

The tempo and mode of gopher mound production in a tallgrass prairie remnant

Benjamin A. Klaas, Kirk A. Moloney and Brent J. Danielson

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To gain better insight into how small-scale disturbances might affect ecological processes, such as the maintenance of plant species diversity, we conducted a two-year study characterizing spatio-temporal patterns of gopher mound production on a tallgrass prairie remnant located at Anderson Prairie, Iowa, USA. The locations of all newly produced gopher mounds were mapped on two 80 × 80 m permanent plots. We used these data to characterize spatio-temporal patterns of mound production across a range of scales. We found that mound production was highly clustered at scales of < 8 m over short periods of time (< 2 weeks), but shifted in location over a 3–4 weeks time period, resulting in a clustered pattern at scales of < 20 m over longer time periods (up to the 2 yr of the study). We also found that patterns of mound production at intermediate spatial scales (> 20 m) remained fairly static over time, although they differed significantly from site to site. The results of this study suggest that small-scale patterns of variability in mound production may increase habitat variability over very short spatial scales, possibly providing a mechanism that can enhance the development and maintenance of species diversity.

B. A. Klaas, and B. J. Danielson, Dept of Animal Ecology, Iowa State Univ., Ames, IA 50011, USA. – K. A. Moloney (correspondence: kmoloney@iastate.edu), Dept of Botany, Iowa State Univ., Ames, IA 50011, USA (present address of B. A. K.: 1117A East Cota, Santa Barbara, CA 93103, USA).

Theoretical and empirical studies suggest that the spatio-temporal architecture of disturbance regimes can be critical in determining the impact of disturbance on ecological processes at the landscape scale (Huston 1979, Runkle 1982, Runkle and Yetter 1987, Armstrong 1988, Foster 1988a, b, Coffin and Lauenroth 1989, Hastings and Wolin 1989, McConnaughy and Bazzaz 1990, Frelich and Lorimer 1991, Colasanti and Grime 1993, Turkington et al. 1993, Moloney and Levin 1996). Historically, most studies of disturbance ecology have focused on the non-spatial components of disturbance, such as the proportion of the landscape affected per unit time and the proximal effects of individual disturbances on local ecological processes. More recently, attention has been paid to the importance of the size and shape of individual disturbances (e.g., Runkle 1982, Runkle and Yetter 1987, Foster

1988b, Halpern 1989, Whitmore 1989, Brokaw and Scheiner 1989, Coffin and Lauenroth 1989, Spies and Franklin 1989, McConnaughy and Bazzaz 1990, Moloney and Levin 1996). However, few studies have examined the importance of spatial and temporal autocorrelation relationships among individual disturbances on ecological processes (although see Lawton and Putz 1988, Moloney 1993, Moloney and Levin 1996, Jetsch et al. 1998). This is curious since autocorrelation relationships may play a very critical role in determining the response of an ecological system to disturbance. For example, modeling studies have indicated that the degree of recurrence of disturbances within localized areas of a landscape may play an equally important (or greater) role in determining the ecological response to disturbance than does the overall landscape-scale rate of disturbance (Moloney and Levin 1996). Clearly,

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more attention needs to be paid to the spatio-temporal architecture of ecological disturbance regimes.

One reason that there have been few, if any, studies fully characterizing the spatio-temporal structure of ecological disturbances is that, until recently, adequate statistical tools have not been readily available for conducting these analyses. Fortunately, major advances in pattern analysis techniques have been introduced over the last decade or so (e.g., see Ripley 1981, Diggle 1983, Dale and MacIsaac 1989, Cressie 1991, Haase 1995) and we can now characterize the impact of disturbance on ecological systems more completely.

In this paper, we will present an analysis of spatio-temporal patterns of disturbance produced by the activity of the plains pocket gopher *Geomys bursarius* in a NW Iowa tallgrass prairie. Pocket gophers create extensive burrow systems, in which they forage for roots. Individual gophers are highly territorial, thus each burrow system is non-overlapping and unconnected with other burrow systems (Reichman et al. 1982, Nowak 1991). Soil from the maintenance and construction of burrow systems is periodically expelled to the surface, creating mounds that bury the local vegetation. These localized disturbances create microhabitats that can differ significantly in soil characteristics (Grant and McBrayer 1981, Koide et al. 1987, Zinnel and Tester 1990) and in the composition of plant species (Grant et al. 1980, Hobbs and Mooney 1985, 1995, Martinsen et al. 1990, Reichman et al. 1993). They may also have an impact on the local abundance of animal species (Huntly and Inouye 1988, Whittaker et al. 1991, Klaas 1996, Klaas et al. 1998). Once created, gopher mounds are stationary in space and their size and shape is fairly constant from mound to mound. Because of these characteristics, mounds can be modeled appropriately as points measured at their centers rather than as non-overlapping circles (see Ripley 1981), greatly simplifying the analysis of spatio-temporal patterns of mound production.

We examine two basic aspects of gopher mound production: 1) the development of pattern over varying lengths of time and 2) the spatial coherence of disturbance patterns produced over different time intervals. These analyses will eventually be used to examine a number of issues that may be important for understanding the impact of disturbance on the tallgrass prairie ecosystem.

