity was calculated for each disturbance treatment, and pairwise t-tests were used to determine if there were significant differences in regional heterogeneity between treatments.

Regional spatial autocorrelation was assessed using the Mantel test (Mantel 1967; Sokal 1979; Schnell *et al.* 1985). For this test, regional heterogeneity was compared to the physical spatial distances between sites measured on 7.5' topographic maps. This test was used to determine if sites that were physically close to each other had more similar composition than sites that were further apart. The Mantel test is a non-parametric comparison of distance or dissimilarity matrices to determine if there is a statistical association between corresponding elements (Schnell *et al.* 1985). If a positive association occurs between 2 variables ( $p < 0.05$ ), such as between heterogeneity and distance, then between-site heterogeneity is a function of distance. Mantel tests were done at each sample time in each treatment.

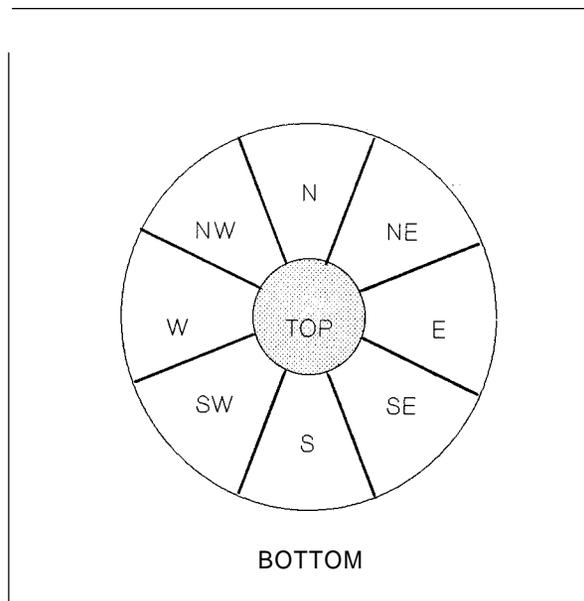


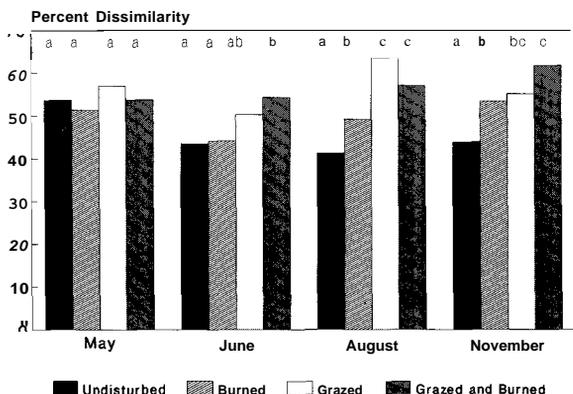
Fig. 2. Aspect categories used to determine differences in aspects of two sites. Eight possible directional slope aspects (N, NE, E, SE, S, SW, W, NW) were coded with one unit difference between adjacent aspects and one unit between a slope aspect and a top or bottom aspect. For example, N and SW were three units apart, and N and top had a one unit difference. The top and bottom aspects were coded as being two units apart.

Mantel's tests were also used to determine if differences in slope, aspect (Fig. 2), elevation, or grazing intensity were consistent with regional heterogeneity within a treatment.

### 2.2.2. Local heterogeneity

Local heterogeneity of plots within a site at each time was also calculated using percent dissimilarity. Percent cover of all species was used to calculate percent dissimilarity between each pair of plots at a site. These percent dissimilarity values were averaged over all pairs of plots at a site as a measure of local heterogeneity (Collins 1989). Average local dissimilarity was averaged over each disturbance treatment and between treatment comparisons were made using pair-wise t-tests.

## Between Sites



**Fig. 3.** Regional percent dissimilarity between tallgrass prairie sites with different burning and grazing treatments in northeastern Kansas. Different letters at the top of bars within a sample time indicate treatments that were significantly different using t-tests @  $p > 0.05$ .

