

Light distribution in mesic grasslands: Spatial patterns and temporal dynamics

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Abstract. Spatial patterns and temporal dynamics of light distribution were investigated using lacunarity analysis, a multi-scale measure of spatial heterogeneity, in three mesic grasslands with different disturbance regimes. Frequency distributions of relative light intensity (RLI) were similar for the two non-disturbed grasslands, despite different composition (forbs vs. caespitose grass) resulting from different historical disturbance regimes prior to 1985, and different from the annually disturbed grassland. Spatial heterogeneity of light distribution was greater at all scales in the native, annually disturbed grassland than in the two non-disturbed grasslands. The disturbance regime affected temporal dynamics of the spatial patterns of light distribution in each grassland. The annually disturbed grassland exhibited a dramatic decrease in lacunarity (heterogeneity) from early to late April, likely the result of considerable growth of a cool-season grass. A general decrease in lacunarity occurred in the native, non-disturbed grassland, although the magnitude was much less than in the annually disturbed grassland. The reverted, non-disturbed grassland did not exhibit an appreciable change in lacunarity until later in the growing season, and then only at smaller scales. Combining the frequency distribution of RLI and the lacunarity curves provided an effective approach to assess relationships between the dynamics of spatial pattern of light distribution and ecological processes as influenced by different disturbance regimes. Integrating lacunarity analysis with more traditional measurements of grassland ecosystems (plant spatial distribution and arrangement and plant species composition and architecture) may be an effective way to assess functional consequences of structural changes in grassland ecosystems.

Keywords: Disturbance; Invasibility; Lacunarity analysis; Light intensity; Risk assessment; Spatial heterogeneity; Tall-grass prairie.

Abbreviations: NAD = Native annually disturbed (prairie); NND = Native no longer disturbed (prairie); RLI = Relative light intensity; RND = Reverted no longer disturbed (prairie).

Nomenclature: Diggs et al. (1999).

Introduction

Spatial patterns and temporal dynamics of light distribution are fundamental to understanding the mechanisms of grassland vegetation dynamics, especially in mesic environments (e.g. Burke et al. 1998). While light distribution has often been studied in forests (Baldocchi & Collineau 1994; Oliveira-Filho et al. 1998; Van Der Meer et al. 1999) it is difficult to quantify in grasslands even though light distribution is recognized as being important for recruitment and seedling establishment (Moretto & Distel 1998; Morgan 1998). The importance of spatial distribution of light in grasslands has, however, received recent attention (Silvertown & Smith 1988; Tang & Washitani 1995; Anten & Hirose 1999; Skálová et al. 1999) with increasing emphasis on how species utilize vertical space and temporal partitioning to absorb light (Anten & Hirose 1999; Skálová et al. 1999).

Light at the soil surface or within the canopy in grasslands can be viewed as a pattern of discrete patches of high-light vs. low-light areas that are classified using an arbitrary threshold of light intensity. Patch-based landscape metrics (Gustafson 1998) can be used to quantify the spatial attributes of such light gap 'landscapes'. Alternatively, the spatial pattern of light distribution, as well as its temporal dynamics, can be quantified using lacunarity analysis (Plotnick et al. 1993, 1996). Lacunarity is a scale-dependent measure of spatial heterogeneity or texture of landscapes (Plotnick et al. 1993, 1996) and lacunarity analysis has been used in several ecological and remote sensing studies for quantifying spatial pattern of binary (two-category) landscapes and of landscape use (Henebry & Kux 1995; Ranson & Sun 1997; With & King 1999; McIntyre & Wiens 2000; Peralta & Mather 2000; Wu et al. 2000). Lacunarity analysis can also be expanded for use with quantitative data (Plotnick et al. 1996; Wu & Sui 2001), such as light intensity. This approach can be used to synthesize spatial patterns of light distribution at all intensity levels rather than the arbitrary single cut-off level used in patch-based analyses. Although lacunarity analysis has been used in large-scale studies, it has

rarely been used for ecological applications at small scales (McIntyre & Wiens 2000).

Many of the factors influencing light distribution at the soil surface in grasslands, including plant spatial distribution, arrangement (van der Maarel 1996; Anten & Hirose 1999), species composition and architecture (Anten & Hirose 1999; Skálová et al. 1999), are sensitive to disturbance. Disturbance may also influence temporal dynamics of light distribution in grasslands. By permitting assessment of both spatial patterns and temporal dynamics of light distribution, lacunarity analysis may provide additional insight into the influence of disturbance on the invasibility of grasslands, as disturbance is often a precursor for invasion (e.g. Burke & Grime 1996).