Methods

Study system

We conducted our study at Anderson Prairie, an 81 ha state preserve in Emmet Co., Iowa, USA, ca 6 km NW of the town of Estherville. Anderson Prairie is a moderately diverse tallgrass prairie that varies greatly in to-

pography and species composition, ranging from wet prairie in low spots to xeric prairie on hilltops. The amount of gopher activity also varies greatly across the prairie, which can be attributed primarily to local habitat preferences (Thomsen et al. 1996, Benedix 1991).

We censused gopher mound production on two 80 × 80 m permanent grids established in May 1994. One of the sample grids (the N grid) was characterized by relatively flat relief on a moderate slope (Fig. 1). Total vertical displacement was ca 6 m. The eastern third of the grid was in an area of moderately wet prairie that differed from the rest of the grid, which was more mesic. The second permanent grid used in the study (the SE grid) was located ca 150 m away from the N grid on a relatively dry hillside, with a total vertical displacement of ca 12 m (Fig. 1). Because of its position, the SE grid was characterized by a great deal of variability with respect to topographic relief.

An initial census of gopher mound production for both grids was conducted on 23 May 1994. After the initial survey, we located and marked all freshly produced mounds at approximately weekly intervals during the 1994 and 1995 growing seasons (Table 1). Mounds produced during autumn and winter of 1994–1995 were censused on 26 March 1995. Using survey equipment, we mapped the locations of the centers of all mounds created on the N grid from 23 May 1994 to 5 August 1995, and all mounds created on the SE grid from 26 March 1995 to 3 August 1995. The N grid was initially chosen for the detailed survey, because of its high level of mound production and relative homogeneity compared to the SE grid (cf. Haase 1995). Mound production on the SE grid was mapped in 1995 to allow a comparison between two dissimilar sites.

Pattern analysis techniques

All pattern analyses were conducted on the more highly disturbed, western 50 × 80 m subsections of the sample grids (Klaas 1996). This was done to eliminate major discontinuities in disturbance intensity, as large-scale trends in pattern data tend to mask the structure of the data at smaller scales (Chatfield 1984, Diggle 1990). The lower rate of gopher mound production in the eastern portion of the N grid was due to moister habitat found in the lower portion of the grid (Klaas 1996). The eastern portion of the SE grid also occupied a lower position than the rest of the grid, however the ecological reasons behind the lower gopher activity there were not apparent.

We used Ripley's L-function analysis to examine pattern production of mounds across a range of scales h . All of the analyses were based on either the univariate L-function $L_{11}(h)$ or its bivariate extension $L_{12}(h)$ (see Ripley 1979, 1981, Cressie 1991, and Bailey and Gatrell 1995 for a more detailed description of the

technique). In the univariate case, $L_{11}(h)$ characterizes the degree of clustering or hyper-dispersion of a set of points (i.e., mounds) relative to a randomly distributed set of the same number of points. In the bivariate case, $L_{12}(h)$ characterizes the degree of clustering or hyper-dispersion of one set of points with respect to a second set of points (Ripley 1979, 1981, Cressie 1991, Bailey and Gatrell 1995). In both cases, the scale h corresponds to a circular area of radius h around individual points. In the present study, the univariate analyses were used to characterize spatial relationships among mounds produced during one time period and the bivariate analyses were used to characterize spatial relationships among mounds produced during two different time periods.

We used the standard formulas given in Bailey and Gatrell (1995, pp. 120–121) for the calculation of $L_{11}(h)$ and $L_{12}(h)$. In the univariate case, the expected value of $L_{11}(h)$ is 0 for a random point pattern at scale h , otherwise $L_{11}(h) < 0$ for an evenly distributed pattern and $L_{11}(h) > 0$ for a clustered pattern. The same is true for the bivariate case, i.e., $L_{12}(h) < 0$ for a set of points that is evenly distributed with respect to a second set of points, whereas $L_{12}(h) > 0$ for a clustered pattern.

Tests for significant departures from the null hypothesis of spatial randomness across a range of scales must be conducted to assess the significance of $L_{11}(h)$ and

$L_{12}(h)$. We did this using Monte Carlo techniques (Ripley 1981, Cressie 1991, Bailey and Gatrell 1995) in estimating 99% confidence intervals around the expected values of $L_{11}(h) = 0$ or $L_{12}(h) = 0$. N_1 points (univariate case) or N_1 and N_2 points (bivariate case) were randomized 99 times and values of $L_{11}(h)$ or $L_{12}(h)$ were calculated each time (Haase 1995). (N_1 and N_2 were equal to the number of mounds in the field samples being analyzed.) Values of $L_{11}(h)$ or $L_{12}(h)$ greater than the maximum $L_{11}(h)$ or $L_{12}(h)$ obtained through Monte Carlo randomization indicated significant clustering among mounds. Values less than the minimum values obtained through randomization indicated significant hyperdispersion or repulsion (cf. Haase 1995). The computer routines used in our analyses were developed through a modification of the computer code provided in Venables and Ripley (1994).