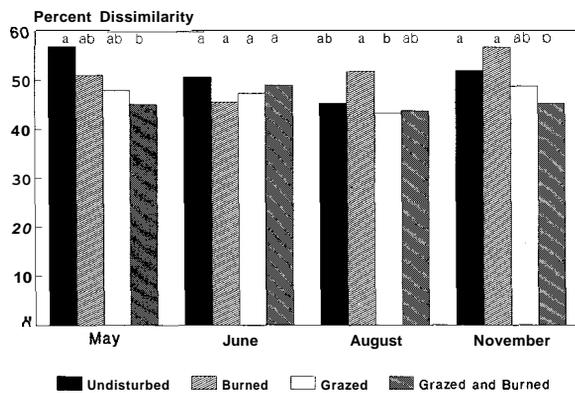
## 3. Results

### 3.1. Regional heterogeneity

Percent dissimilarity between sites was not significantly different between treatments in May (Fig. 3). In June, grazed-only treatments and grazed + burned treatments were more heterogeneous than other treatments. By August, heterogeneity was significantly greater between sites with grazing compared to sites that were ungrazed, regardless of burning treatment. In August and November, heterogeneity was significantly lower between undisturbed sites than between sites with other treatments. Therefore, throughout the year, sites that were undisturbed were regionally more similar to each other than sites that were disturbed, especially by grazing (Fig. 3).

Sites in undisturbed treatments and burned-only treatments were all found on Konza Prairie, with average distances between sites of 1.8 and 3.0 km, respectively. Grazed-only sites and grazed + burned sites were spread across the study area with average distances between sites of 10.8 and 7.3 km, respectively. However, spatial distances between sites and percent dissimilarity were not significantly associated using the Mantel test ( $p > 0.05$ ) at any sampling

## Within Sites



**Fig. 4.** Local percent dissimilarity between plots within sites in tallgrass prairie sites with different burning and grazing treatments in northeastern Kansas. Different letters at the top of bars within a sample time indicate treatments that were significantly different using t-tests ( $p > 0.05$ ).

time within any grazing/burning treatment. Therefore, sites that were close together did not consistently have similar species compositions.

Differences in slope, aspect, elevation, or grazing pressure were not significantly associated with percent dissimilarity in any treatment at any sample time when tested using the Mantel statistic ( $p > 0.05$ ). Therefore, greater variation in these factors in some treatments could not account for high percent dissimilarity between sites.

### 3.2. Local heterogeneity

We analyzed local heterogeneity within sites with different burning and grazing treatments. Undisturbed sites and burned-only sites were often the most heterogeneous, and grazed-only sites and grazed + burned sites were often the least heterogeneous (Fig. 4). Only in June were there no significant differences between treatments (Fig. 4). In general, patterns of local heterogeneity were opposite to patterns of regional heterogeneity.

#### 4. Discussion

Regional responses to disturbance in tallgrass prairie communities varied with type of disturbance. Species composition was more variable between sites with cattle grazing treatments than between sites that were undisturbed or sites with burned-only treatments. The variability imposed by grazing masked the effects of fire, because sites that were both grazed and burned were very different in composition while burned-only sites were relatively homogeneous. Even though grazed-only sites and grazed + burned sites were spread across a larger area and a greater variety of topographic positions than burned-only and undisturbed sites, these factors did not explain the increased variability of grazed-only treatments or grazed + burned treatments. Distance between sites and differences in composition were not closely related; sites that were very close together with similar slopes and aspects often had different species composition.

The observed patterns in regional heterogeneity may result from community response to disturbance. Community response following a disturbance depends on both initial conditions (Glenn-Lewin 1980; Armesto and Pickett 1985) and individualistic responses of the species (Gibson and Hulbert 1987). Spatial and temporal factors interacting with successional processes may lead to communities with different species composition. Grazing is a relatively heterogeneous process at regional scales (Bakker *et al.* 1984; Senft *et al.* 1987), and often results in increased diversity (Peet *et al.* 1983; Collins 1987) in tallgrass prairie. Diversity also increased with clipping in a variety of grassland systems (Bobbink *et al.* 1987), even though clipping may not accurately represent grazing (Facelli *et al.* 1988). Grazing reduces dominance of tall prairie grasses and releases space for colonization by other species (Collins 1987). Therefore, species that colonize a grazed site will vary, depending on the composition of the surrounding communities that are the source of immigrants.

