Experimental Analysis of Patch Dynamics in Tallgrass Prairie Plant Communities

Susan M. Glenn; Scott L. Collins

Experimental analysis of patch dynamics in tallgrass prairie plant communities

Glenn, Susan M.[1]* & Collins, Scott L.[2]

[1]*Oklahoma Biological Survey and* [2]*Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA; *Tel. +1 405 3255374; Fax +1 405 3257702; E-mail AC2020@UOKMVSA*

Abstract. Previous research has indicated that patch structure at small spatial scales ($< 100 \, m^2$) in tallgrass prairies was defined by a diverse array of infrequent species because dominant species occurred in all samples at this scale. Also, patch structure was not significantly different from that derived from random species associations. Based on these results, we hypothesized that removal of a dominant species would have no effect on patch structure in these prairies. We tested this hypothesis by removing a dominant grass, *Schizachyrium scoparium* (*Poaceae*), from half of each of four $10 \, m \times 10 \, m$ study blocks, and comparing differences in patch structure between control and removal halves before and after removal. The minimum resolution in our study was $1 \, m^2$. Patches of similar species composition were defined by cluster analysis of presence/absence data and cover data. Patch sizes ranged from 1 to $34 \, m^2$.

Following the removal of *S. scoparium* there was an overall increase in the number of species in the removal half of each block compared to pre-treatment levels. However, the number of patch types and number of spatially mapped groups, based on presence/absence or cover data, did not change between control and removal plots after the removal of *S. scoparium*. This supports the hypothesis that removal of a large, dominant species would have no effect on patch structure at this scale of resolution in these prairies. Thus, patch structure, as defined here, is an emergent property in these grasslands that is not predictable from changes in species composition. This property of stochastic patch structure results from interactions of processes operating at scales both larger and smaller than our scale of resolution. Stochastic models may provide a reasonable approach to modelling small-scale patch dynamics in tallgrass prairie communities.

Keywords: Grassland community; Patch structure; Removal experiment; *Schizachyrium scoparium*.

Nomenclature: Barkley (1986).

Introduction

Within any community, a patch can be defined as a locally distinct assemblage of species, potentially repeatable over space and time (Forman & Godron 1986).

Patch structure can be described as the number, size and distribution of patches in an area. Most studies of patch dynamics have focused on the relationship between disturbance regime and patch dynamics (Sousa 1984; Pickett & White 1985). These studies emphasise succession following disturbances, and the collective effects of different-aged patches on community structure and dynamics (Rabinowitz & Rapp 1985; Rapp & Rabinowitz 1985; Belsky 1986). Under complex disturbance regimes, community structure may be highly variable and reflect response to the interaction of multiple disturbance events (e.g. Collins & Barber 1985; Collins 1987; Chaneton & Facelli 1991; Glenn, Collins & Gibson in press).

Recently, there has been increasing interest in the small-scale dynamics of patches in the absence of disturbance (Glenn & Collins 1990; van der Maarel & Sykes 1993; Herben et al. 1993). A dynamic mosaic of patches in the absence of disturbance may be maintained where there are many species with similar requirements (e.g. van der Maarel & Sykes 1993; Agnew, Wilson & Sykes 1993). Thus, factors such as regional dispersion of species (Whittaker & Levin 1977) and high species richness (Grubb 1986) become important constraints on patch dynamics.

Species richness in tallgrass prairies is generally a function of a large component of sparsely distributed 'satellite' species and a smaller number of dominant 'core' species that are often widely distributed spatially (Gotelli & Simberloff 1987; Collins & Glenn 1990). This type of community structure is consistent with the core-satellite model of Hanski (1982, 1991). Hanski's model also predicts that the occurrence of many species is highly dynamic over space and time. Rapid dynamics in species occurrences at large spatial scales (km^2) have been reported for tallgrass prairie communities (Collins & Glenn 1991). Dynamics at this scale are driven by interactions among several processes including annual variations in climate, and differences in fire frequency among sites in a region. At local spatial scales ($100 \, m^2$) patch structure varied within and between growing seasons in tallgrass prairies *independent* of disturbance

(Glenn & Collins 1990). In this case, patches were defined as areas with similar species composition based on presence/absence data. Differences among patches at this local scale resulted from differences in the presence and absence of sparsely distributed satellite species.