This paper addresses the influence of disturbance on light distribution and dynamics at the soil surface in mesic grasslands. Specifically, we examined the frequency distribution and spatial heterogeneity of light intensity at multiple scales using lacunarity analyses.

Material and Methods

This study was conducted on three mesic grasslands with different disturbance regimes at the Grassland, Soil and Water Research Laboratory near Riesel, Texas (31° 28' N; 96° 52' W). Long-term (62 yr) mean annual precipitation is 896 ± 220 (S.D.) mm, with peaks in May and October. Grasslands studied include: (1) native tall-grass prairie that is disturbed annually by hay-making in late June, as is typical in this region (hereafter referred to as NAD), (2) native tall-grass prairie that was annually disturbed by hay-making prior to 1985, but has not been disturbed by hay-making or fire since (hereafter NND) and (3) reverted tall-grass prairie on a site that was cultivated prior to 1939, allowed to naturally revegetate and hayed annually from 1940 to 1985. This prairie has not been disturbed since 1985 (hereafter RND). The three grasslands are small (< 2 ha), immediately adjacent to each other and surrounded by croplands or permanent pastures.

The NAD grassland is dominated by climax vegetation for this tall-grass prairie: *Nassella leucotricha*, *Schizachyrium scoparium*, *Sporobolus compositus*, *Bouteloua curtipendula* and *Sorghastrum nutans*. These tall grasses have been mostly replaced by mid-successional forbs, *Ambrosia trifida* var. *texana*, *Ratibida columnifera* and *Aster* spp. in the NND grassland. Large clones of *S. scoparium* dominate the RND grassland.

10 1-m² plots were randomly located in each of the grasslands on 20 March 1998. Corners of each plot were permanently marked. For seven of the 10 plots, photosynthetically active radiation (PAR) was measured with a SunScan Canopy Analysis System (Delta T Devices

Ltd. Cambridge, UK) using a 0.015 m × 1 m wand containing 64 photodiodes. Preferred weather and light conditions were within 3 h of solar noon, solar zenith angles < 60°, slowly changing conditions and full sun in blue sky. Readings were stored on a lightweight field data collection unit (Psion Workabout). Measurements were taken at ground level between 12:00 and 15:00 h (CST) on 2 April, 30 April, 29 May and 26 June 1998. The entire plot was sampled by locating transects at 5 cm increments on the east and north sides of the plot, resulting in 2432 PAR measurements per plot. Prior to and following measurements in each plot, a measurement was taken above the canopy to determine ambient PAR. PAR measurements within each plot were expressed as RLI (light intensity which is incident at the soil surface relative to that which occurs above the vegetation canopy):

$$RLI = (\text{soil surface PAR}/\text{above canopy PAR}) \times 100 \quad (1)$$

Five 0.25-m² quadrats randomly located in the remaining plots were clipped to ground level at each sampling date to estimate standing crop. On 1 July, biomass was clipped at ground level from the seven plots used for PAR measurements. All biomass was dried at 60 °C for five days and weighed.

The 2432 RLI measurements and spatial co-ordinates in each plot were imported into ArcView GIS (Anon. 1998) as a point theme, then spatially interpolated to generate a continuous surface of RLI for the plot at 0.5 cm × 0.5 cm resolution. The Inverse Distance Weighted (IDW) interpolator in ArcView Spatial Analyst (Anon. 1998) was used for spatial interpolation. RLI values at unsampled locations were determined with a weighted mean of RLI values from the closest 12 sampled locations. Weights were determined using the inverse of the distance between the unsampled location and each of the sampled locations. This is based on the concept of spatial continuity, i.e. samples close together are more similar than those that are further apart (Isaaks & Srivastava 1989; Rossi et al. 1992). Point themes were also interpolated using variography and kriging (Isaaks & Srivastava 1989; Goovaerts 1997), but these methods were rejected because experimental variograms varied greatly for different plots. The selection of variogram models and parameters for each of the 81 repeated plots could introduce considerable subjectivity and artificial variation among RLI surfaces of different plots generated using kriging, which would diminish the potential gains of kriging over the inverse distance method.