Local diversity is a direct function of regional diversity (Ricklefs 1987). Variability in successful immigrants from the surrounding region affects community heterogeneity. At Konza Prairie, im-

migration was highly variable at scales ranging from 50 m<sup>2</sup> to all of Konza Prairie (Glenn and Collins 1992). As noted by Hengeveld (1988), regional immigration processes are often consistent with predictions from stochastic models as opposed to predictions from deterministic models. Thus, the interaction between grazing and stochastic patterns of immigration leads to high heterogeneity at a regional scale. Therefore, immigration may account for high regional heterogeneity between sites that were grazed + burned. Grazing of burned tallgrass prairie increased species richness compared to burning alone (Collins and Barber 1985; Collins 1987). Spring burning opens the canopy of dominant grasses early in the growing season and may enhance germination of the seed bank (Collins 1987). Grazing following burning then maintains an open canopy which allows establishment of rarer species, that would otherwise be competitively excluded in ungrazed prairies (Collins 1987). High regional heterogeneity between sites that were grazed, or grazed + burned, was consistent with non-equilibrium concepts of disturbance, where diversity is enhanced by disturbance if species are spatially and temporally dynamic (DeAngelis *et al.* 1985). On Konza Prairie, these dynamics of species abundance and distribution are rapid (Collins and Glenn 1990; Glenn and Collins 1990, 1992), with approximately nine immigrations and nine extinctions of species on each watershed per year (Collins and Glenn 1991).

Burning alone enhanced the growth of dominant grasses, such as *Andropogon gerardii*, and resulted in similar community composition and reduced heterogeneity because of deterministic competitive interactions (Collins 1987, 1992). In tallgrass prairie, species richness initially increased in the year following a spring fire; however, annual burning decreased species richness (Collins 1987; Collins and Gibson 1990) probably as a function of a smaller seed bank (Abrams 1988) and decreased soil nutrient availability (Seastedt and Ramundo 1990). The regional analyses reported here indicated that burned-only treatments were not significantly more homogeneous than undisturbed treatments (Fig. 3).

It is interesting to note that the effects of disturbance treatments at the local scale were opposite

those found at the regional scale. Plots within grazed-only sites and grazed +burned sites tended to be more homogeneous than those within burned-only sites or undisturbed sites (Fig. 4). Variation in fire temperatures may account for within-site heterogeneity in burned grasslands (Gibson *et al.* 1990). Interactions between fine-scale disturbances, such as gopher mounds, and the time of year of burning may also contribute to increases in heterogeneity with burning (Collins and Barber 1985, Biondini *et al.* 1989). Grazing is considered a patchy phenomenon (Bakker *et al.* 1984), that tends to increase community diversity (Collins and Barber 1985; Collins 1987). However, sites with high grazing pressure are thoroughly and consistently grazed, which may mask environmental heterogeneity and produces grazing lawns that reduce within-site heterogeneity (McNaughton 1984; Facelli *et al.* 1989). Therefore, the entire sample area could fall in one grazing patch, and local extinction of palatable grasses would occur over the entire site. Similar mechanisms have been shown to account for decreased diversity at high predation levels in a rocky intertidal community (Menge *et al.* 1985) and are incorporated in the intermediate disturbance hypothesis (Connell 1978). These results are also consistent with disturbance models in which large disturbances result in low probabilities of coexistence among species with dispersal distances that are smaller than the disturbance size (Armstrong 1988).

In summary, disturbances in tallgrass prairies effect community heterogeneity differently at different spatial scales. The local and regional scales of this study reflect patterns seen at the 'local' and 'community' scales of Collins and Glenn (1990). Few species were found at all sites at the regional scale, but many species were found in all plots at a local scale (Collins and Glenn 1990). Scale-dependent effects found in this study may have resulted from interactions between scale-dependent patterns in both species dispersal and disturbances. Establishment of immigrants in space made available by disturbances is more variable at a regional scale than at a local scale. Locally, dispersal is considered to be a function of distance from the parent plant, but regionally, dispersal is more variable because the scale is beyond the influence of the in-

dividual plant. Burning appears more heterogeneous at a local scale and grazing appears more heterogeneous at a regional scale. The regional effects observed were not predictable from within-site analyses and vice versa. Perhaps the diverse scale-variant interactions of disturbance, immigration, competition and extinction resulted in interference patterns which enhance the unpredictable nature of grassland community structure (Hoekstra *et al.* 1991). This understanding of community structure will be facilitated by analysis of patterns at a series of scales of resolution.