In addition to changes in patch composition, patch structure (e.g. number of patch types, average patch size) in tallgrass prairies in Kansas and Oklahoma, USA, was not significantly different from patch structure generated by data with random species associations (Glenn & Collins 1990). This was found for both compositional and spatial structure indices based on presence/absence data. Such a result implies that factors controlling species association were not important controls of patch structure. This is surprising because previous studies have shown that species dominance is correlated with frequency in this system (Gotelli & Simberloff 1987; Collins & Glenn 1990). Thus, it seems logical to assume that dominant species would impose considerable influence on patch composition and structure.

The purpose of this study is to determinate the importance of core species in controlling local patch structure and dynamics in tallgrass prairies. This would reflect the importance of competition as a deterministic constraint on patch structure. To do this, we experimentally removed the core species *Schizachyrium scoparium* (*Poaceae*) from half of each of four permanent study blocks and compared differences in patch structure between control and removal halves to determine if these differences were affected by removal of a locally dominant species.

Methods

Field methods

Local patch structure was measured in 10 m × 10 m permanent blocks in tallgrass prairies in Kansas and Oklahoma. Two blocks were established at the USDA Livestock and Forage Research Station at El Reno, Oklahoma, in May, 1986. A large fenced enclosure was constructed in 1986 prior to the beginning of the experiment to prevent grazing by cattle. The site was last burned in April 1984. Two permanent blocks were established in June 1987 in tallgrass prairie at Konza Prairie Research Natural Area, near Manhattan, Kansas. Cattle were excluded from this site in 1971 and the site was burned in 1981 and 1991. Percent cover of living above-ground parts of each species in 100 contiguous quadrats (1 m²) in each block was visually estimated one to three times each year after the plots were established (1986-1991).

Individual clones of *Schizachyrium scoparium* were removed from one-half of each block in February 1989.

A shovel was used to cut across the base of the meristems of this bunchgrass. At the time of removals, the ground was frozen; therefore, soil disturbance was minimal. Large, conspicuous clumps were removed, but small clumps were left because removing them would potentially disrupt too many neighbouring plants. The sites were visited in May 1989 and very little *S. scoparium* was growing from the remaining meristems in the removal sites. Because regrowth was minimal and winds were typically high, chemical herbicides were not used to kill the few remaining tillers.

Numerical methods

To document the efficacy of removal of *S. scoparium,* average cover of this species was calculated for each half-block at each sample time in 1987, 1988 and 1989. The differences in cover of *S. scoparium* in the 1987 and 1988 samples were used to determine the initial differences in cover between the control and removal halves of each block. The same was done for the post-removal 1989 samples. Two sample *t*-tests were used to determine if the average differences in *S. scoparium* cover between control and removal halves was significantly reduced by the removal (Taylor 1977).

Patch types were determined using both quantitative (cover) and qualitative (presence/absence) measures of species occurrence. Patch types were calculated for the removal and control halves separately. Euclidean distance was used to determine the similarity among 1-m² quadrat samples within each half block based on species cover data. Jaccard's coefficient was used to calculate similarity among 1-m² quadrat samples within each half block based on species presence data (Romesburg & Marshall 1984). Patch types were defined by unweighted pair group cluster analysis using SYNTAX IV (Podani 1990). For qualitative data, patch types were defined as quadrats with similarity values greater than 0.63. At this similarity level, the resulting dendrograms were divided into discrete clusters with few single quadrat groups (Glenn & Collins 1990). A distance value of 24.2 between quadrats was used as the cut-off level to define patch types because this value corresponded to 0.63 when scaled to the dendrograms based on qualitative data.