Lacunarity analysis (Plotnick et al. 1996) was used to determine the spatial pattern of RLI and its temporal dynamics. Lacunarity (*A*) was determined using a glid-

ing box algorithm at eight different spatial scales with corresponding box sizes (side length of the gliding box, r) of 0.5, 1, 2, 4, 8, 16, 32 and 64 cm. Lacunarity measures the ‘gappiness’ of the landscape element of interest (Plotnick et al. 1993) and the element of interest is represented by higher density (greater value) in the case with continuous data or by ‘1’ in the case with binary data. Since lacunarity analysis may give different results for complementary patterns (Dale 2000) lacunarity of 1-RLI, a measure of shading, was determined to quantify the spatial pattern of a micro-landscape that is shaded by vegetation cover (high 1-RLI) and has lighted gaps in areas with no, or sparse, vegetation cover (low 1-RLI). The gliding box of a given size (r) was first placed at one corner of the plot and the ‘box mass’ $S(r)$, the sum of 1-RLI of the pixels within the box, determined. The box was then systematically moved through the plot one pixel at a time and box mass determined at each location. The lacunarity for box size r is calculated as one plus the ratio of the variance and the mean square of the box mass:

$$\Lambda(r) = \text{var}[S(r)] / E[S(r)]^2 + 1. \quad (2)$$

The lacunarity curve, a log-log plot of lacunarity $\Lambda(r)$ against box size r , was then used to quantify spatial heterogeneity of light distribution at different scales. Since the ratio of the variance and the mean square of the box mass decreases with increasing box size, a lacunarity curve has its maximum value at the smallest box size (a single pixel) and decreases with increasing box size. Typically, when the box size is smaller than the scale of the spatial pattern, the lacunarity curve decreases slowly with a convex shape; once the box size reaches and passes the scale of the spatial pattern, the lacunarity curve decreases quickly and approaches zero with a concave shape. The rapid decrease of the lacunarity curve indicates a general range for the domain of scale of the spatial pattern. There is, however, no proven approach to determine the precise domain of scale of a spatial pattern using lacunarity analysis (Dale 2000). ArcView Spatial Analyst was used to calculate lacunarity for each plot (Wu & Sui 2001). Given the repeated measure design, multivariate analysis of variance (MANOVA) with Pillai’s trace statistic (Zar 1999) was used to evaluate the effect of different disturbance regimes on spatial heterogeneity (lacunarity) for each scale (box size) and all scales combined. Analysis of variance (ANOVA) was then used to test the effect of disturbance regime at each scale on each sampling date and the effect of date (seasonal dynamics) at each scale under each disturbance regime. Multiple comparisons were conducted for significant ANOVA tests using the Tukey test (Zar 1999). Frequency distributions of RLI between grasslands at each date were compared using the Kolmogorov-Smirnov two-sample test (Conover

1980). S-PLUS software was used for performing these statistical tests (Anon. 1997).

Results

Standing biomass was consistently highest in reverted (RND) and lowest in annually disturbed (NAD) grassland (Table 1). Standing crop in undisturbed since 1985 (NND) and NAD grasslands was 18-29% and 54-82%, respectively, of that in RND grassland across all sampling dates.

Frequency distributions of RLI were similar for the two non-disturbed grasslands at all sample dates, but were significantly ($p < 0.05$) different at each date from distributions in the annually disturbed grassland (Fig. 1). A high proportion (70-86%) of sample points within RND and NND grasslands had RLI values $\leq 25\%$ across all sample dates, while only 6-45% of the sample points in the NAD grassland fit this criterion. Frequency distributions of RLI values in RND and NND grasslands exhibited an exponential decline across all sampling dates.

MANOVA tests using the lacunarity values at the four sampling dates as the repeated response variables showed a significant effect of disturbance regime on spatial heterogeneity of light distribution for each individual scales and for all scales combined. ANOVA F -tests indicated a significant ($p < 0.05$) effect of disturbance regime on spatial heterogeneity of light distribution at all scales except the largest (box size = 64 cm) and throughout the season (Fig. 2). Multiple comparisons using the Tukey test for the significant ANOVA tests showed no significant difference between RND and NND grasslands in their spatial heterogeneity at any scale on any sampling date. Spatial heterogeneity was significantly greater in NAD than in RND and NND grasslands at every scale throughout the season,

Table 1. Mean (\pm s.e.) standing biomass (g/m^2) of plots in three mesic grasslands with different disturbance regimes (NAD = native prairie with annual disturbance, NND = native prairie without annual disturbance since 1985 and RND = revegetated prairie). Five 0.25-m^2 plots were clipped in each grassland in April and May, while seven 1-m^2 plots were clipped in June. Letters indicate significant ($P < 0.05$) differences between grasslands within a sampling date.