Pattern accumulation through time

Spatial patterns of mounds produced over time periods ranging from one week to two years were analyzed using univariate L-analysis. By characterizing the development of disturbance patterns in the prairie community over several different time intervals, we will be able to examine the impact of mound production on distur-

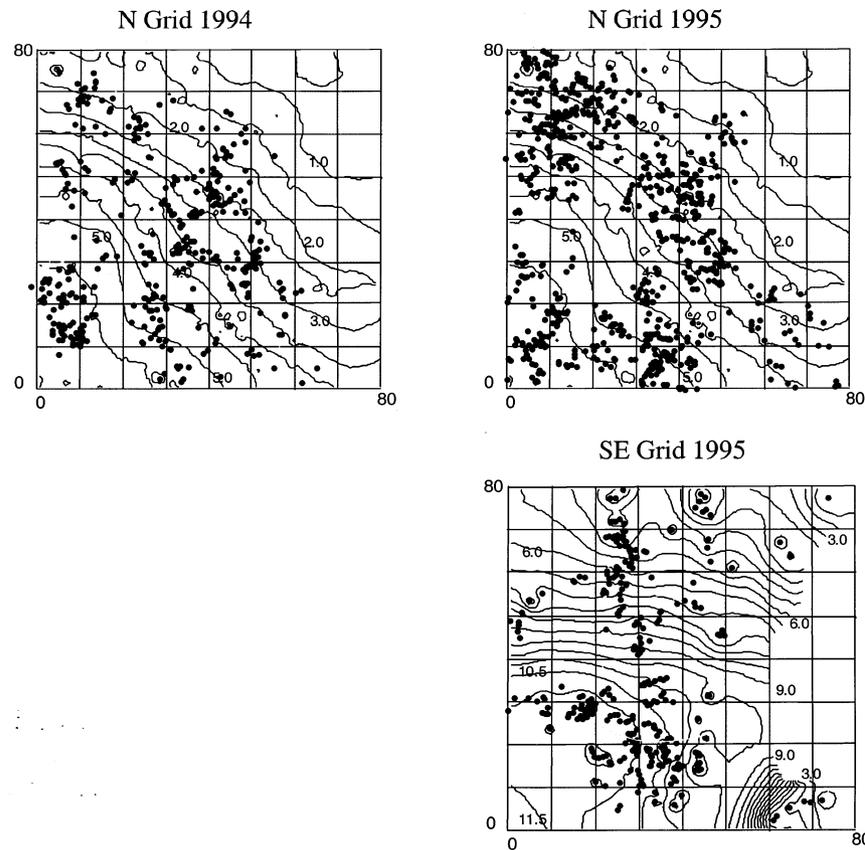


Fig. 1. Maps of gopher mound production at Anderson Prairie on the N grid between 24 May and 10 August 1994 and on the N and SE grids between 26 May and 3 August 1995. Contour intervals, using 0.5 m increments, are indicated on the maps and represent relative elevations within the grids. Contours for the SE grid are not included for the eastern most section due to a lack of survey points.

Table 1. Census dates, number of new mounds produced, and average mound production rates for 1994 and 1995 on the N and SE grids of Anderson Prairie. Rows in bold indicate censuses used in the more detailed analyses (see Methods).

Census date	Days in census		N Grid		SE Grid		
			No. of new mounds	Production rate (mounds/day)	No. of new mounds	Production rate (mounds/day)	
1994	3 Jun	12	24	2.00	15	1.25	
	10 Jun	7	30	4.29	13	1.86	
	17 Jun	7	22	3.14	NA	NA	
	21 Jun	4	35	8.75	31	2.82	
	1 Jul	10	59	5.90	23	2.30	
	8 Jul	7	25	3.57	11	1.57	
	17 Jul	9	44	4.89	12	1.33	
	21 Jul	4	24	6.00	15	3.75	
	29 Jul	8	51	6.38	12	1.50	
	5 Aug	7	17	2.43	8	1.14	
	17 Sep	43	72	1.67	42	0.98	
	1995	26 Mar	190	89	0.47	82	0.43
		19 Apr	24	23	0.96	12	0.50
		26 Apr	7	8	1.14	5	0.71
11 May		15	34	2.27	13	0.87	
18 May		7	14	2.00	8	1.14	
25 May		7	13	1.86	15	2.14	
1 Jun		7	61	8.71	19	2.71	
8 Jun		7	59	8.43	30	4.29	
15 Jun		7	72	10.29	28	4.00	
22 Jun		7	67	9.57	38	5.43	
29 Jun		7	30	4.29	12	1.71	
6 Jul		7	25	3.57	36	5.14	
13 Jul		7	43	6.14	16	2.29	
20 Jul		7	16	2.29	15	2.14	
27 Jul		7	42	6.00	39	5.57	
3 Aug		7	34	4.86	27	3.86	

bance-sensitive, tallgrass-prairie species characterized by different generation times and dispersal rates (cf. Platt and Weiss 1985). For the analysis of 1–12 weeks intervals, a 12 weeks subset of the 1995 mound data was used (see Table 1). Data were pooled for each grid in increments of 7-d periods to produce all 12 possible one-week data sets, all 11 possible consecutive two-week data sets and so on, up to a single 12-weeks data set. Disturbance patterns over the growing season were characterized by analyzing all mounds created from 23 May to 5 August 1994 for the N grid and all mounds created from 26 March to 3 August 1995 for the N and the SE grids. Finally, data from the 1994 and 1995 data sets for the N grid were pooled to examine pattern formation over a 2 yr time period. $L_{11}(h)$ values for each time period within each grid were calculated by averaging the $L_{11}(h)$ values from all applicable data sets (e.g., 11 data sets for the two-week data).