We defined patch types using both analyses because dendrograms based on qualitative data are affected by the presence of infrequent satellite species, whereas dendrograms based on quantitative data are sensitive to shifts in dominance, as well as changes in presence/absence of species (Rahal 1990).

For each half block at each sampling date, the number of patch types was determined from the dendrograms. These patches were then mapped onto a 5 × 10 template (Fig. 1). From these maps we then determined the number of spatial groups, regardless of patch type. The number
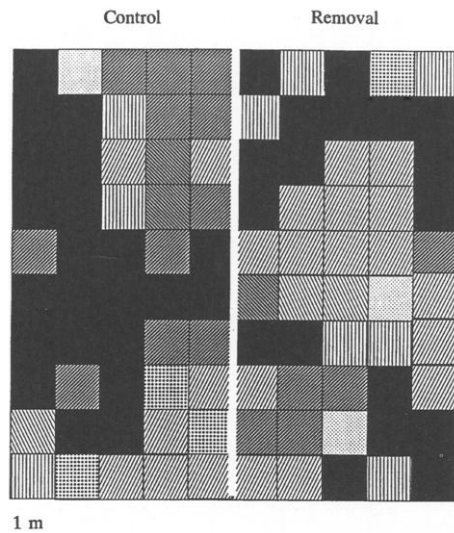
Control   Removal

1 m

Fig. 1. Example of patch structure in two 5 m × 10 m blocks of tallgrass prairie. Individuals of *Schizachyrium scoparium* have been removed from the block on the right. Each pattern represents a patch type based on cluster of cover data. The number of patch types is eight in both control and removal treatments. The number of spatial groups regardless of patch type is 21 on the removal half and 20 on the control half.

Table 1. Mean differences (c – r) and mean percent differences $[100 \; (c - r)/c]$ in cover of *Schizachyrium scoparium* between control (c) and removal (r) halves of each block in 1987/1988 versus 1989. Standard deviations (s.d.) and number of samples (n) for each block are shown and two-sample t-test values (t) comparing 1987/1988 and 1989 values. All t-tests indicated that significantly more *S. scoparium* was found in the removal halves in 1987/1988 than in 1989 $(p < 0.05)$.

	1987/88			1989			t
	mean	s.d.	n	mean	s.d.	n	
Oklahoma							
Block 1							
$c - r$	– 3.8	4.7	4	+20.5	3.3	3	8.02
$100 \; (c - r)/c$	– 18.6	22.9	4	+57.8	7.1	3	6.29
Block 2							
$c - r$	+ 2.3	4.0	3	+35.9	4.0	3	11.7
$100(c - r)/c$	– 4.7	29.5	3	+81.0	3.0	3	5.00
Kansas							
Block 1							
$c - r$	– 2.0	1.4	5	+ 5.5	1.5	3	7.02
$100(c - r)/c$	– 14.9	11.1	5	+55.3	10.5	3	8.96
Block 2							
$c - r$	– 6.9	3.2	4	+ 3.0	0.9	3	5.88
$100(c - r)/c$	– 28.3	8.0	4	+13.8	3.1	3	9.61

of patch types and spatial groups was calculated for both qualitative and quantitative data for each half block. The differences in these indices between control and removal halves of the blocks were calculated for each sample. A t-test was used to determine if initial differences between control halves and removal halves were significantly altered by removing *S. scoparium*. These t-tests were calculated for each block, site, and all blocks combined.

To determine if there were any treatment effects on community structure, we calculated species richness for each half-block. A t-test was used, for each block and for all blocks combined, to determine if the average difference in species richness between the control and removal halves in pre-removal samples was significantly different from post removal samples.