Grassland	Standing crop biomass (g/m^2)			
	2 Apr	30 Apr	29 May	26 June
NAD	217 \pm 16 ^a	269 \pm 10 ^a	245 \pm 16 ^a	280 \pm 10 ^a
NND	646 \pm 40 ^b	776 \pm 61 ^b	818 \pm 31 ^b	788 \pm 66 ^b
RND	1186 \pm 183 ^c	1477 \pm 176 ^c	1042 \pm 119 ^c	962 \pm 85 ^b

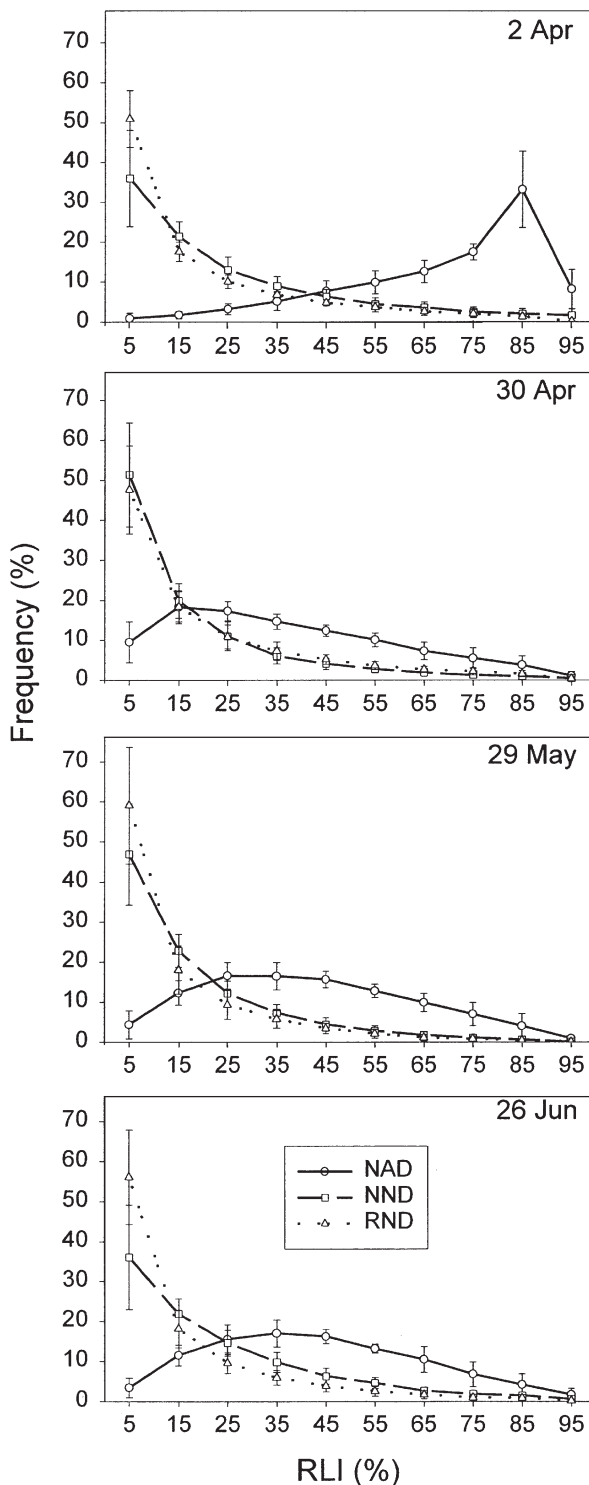


Fig. 1. Mean (\pm 1SD, $n = 7$) frequency distribution of relative light intensity (RLI) measurements at the soil surface for four dates in 1-m² plots in three mesic grasslands: NAD = native prairie with annual disturbance, NND = native prairie without annual disturbance since 1985 and RND = reverted prairie without annual disturbance since 1985.

with the exception of 30 April when NAD and RND grasslands were not significantly different.

Patterns of seasonal dynamics in spatial heterogeneity of light distribution in the three grasslands were more complex (Fig. 3). Significant seasonal dynamics occurred at box sizes of 0.5 to 16 cm in the NAD grassland, with a consistent pattern of decreased lacunarity as the season progressed. Spatial heterogeneity on 2 April was significantly greater than those of all other dates for NAD grassland. The NND grassland also exhibited significant seasonal dynamics across all scales, but with different patterns at different scales. Spatial heterogeneity was significantly greater on 2 April than on 30 April and 29 May at box sizes 0.5 to 16 cm, and was greater on 2 April than on other dates at a box size of 32 cm. In RND grassland, significant seasonal changes occurred only at box sizes of 0.5 to 8 cm. Spatial heterogeneity was significantly lower at these scales on 29 May than on 2 April and 30 April. Spatial heterogeneity was highest at the beginning of the season and decreased significantly early in the season in both NAD and NND grasslands, but changed little in RND grassland until decreasing from 30 April to 29 May. There was an apparent increase in spatial heterogeneity later in the season (26 June) in all three grasslands.