Pattern coherence through time

In addition to characterizing pattern development accumulated over varying lengths of time, we were also interested in examining spatial relationships among mounds produced at different times, since the long-term impact of a particular disturbance regime may

depend upon long term trends in the spatial distribution of disturbances. We analyzed patterns of mound production separated by different temporal lags (t) using the bivariate $L_{12}(h)$ function. For lags of 1–5 weeks, we used the same 12 weeks data sets that were used in the previous analyses. This resulted in 11 comparisons for mounds produced one week apart ($t = 1$), 10 comparisons for mounds produced 2 weeks apart ($t = 2$), etc. As in the previous analysis, we calculated average values for $L_{12}(h)$. Results were then compared to the average pattern found for mounds produced within a contiguous 7 d time period ($t = 0$), as determined through the univariate analysis described in the previous section.

Spatial relationships among mounds produced 52 weeks apart were determined for the N grid using mound data from 1994 and 1995. Although census intervals in 1994 were more variable than in 1995 (Table 1), 7-d data sets were paired so that they were separated as closely as possible by a 52 weeks time interval.

In one final analysis, we characterized the spatial relationships for mounds produced on the N grid in 1994 (all mounds produced from 23 May to 5 August) with those produced in 1995 (all mounds produced from 26 March to 3 August). In this case, we were interested in the coherence of overall mound production patterns between years.

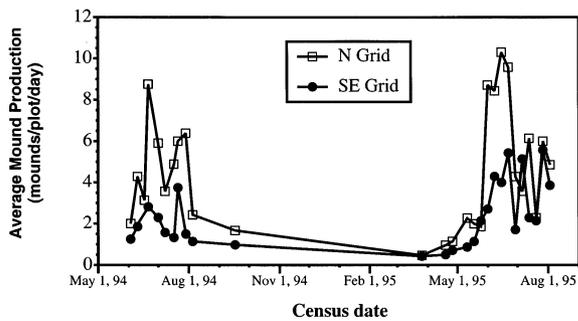


Fig. 2. Average rate of mound production calculated for the period of time between the indicated census and the preceding census for the N and SE grids during 1994 and 1995. Rates were determined by dividing the number of mounds produced between census periods by the number of days between censuses.

Results

General patterns of disturbance

A large number of mounds were produced by gopher activity on Anderson Prairie during 1994 and 1995 (Table 1). The rate of mound production was greatest during mid summer and tapered off during autumn and winter (Fig. 2). 331 new gopher mounds were created on the N grid between 24 May and 10 August 1994 (Table 1, Fig. 1). During that same period of time, 140 new mounds were produced on the SE grid. Mound production was even greater in 1995, with 449 mounds being produced on the N grid and 260 on the SE grid from 26 May through 3 August.

Overall disturbance rates for the N and SE grids during individual growing seasons ranged from 0.8% to 1.3% of the total grid area, given that the average area covered by an individual mound was 0.18 m^2 (long axis $\bar{x} = 0.58 \text{ m}$, $SD = 0.17 \text{ m}$; short axis $\bar{x} = 0.39 \text{ m}$, $SD = 0.12 \text{ m}$; $n = 61$ mounds). (Rates of disturbance were discounted for the area of overlap among individual mounds.) However, the probability of a disturbance being produced at any particular location within a grid varied greatly over relatively short distances ($< 10 \text{ m}$) and differed significantly in spatial distribution among sites (Fig. 3). Disturbance activity on the N grid was widely distributed within 4 or 5 general areas of activity, whereas the activity on the SE grid was more localized around what appear to be tunnel systems.

Survey error

In all of the pattern analyses, we found a sharp decline from a highly clustered pattern (high L-values), at scales of ca 1–20 m, to a pattern showing a strong tendency towards randomness at scales below 1 m (cf. Figs 5, 6 and 7). The tendency towards randomness at the smaller spatial scales was due primarily to survey error, as error in measuring the location of widely separated, fixed points (i.e., $> 50 \text{ m}$) was ca $\pm 0.5 \text{ m}$ between independent surveys. As a consequence, we cannot accurately resolve patterns at a scale finer than ca 0.5 m. However, we expect mound production patterns to be highly clustered at these scales, as mounds are commonly produced in close proximity to one another during periods of high mound production activity; and, in fact, often overlap.