Results

During the growing season following removal, cover of *Schizachyrium scoparium* was significantly reduced in the removal halves of each block compared to the controls. Cover of *S. scoparium* increased slightly over time on the removal treatments, but remained below pretreatment levels. The actual difference in cover and percent difference between the control and removal halves was significantly different in 1989 from samples from the previous two years (Table 1). For example, in

Oklahoma block 1, total cover of *S. scoparium* on the control half was 18.6 % less than on the removal half, whereas following the removal, cover of *S. scoparium* was 57.8 % higher on the control versus removal half.

The difference between the control and removal halves of the blocks in the number of patch types (either qualitative or quantitative data) did not change significantly after removing *S. scoparium*. There were no significant differences in patch structure between control and removal halves within a site or a block.

There was a significant difference in species richness between the control and removal halves of the block after the removal experiment (Fig. 4). On average, there were 3.5 × more species on the removal halves of the blocks after the removal occurred as opposed to a pre-removal difference of 0.04 species $(t = 3.498, P = 0.001)$. The removal halves of the blocks tended to have more species than the control halves. This implies that although patch structure was not significantly different between the control and removal halves, patch composition was different. There were no significant changes in differences between the number of species between control and removal halves within a site or block.

Discussion

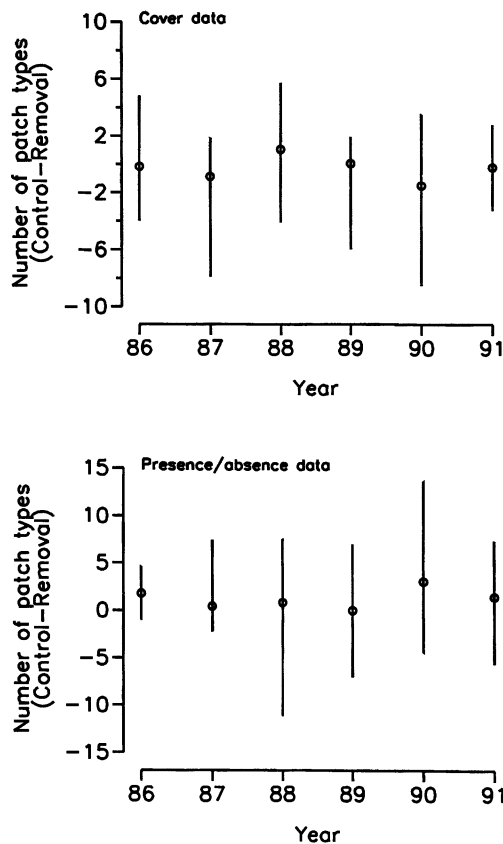The experimental treatment was effective in reducing

Fig. 2. Differences in number of patch types in control and removal halves of four 100-m² tallgrass prairie study blocks over six growing seasons. Values are means (±s.e.) of similar treatments over time and site within a year. Individuals of *Schizachyrium scoparium* were removed from half of each block prior to the 1989 growing season. Patch types were based on either quantitative cover data (A), or presence/absence data (B). Patches were defined by cluster analysis. There were no significant changes in the difference between control and removal halves of each block when the pre-removal data were compared to the post-removal data.

Fig. 3. Differences in number of spatial groups between control and removal halves of tallgrass prairie study blocks over six growing seasons. Spatial groups were counted from maps as in Fig. 1. Spatial groups were based on either quantitative cover data or qualitative presence/absence data. There were no significant changes in the difference between control and removal halves when pre-removal data were compared to post-removal data.