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## References

- Abrams, M.D. 1988. Effects of burning regime on viable buried seed pools and canopy coverage in a northeast Kansas tallgrass prairie. *Southwestern Naturalist*, 33: 65–70.
- Abrams, M.D. and Hulbert, L.C. 1987. Effect of topographic position and fire on species in tallgrass prairie in northeast

- Kansas. *American Midland Naturalist*, **117**: 442–445.
- Allen, T.F.H. and Starr, T.B. **1982**. *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago.
- ARMesto, J.J. and Pickett, S.T.A. **1985**. Experiments on disturbance in old-field plant communities: Impact on species richness and abundance. *Ecology*, **66**: 230–240.
- Armstrong, R.A. **1988**. The effects of disturbance patch size on species coexistence. *Journal of Theoretical Biology*, **133**: 169–184.
- Axelrod, D.I. **1985**. Rise of the grassland bioma, central North America. *Botanical Review*, **51**: 163–202.
- Bakker, J.P., Leeuw, J. de, and Wieren S.E. van. **1984**. Micro-patterns in grassland vegetation created and sustained by sheep grazing. *Vegetatio*, **55**: 153–161.
- Beatty, S.W. **1988**. Mass movement effects on grassland vegetation and soils on Santa Cruz Island, California. *Annals Association of American Geographers*, **78**: 491–504.
- Belsky, A.J. **1988**. Regional influences on small-scale vegetational heterogeneity within grasslands in the Serengeti National Park, Tanzania. *Vegetatio*, **74**: 3–10.
- Biondini, M.E., Steuter, A.A. and Grygiel, C.E. **1989**. Seasonal fire effects on the diversity patterns, spatial distribution and community structure of forbs in northern mixed prairie, USA. *Vegetatio*, **85**: 21–31.
- Bobbink, R., During, H.J., Schreurs, J., Willems, J. and Zielman, R. **1987**. Effects of selective clipping and mowing time on species diversity in chalk grassland. *Folia Geobotanica et Phytotaxonomica*, **22**: 363–376.
- Bock, C.E., Bock, J.H., Kenny, W.R. and Hawthorne, V.M. **1984**. Responses of birds, rodents and vegetation to livestock enclosure in a semidesert grassland site. *Journal of Range Management*, **37**: 239–242.
- Collins, S.L. **1987**. Interaction of disturbances in tallgrass prairie: A field experiment. *Ecology*, **68**: 1243–1250.
- Collins, S.L. **1989**. Experimental analysis of patch dynamics and community heterogeneity in tallgrass prairie. *Vegetatio*, **85**: 57–66.
- Collins, S.L. **1992**. Fire frequency and community heterogeneity in tallgrass prairie vegetation. *Ecology*, **73**: *in press*.
- Collins, S.L. and Barber, S.C. **1985**. Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio*, **64**: 87–94.
- Collins, S.L. and Gibson, D.J. **1990**. Effects of fire on community structure in tall and mixed-grass prairie. *In Fire in North American Tallgrass Prairies*. pp. 81–98. Edited by S.L. Collins and L.L. Wallace. University of Oklahoma Press, Norman.
- Collins, S.L. and Glenn, S.M. **1988**. Disturbance and community structure in North American prairies. *In Diversity and Pattern in Plant Communities*. pp. 131–143. Edited by H.J. During, M.J.A. Werger and J.H. Willems, SPB Academic Publishing, The Hague.
- Collins, S.L. and Glenn, S.M. **1990**. A hierarchical analysis of species abundance patterns in grassland vegetation. *American Naturalist*, **135**: 633–648.
- Collins, S.L. and Glenn, S.M. **1991**. Importance of spatial and temporal dynamics in species regional distribution and distribution. *Ecology*, **72**: 654–664.
- Connell, J.H. **1978**. Diversity in tropical rainforests and coral reefs. *Science*, **199**: 1302–1310.
- Daubenmire, R. **1959**. A canopy-coverage method of vegetational analysis. *Northwest Science*, **33**: 43–66.
- DeAngelis, D.L., Waterhouse, J.C., Post, W.M. and O'Neill, R.V. **1985**. Ecological modelling and disturbance evaluation. *Ecological Modelling*, **29**: 399–419.