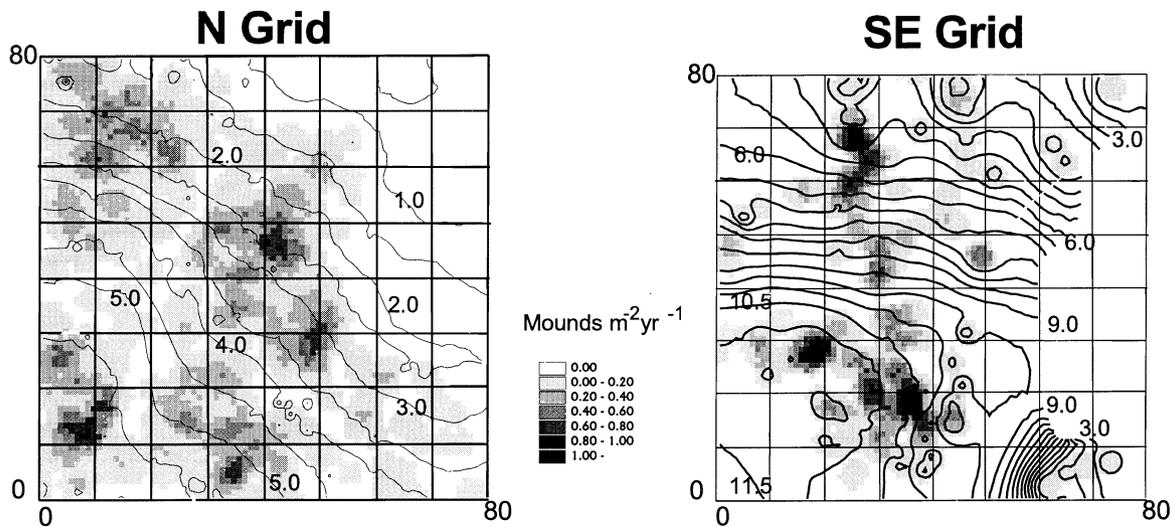
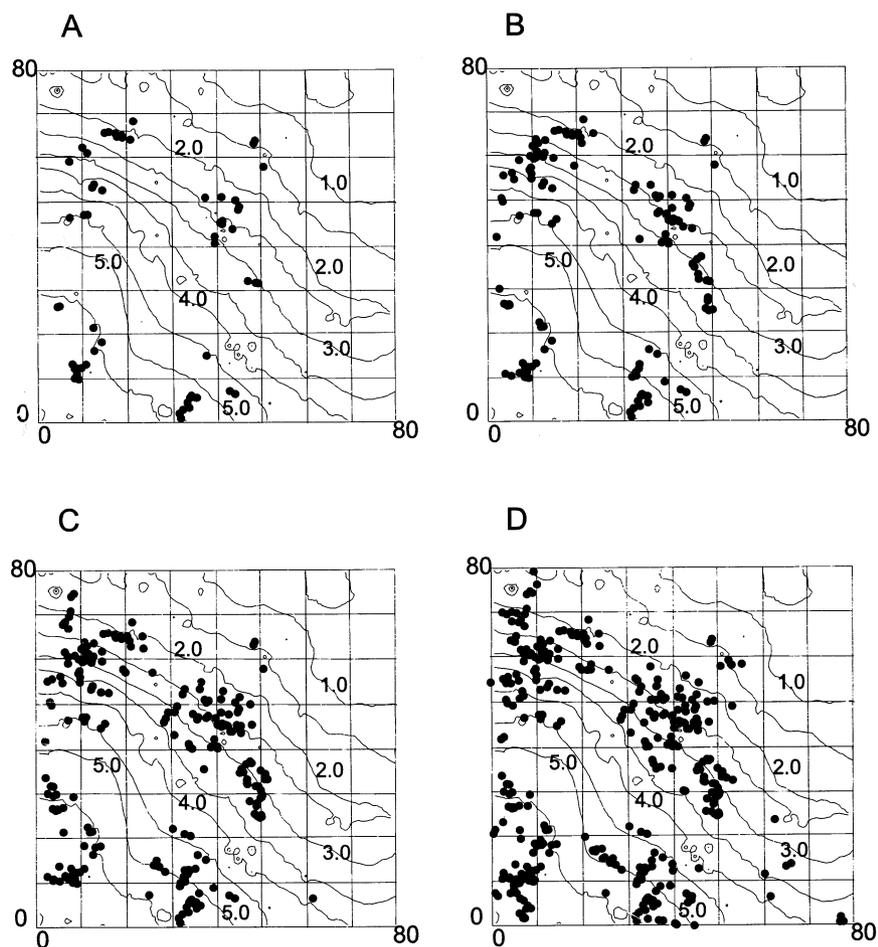


Fig. 3. Map of expected mound production rates (i.e., average number of mounds produced $\text{m}^{-2} \text{ yr}^{-1}$) as determined from mound surveys on the N and SE grids of Anderson Prairie. Rates were calculated for each $\text{m} \times \text{m}$ cell within a grid by tallying the number of mounds produced within a 20 m^2 area centered on the midpoint of each cell. This value was then divided by the sample area (20 m^2) and rescaled to reflect the annual rate of mound production observed on each of the grids. Calculations were done using the Arc View GIS.

Fig. 4. New mound production accumulated over different periods of time on the N grid at Anderson Prairie: (A) 7 d of mound production: 2–8 June 1995; (B) 14 d of mound production: 2–15 June 1995; (C) 28 d of mound production: 2–29 June 1995; (D) 56 d of mound production: 2 June–27 July 1995.



Pattern development over time

In characterizing disturbance patterns produced over varying lengths of time (e.g., Fig. 4), we found that mound production over a one-week period was highly concentrated at spatial scales centered around 5 m on the N grid and more broadly concentrated at scales around 8 m on the SE grid (Fig. 5). At broader scales, there was a tendency towards a more random pattern of mound production, as indicated by a decline in L-values above the scales associated with peak clustering. And, in fact, at scales above ca 25 m, mounds on the N grid were significantly hyperdispersed (evenly distributed).

As data were pooled over longer time periods, the pattern of clustering from 1 m to ca 20 m diminished in intensity, with the peak in the distribution shifting to broader scales (Fig. 5). This trend arose from the general tendency for mound building activity to spread over a broader area during the growing season (e.g., Fig. 4). In contrast, we found less change in pattern at scales above 20 m as mounds were accumulated over increasing periods of time (Fig. 5). This

suggests that the pattern of mound production is more constrained at the broader scales over individual growing seasons. However, when we pooled data from the 1994 and 1995 growing seasons on the N grid, we did see some change in pattern at the broader scales. Specifically, the pattern at scales above 25 m was no longer significantly hyperdispersed, indicating a subtle shift in broader scale patterns of activity from one year to the next (Fig. 5).