cover of *Schizachyrium scoparium* and opening space for colonization by additional species. More species were found, on average, on the removal halves compared to the control halves. However, differences in patch structure between the removal and control halves of blocks as a result of the removal of *S. scoparium* were not detectable. Patch structure on these blocks prior to removal of *S. scoparium* was not different from that produced by simulated data with random species associations. Fractal dimensions of patches were slightly lower in maps with random species associations suggesting that patch complexity may be more a function of species associations and perhaps competition (Glenn & Collins 1990). However, removal of a dominant core species did not alter any
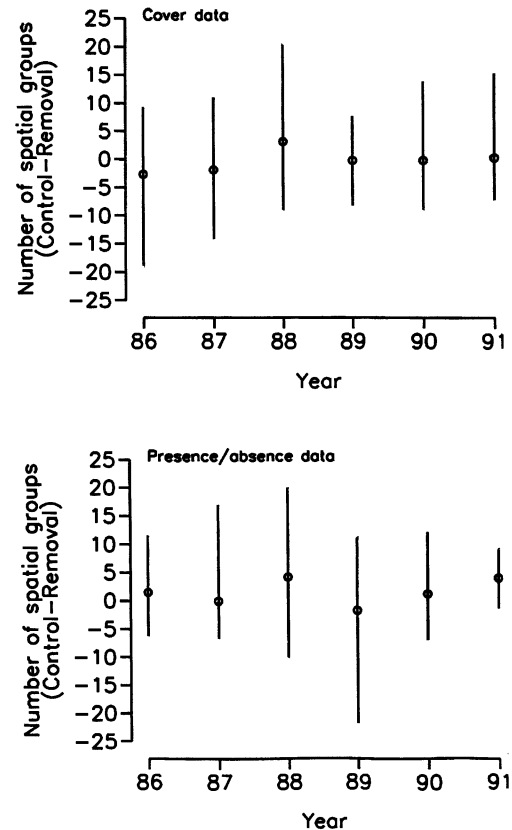
index of patch structure. The original simulation model was based on presence/absence data, but in this study neither qualitative nor quantitative data indicated any effect of removal on measures of patch structure. Therefore, *at this spatial scale of analysis*, the presence of a core species, presumably able to compete for and maintain a large proportion of space in the community, had little effect on patch structure in these prairies.

The apparent lack of control by the core component in tallgrass prairie plant communities on patch structure at this scale implies that stochastic models may apply to these communities. Structure at this scale may conform to 'middle number systems' that cannot be modelled using statistical or deterministic equations (Allen & Starr 1982). In addition, our results are similar to those of van der Maarel & Sykes (1993) and Herben et al. (1993) showing that grasslands are highly dynamic and unpre-
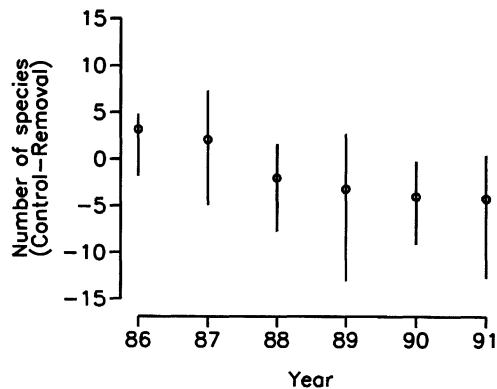
Fig. 4. Differences in number of species between control and removal halves in tallgrass prairie study blocks over six growing seasons. Prior to removal of *Schizachyrium scoparium* in 1989, the number of species was, on average, equal on both halves of each block (control side richness - removal side richness $X = 0.04$). After removal, there were more species on average on the removal side compared to the control (control side richness – removal side richness $X = 3.5$). Therefore, there was a significant increase in the number of species on the removal halves when prior differences between control and removal halves were taken into account ($t = 3.5$, $P = 0.001$).

dictable at small spatial scales. These studies showed that in very small samples (ca. 25 cm²), species moved rapidly into and out of sample units. However, the overall composition of study plots remained the same despite the small scale changes in vegetation. Our plot size of 1 m² was much larger than in these studies, to accommodate the very large individuals of the dominant C₄ grasses, *Schizachyrium scoparium* and *Andropogon gerardii* along with other satellite species. Nevertheless, even at this scale of resolution, patch composition and structure were found to be highly dynamic in these prairies.