- Facelli, J.M., Leon, R.J.C. and Deregibus, V.A. **1989**. Community structure in grazed and ungrazed grassland sites in the flooding pampus, Argentina. *American Midland Naturalist*, **121**: 125–133.
- Facelli, J.M., Montero, C.M. and Leon, R.J.C. **1988**. Effect of different disturbance regimen on seminatural grasslands from the subhumid pampa. *Flora*, **180**: 241–249.
- Gibson, D.J., Hartnett, D.C. and Merrill, G.L. **1990**. Fire temperature heterogeneity in contrasting fire prone habitats: Kansas tallgrass prairies and Florida sandhill. *Bulletin of the Torrey Botanical Club*, **117**: 349–356.
- Gibson, D.J. and Hulbert, L.C. **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 Collins, S.L. **1990**. Patch structure in tallgrass prairies: dynamics of satellite species. *Oikos*, **57**: 229–236.
- Glenn, S.M. and Collins, S.L. **1992**. The effects of scale and disturbance on rates of immigration and extinction of species in prairies. *Oikos*, **62**: 273–280.
- Glenn-Lewin, D.C. **1980**. The individualistic nature of plant community development. *Vegetatio*, **43**: 141–146.
- Hengeveld, R. **1987**. Scales of variation: their distinction and ecological importance. *Annales Zoologica Fennici*, **24**: 195–202.
- Hengeveld, R. **1988**. Mechanisms of biological invasions. *Journal of Biogeography*, **15**: 819–828.
- Hoekstra, T.W., Allen, T.F.H. and Flather, C.H. **1991**. Implicit scaling in ecological research. *Bioscience* **41**: 148–154.
- Mantel, N.A. **1967**. The detection of disease clustering and a generalized regression approach. *Cancer Research* **27**: 209–220.
- McGuinness, K.A. **1987a**. Disturbance and organisms on boulders I. Patterns in the environment and the community. *Oecologia*, **71**: 409–419.
- McGuinness, K.A. **1987b**. Disturbance and organisms on boulders II. Causes of patterns in diversity and abundance. *Oecologia*, **71**: 420–430.
- McNaughton, S.J. **1983**. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs*, **53**: 291–320.
- McNaughton, S.J. **1981**. Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist*, **124**: 863–886.
- Menge, B.A., Lubchenco, J. and Ashkenas, L.R. **1985**. Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. *Oecologia*, **65**: 394–405.
- Peet, R.K., Glenn-Lewin, D.C. and Walker Wolf, J. **1983**. Prediction of man's impact on plant species diversity. *In Man's Impact on Vegetation*. pp. 41–54. Edited by W. Holzner, M.J.A. Werger and I. Ikusima. Junk, The Hague.
- Poole, R.W. **1974**. *An Introduction to Quantitative Ecology*.

- McGraw Hill, New York.
- Reichman, O.J. **1987**. Konza Prairie: A Tallgrass Prairie Natural History. University Press of Kansas, Lawrence.
- Ricklefs, R.E. **1987**. Community diversity: relative roles of local and regional processes. *Science*, **235**: 167–171.
- Seastedt, T.R. and Ramundo, R.A. **1990**. The influence of fire on belowground processes of tallgrass prairie. *In* Fire in North American Tallgrass Prairies. pp. 99–117. Edited by S.L. Collins and L.L. Wallace. University of Oklahoma Press, Norman.
- Schnell, G.D., Watt, D.J. and Douglas, M.E. **1985**. Statistical comparison of proximity matrices: applications in animal behavior. *Animal Behavior* **33**: 239–253.
- Sellers, P.J., Hall, F.G., Asrar, G., Strebel, D.E. and Murphy, R.E. **1988**. The First ISLSCP Field Experiment (FIFE). *Bulletin of the American Meteorological Society*, **69**: 22–27.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. and Swift, D.M. **1987**. Large herbivore foraging and ecological hierarchies. *BioScience*, **37**: 789–799.
- Sokal, R.R. **1979**. Testing statistical significance of geographic variation patterns. *Systematic Zoology*, **28**: 227–231.