Comparison of pattern at different times

The spatial integrity of the disturbance regime over time was examined by comparing patterns of mound production separated by varying time intervals. The degree of spatial clustering in mound production at small scales (up to ca 15 m) decreased for both grids as time between disturbance events increased, although the rate of decline was more rapid on the N grid ($t > 1$; Fig. 6). A substantial decrease in the degree of spatial clustering was observed for mounds

produced only one week apart ($t = 1$), when compared to mounds produced within the same week ($t = 0$), and there was an even greater decline for mounds produced two weeks apart ($t = 2$) (Fig. 6). Further decreases were seen with increasing time interval, although the change was relatively small for $t > 2$. For both grids, the pattern at broader scales (> 15 m) was essentially the same as in the previous analysis (cf. Figs 5, 6), although there

was more scatter in values of $L_{12}(h)$, due to smaller sample sizes.

Comparison of mound production patterns in 1994 to patterns in 1995 for the N grid show a positive spatial association among mounds between years at scales ranging from 0.3 to 17.5 m; however, at scales > 20 m, mounds were more evenly distributed than expected at random (Fig. 7).

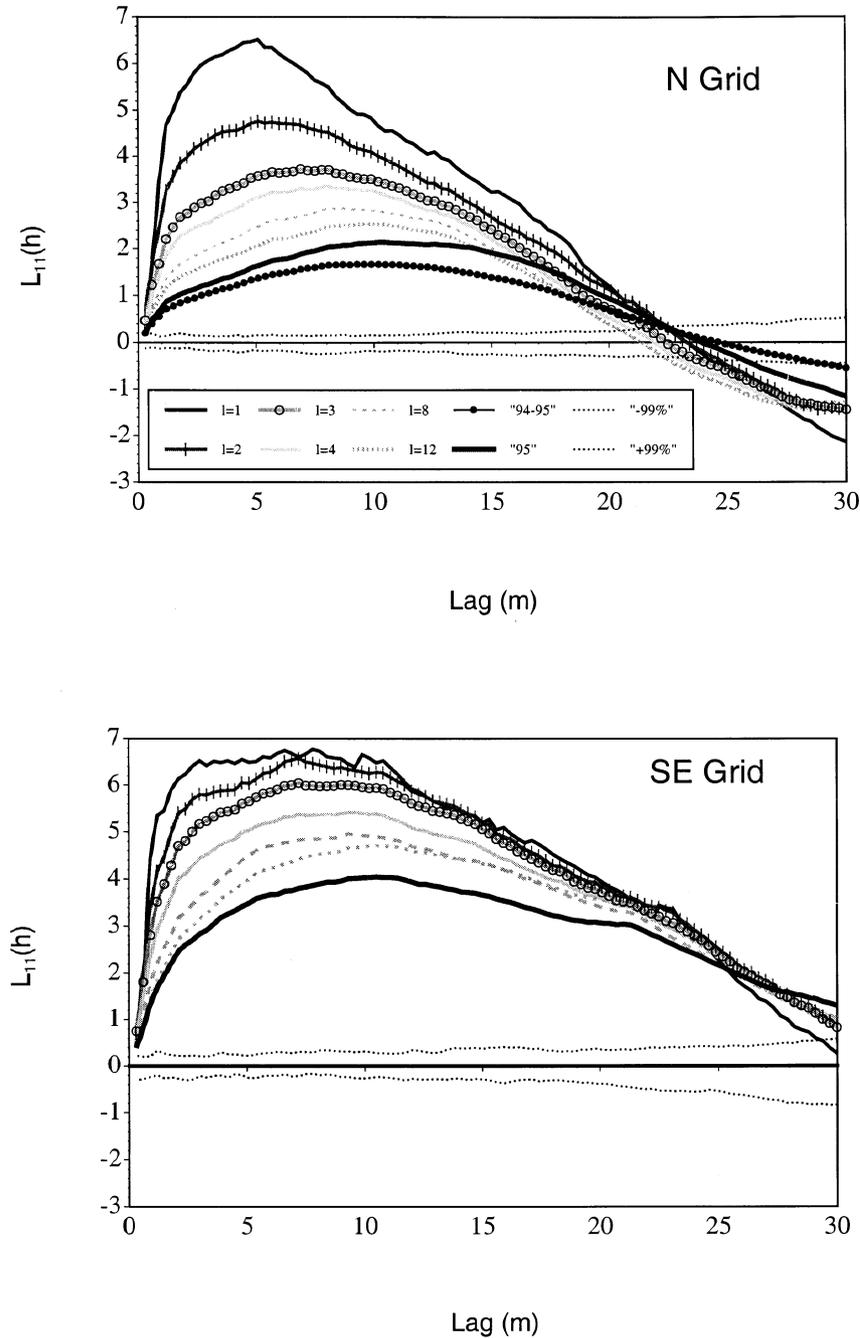
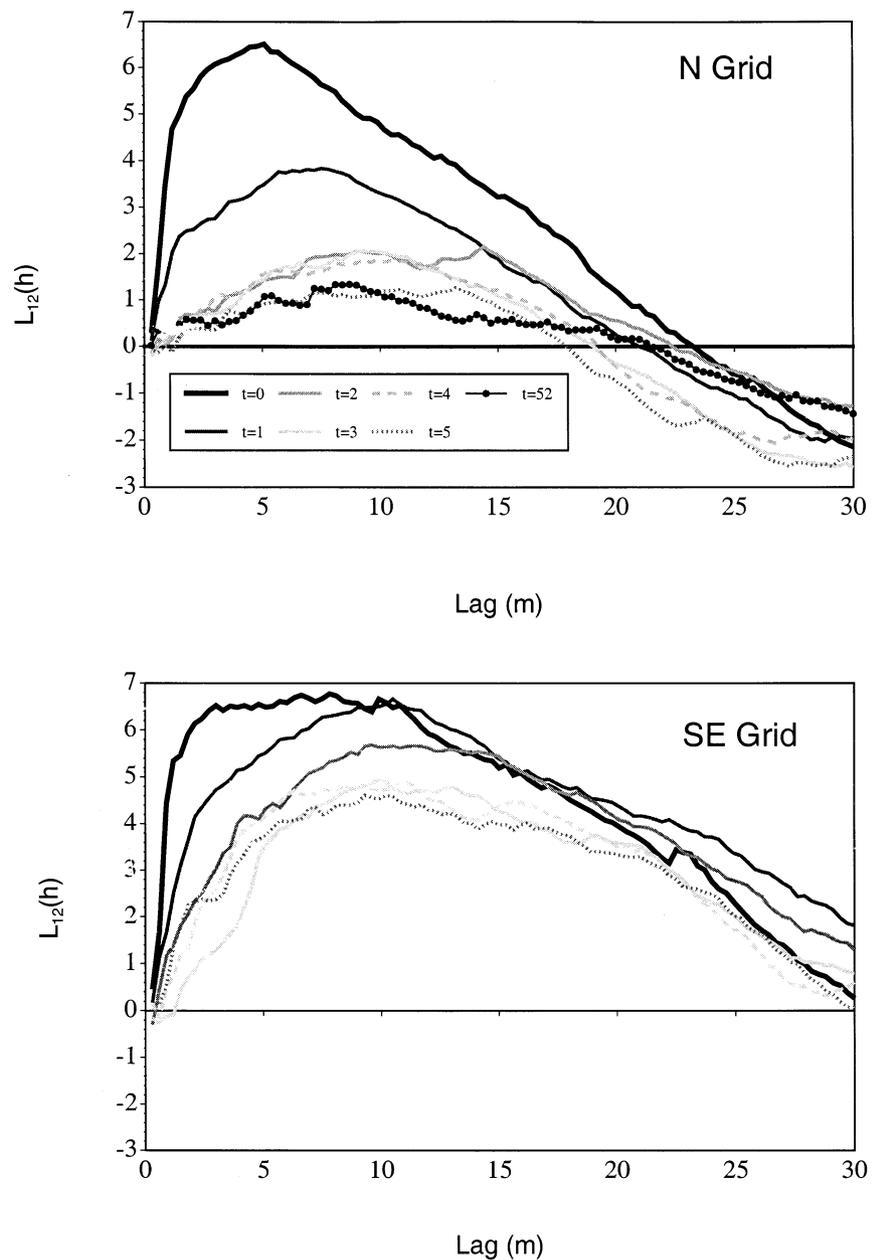