In our case, the core C₄ grasses were spatially stable. It has been assumed that two-tiered competitive hierarchy exists in this system, and experiments have suggested that several of the dominant species have similar competitive abilities (Rabinowitz, Rapp & Dixon 1981; Tilman & Wedin 1991). The satellite species, on the other hand, are spatially dynamic within the stable matrix of core species (Collins & Glenn 1991). The unpredictable dispersion of subdominants within a framework of dominant species has been found in other systems (Grubb 1986; Halpern 1988; Houle & Philips 1989).

There are constraints on the degree of temporal heterogeneity in a community. One probable constraint involves rates of local extinction and immigration. Extinction, in particular, is often positively correlated with the total number of species. That is, patches with high species richness may suffer high rates of local extinction

because a larger number of these species are likely to be rare. This type of constraint is common in models of non-equilibrium coexistence involving either intrinsic dynamics of populations or extrinsic temporal variation caused, for example, by disturbance (Briand 1983; Chesson 1986; Yodzis 1989). Thus, average rates of immigration to patches and extinction from patches can be calculated, but these averages have high variances. Within these confidence limits, species richness may fluctuate stochastically (Glenn & Collins 1992). The ultimate result is an interference pattern (Hoekstra, Allen & Flather 1991) as rates of different processes operating at a variety of spatial and temporal scales interact at our pre-defined scale of analysis.

Given that patch structure at this spatial scale is unpredictable in these grasslands, other commonly accepted notions regarding tallgrass prairie community structure need to be reconsidered. The scale of this analysis used a 1-m² quadrat that is commonly prescribed in studies of herbaceous communities. Sampling at larger or smaller scales may yield more predictable patterns of patch dynamics in this system, although evidence from van der Maarel & Sykes (1993) and Herben et al. (1993) would suggest otherwise for smaller scales. A general assumption in the analysis of most spatial information is that spatial auto-correlation is a significant factor (Legendre & Fortin 1989). However, this analysis seems to indicate that spatial autocorrelation may be low at this scale, or at least the degree of spatial auto-correlation changes over relatively short time spans. This could explain the lack of spatial pattern in species composition found in some previous studies in tallgrass prairies (Collins & Gibson 1990).

The apparent phenomenon of variable patch structure which is not correlated with species composition may be found at other spatial scales in other communities. To determine the extent of this phenomenon, it will be necessary to investigate patch structure and dynamics in our grasslands at different spatial scales, and in other systems at a range of scales. Nevertheless, the results from this study conform to an emerging consensus that grasslands are highly dynamic and unpredictable at relatively small spatial scales.

References

Agnew, A. D. Q., Wilson, J. B. & Sykes, M. T. 1993. A vegetation switch as the cause of a forest/mire ecotone in New Zealand. *J. Veg. Sci.* 4: 273-278.

Allen, T. F. H. & Starr, T. B. 1982. *Hierarchy: perspectives for ecological complexity.* University of Chicago Press, Chicago, IL.

Barkley, T. M. (ed.) 1986. *Flora of the great plains.* Univ. Press Kansas, Lawrence, KS.

Belsky, A. J. 1986. Population and community processess in a mosaic grassland in the Serengeti, Tanzania. *J. Ecol.* 74: 841-856.

Briand, J. 1983. Environmental control of food web structure. *Ecology* 64: 253-263.

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

Chesson, P. L. 1986. Environmental variation and the coexistence of species. In Diamond, J. & Case, T. J. (eds.) *Community Ecology*, pp. 240-256. Harper & Row, New York, NY.

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

Collins, S. L. & Barber, S. C. 1985. Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* 64: 87-94.

Collins, S. L. & Gibson, D. J. 1990. Effects of fire structure in mixed- and tallgrass prairies. In: Collins, S. L. & Wallace, L. L. (eds.) *Fire in North American tallgrass prairies*, pp. 81-98. University of Oklahoma Press, Norman, OK.

Collins, S. L. & Glenn, S. M. 1988. Disturbance and community structure in North American prairies. In: During, H. J., Werger, M. J. A. & Willems, J. H. (eds.) *Diversity and pattern in plant communities*, pp. 131-143. SPB Academic Publishers, The Hague.