Fig. 5. Spatial patterns of mound production accumulated over varying lengths of time on the N and SE grids of Anderson Prairie, as determined by Ripley's univariate L-analysis. In the legend, " $l = x$ " indicates the number of weeks x of mound production included in individual analyses, "95" represents mounds produced from 26 March to 3 August 1995, and "94-95" represents mounds produced from 23 May 1994 through 3 August 1995. Ninety-nine percent confidence intervals around the expected value of $L_{12}(h) = 0$ were calculated for the "95" analysis of each grid. (See Methods for a more complete description of the analyses.)

Fig. 6. Spatial relationships among mounds produced during two different 7-d periods and separated by varying lengths of time, as determined by Ripley's multivariate L-analysis. In the legend, "t = x" denotes the number of weeks x separating the pairs of 7-d mound samples in the analysis. No confidence intervals are presented due to the great deal of variability in the numbers of mounds included in determining the average values for each analysis. (See Methods for a more complete description of the analyses.)



Discussion

Often, the primary goal of spatial pattern analysis is the detection of critical scales involved in ecological pattern formation (e.g., Gardner et al. 1987, Krummel et al. 1987, Palmer 1988, Dale and MacIsaac 1989, Milne 1992, Moloney 1993, Wiegand et al. 1998). Pattern analysis is particularly important as an exploratory tool when there is a need to identify the processes involved in producing pattern within ecological landscapes. By analyzing the development of disturbance patterns over time at Anderson Prairie, we

found two characteristic scales involved in the mound-building process. At small spatial scales (< 20 m), mounds are produced in a clustered pattern due to mound-building activity within individual burrow systems (Adams 1966). Mound production activity tends to be concentrated within smaller areas (< 8 m) over short time periods (1–2 weeks), but broadens out significantly after a period of only 3 to 4 weeks. At intermediate spatial scales (> 20 m and < 30 m), patterns of mound production differ between study sites, but change little over the course of time. In

fact, changes in pattern formation at the broader spatial scales were only apparent in comparing patterns of mound production over more than one year.

The fact that gopher mounds are significantly clustered at small spatial scales (< 8 m) over short time intervals (< 2 weeks) is not surprising; other studies have shown that mounds created by other species of gophers (e.g., *Thomomys* spp.) are significantly clustered at these scales (Adams 1966, Hobbs and Mooney 1991, Moloney 1993, Benedix pers. comm.). Also, as gophers are solitary and territorial (Hansen and Miller 1959), we would expect their mounds to exhibit a high degree of clustering within individual territories over longer periods of time (e.g., the average lifespan of a burrow system). However, the pattern to be expected over intermediate time periods and at broader spatial scales is not so obvious. Disturbance patterns could potentially vary over intermediate periods of time, particularly if gophers systematically alter their activities in response to changing patterns of resource availability during the growing season or between growing seasons. We do see some evidence of this as mound building activity shifted to somewhat different areas of the N grid within a single year (Fig. 4) and between years (Fig. 1).

One of the more interesting results of this study derives from differences seen in the broader scale patterns on the N and SE grids. On the N grid, there were 4 or 5 fairly distinct areas of mound building activity, separated by regions with little, if any, mound production (Fig. 3). The areas of greatest activity were ca 30–55 m apart and relatively evenly spaced, resulting in significant hyperdispersion in mound production at scales > 20 m (Figs 5–7). In contrast, the distribution of mounds on the SE grid resulted in a pattern with significant clustering at the broader scales (Figs 5–6). The differences in broad scale patterns for the N and

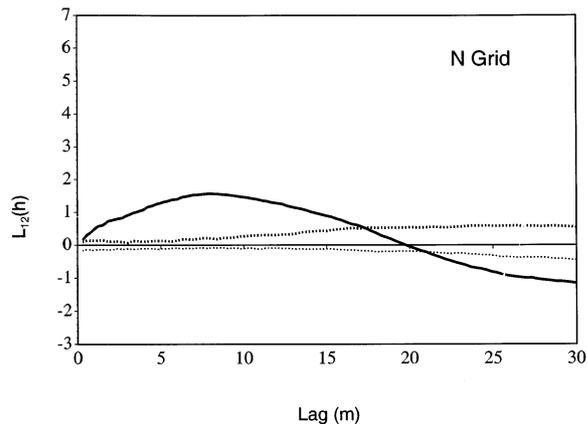


Fig. 7. Spatial relationships on the N grid among mounds produced in 1995 compared to mounds produced in 1994, as determined by Ripley's multivariate L-analysis. Ninety-nine percent confidence intervals around the expected value of $L_{12}(h) = 0$ are indicated by dotted lines. (See Methods for a more complete description of the analyses.)

SE grids may be related, in part, to differences in topographic variability. The SE grid was located on a hillside, whereas the N grid was on less variable terrain with a fairly constant slope and aspect throughout. This may affect the spatial architecture of the burrow systems, as the size and shape of the burrow systems of some species of gophers are known to be influenced by local environmental conditions (cf. Reichman et al. 1982).

Our finding 1) that mound production is highly clustered over short periods of time, 2) that mound production expands to cover a broader area of activity over a period of 3 to 4 weeks and 3) that rates of mound production vary greatly over short distances (< 10 m) has important implications for the ecological community at Anderson Prairie, and perhaps for tallgrass prairie ecosystems in general (cf. Moloney and Levin 1996). Most importantly, the high variability in rates of mound production over short distances may act to enhance the establishment of a more diverse ecological community. For example, it is well known that there is a guild of colonizing or "fugitive" species in tallgrass prairie ecosystems that have a much better chance of establishing on disturbed sites than in the intact prairie sod (Platt 1975, Brotherson 1982, Platt and Weiss 1985). Once established, survival of these species will be enhanced if there is a high probability that new mounds will be regularly produced nearby, since plants in general tend to disperse to sites near the parent plant (Levin and Kerster 1974). Other species that require relatively undisturbed habitat to persist can coexist nearby, if there are also locations that receive very little, if any, disturbance from gopher activity.

We have shown that a combination of factors exists at Anderson Prairie, which may provide ideal conditions for increasing species diversity by allowing species with different tolerances for disturbance to coexist in close proximity (cf. Platt and Weiss 1985). And, although our conjecture that local variability in disturbance rates acts to increase plant species diversity remains to be proven, a preliminary analysis does show a significant correlation between plant community composition and local disturbance rates at Anderson Prairie (Wolfe-Bellin and Moloney unpubl.). Elsewhere (Klaas et al. 1998), we have also shown that small, herbivorous mammals (e.g., *Microtus pennsylvanicus*) alter their patterns of activity in response to local variation in the disturbance regime, typically avoiding disturbed areas. This may act to heighten the impact of the disturbance gradient on the composition of the plant community, as more highly disturbed areas may offer a partial refuge from herbivory, which may be particularly important at the seedling stage for some plant species.

Clearly, there is a great deal of work to be done in clarifying the role of disturbance in structuring tallgrass prairie ecosystems. However, we now have a more precise understanding of the spatio-temporal scales in-

volved through the direct application of pattern analysis to field data. Although relatively large-scale disturbances, such as fire and grazing, play a very important role in maintaining the integrity and diversity of tall-grass prairie ecosystems (cf. Leach and Givnish 1996), our results show that small-scale processes, such as the ones studied here, may also be important.

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