Collins, S. L. & Glenn, S. M. 1990. A hierarchical analysis of species abundance patterns in grassland vegetation. *Am. Nat.* 135: 633-648.

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

Forman, R. T. T. & Godron, M. 1986. *Landscape ecology.* John Wiley & Sons, New York.

Glenn, S. M. & Collins, S. L. 1990. Patch structure in tallgrass prairies: dynamics of satellite species. *Oikos* 57: 229-236.

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

Glenn, S. M., Collins, S. L. & Gibson, D. J. In press. Disturbances in tallgrass prairie: local versus regional effects on heterogeneity. *Landscape Ecol.*

Gotelli, N. J. & Simberloff, D. 1987. The distribution and abundance of tallgrass prairie plants: a test of the core-satellite hypothesis. *Am. Nat.* 130: 18-35.

Grubb, P. J. 1986. Problems posed by sparse and patchily distributed species-rich plant communities. In: Diamond, J. & Case, T. J. (eds.) *Community ecology*, pp. 207-225. Harper & Row, New York.

Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69: 1703-1715.

Hanski, I. 1982. Dynamics of regional distribution: the core

and satellite species hypothesis. *Oikos* 38: 210-221.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biol. J. Linn. Soc.* 42 17-38.

Herben, T., Krahulec, F., Hadincová, V. & Skálová, H. 1993. Small-scale variability as a mechanism for large-scale stability in mountain grasslands. *J. Veg. Sci.* 4: 163-170.

Hoekstra, T. W., Allen, T. F. H. & Flather, C. H. 1991. Implicit scaling in ecological research. *BioScience* 41: 148-154.

Houle, G. & Philips, D. L. 1989. Seasonal variation and annual fluctuation in granite outcrop plant communities. *Vegetatio* 80: 25-35.

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

Pickett, S. T. A. & White, P. S. (eds.) 1985. *The ecology of natural disturbance and patch dynamics.* Academic Press, New York.

Podani, J. 1990. *SYN-TAX IV. Computer programs for data analysis in ecology and systematics on IBM-PC and Macintosh computers.* International Centre for Science and Technology, Trieste.

Rabinowitz, D. & Rapp, J. K. 1985. Colonization and establishment of Missouri prairie plants on artificial soil disturbances. III. species abundance distributions, survivorship and rarity. *Am. J. Bot.* 72: 1635-1640.

Rabinowitz, D., Rapp, J. K. & Dixon, P. M. 1984. Competitive abilities of sparse grass species: means of persistence or cause of abundance. *Ecology* 65: 1144-1154.

Rahal, F. J. 1990. The hierarchical nature of community persistence: a problem on scale: *Am. Nat.* 136: 328-344.

Rapp, J. K. & Rabinowitz, D. 1985. Colonization and establishment of Missouri prairie plants on artificial soil disturbances.I. Dynamics of forb and graminoid seedlings and shoots. *Am. J. Bot.* 72: 1618-1628.

Romesburg, H. C. & Marshall, K. 1984. *CLUSTAR/CLUSTID computer programs for hierarchical cluster analysis.* Lifetime learning Publications, Belmont, CA.

Sousa, W. P. 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15: 353-391.

Taylor, P. J. 1977. *Quantitative methods in geography: an introduction to spatial analysis.* Houghton Mifflin Co., Boston, MA.

Tilman, D. & Wedin, D. A. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* 72: 685-700.

van der Maarel, E. & Sykes, M. 1993. Small-scale plant species turnover in a limestone grassland: the caroussel model and some comments on the niche concept. *J. Veg. Sci.* 4: 179-188.

Whittaker, R. H. & Levin, S. A. 1977. The role of mosaic phenomena in natural communities. *Theor. Pop. Biol.* 12: 117-139.

Yodzis, P. 1989. *Introduction to theoretical ecology.* Harper & Row, New York.