Discussion

Current disturbance regimes had a strong influence on both the frequency distribution and spatial pattern of RLI in these grasslands. Frequency distribution of RLI in annually disturbed native grassland (NAD) differed from that in the undisturbed since 1985 native grassland (NND) and reverted grassland (RND). RLI was higher, especially early in the season (Fig. 1) and spatial heterogeneity of light distribution at almost all scales throughout the season was significantly greater in NAD grassland than in non-disturbed grasslands (Fig. 2). The large proportion of area in NAD grassland with higher levels of RLI provided the necessary condition for spatial pattern with a large range of gap sizes that resulted in high levels of spatial heterogeneity. In contrast, accumulated standing crop biomass decreased light availability at the soil surface as well as spatial heterogeneity of RLI distribution in non-disturbed grasslands (Figs. 1 and 2). Although these grasslands differed in composition, they exhibited similar frequency distribution and spatial pattern of RLI. Thus, 'historical' (cultivation) and current disturbances similarly influenced light distribution and spatial heterogeneity in these grasslands.

Disturbance regimes also had a strong influence on seasonal dynamics of both frequency distribution and

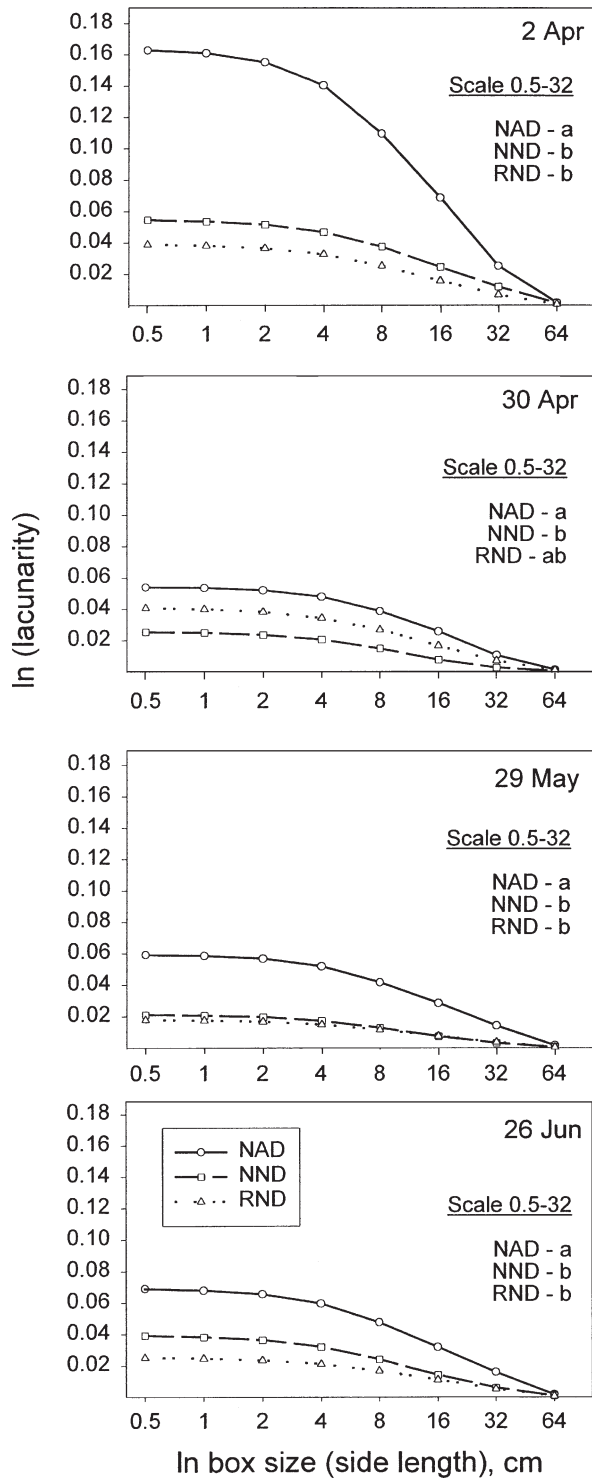


Fig. 2. Effect of disturbance regime on spatial heterogeneity of relative light intensity (RLI) at the soil surface for four dates in 1-m² plots ($n = 7$) in three mesic grasslands: NAD = native prairie with annual disturbance, NND = native prairie without annual disturbance since 1985 and RND = reverted prairie without annual disturbance since 1985. Letters indicate significant ($P < 0.05$) differences between disturbance regimes.

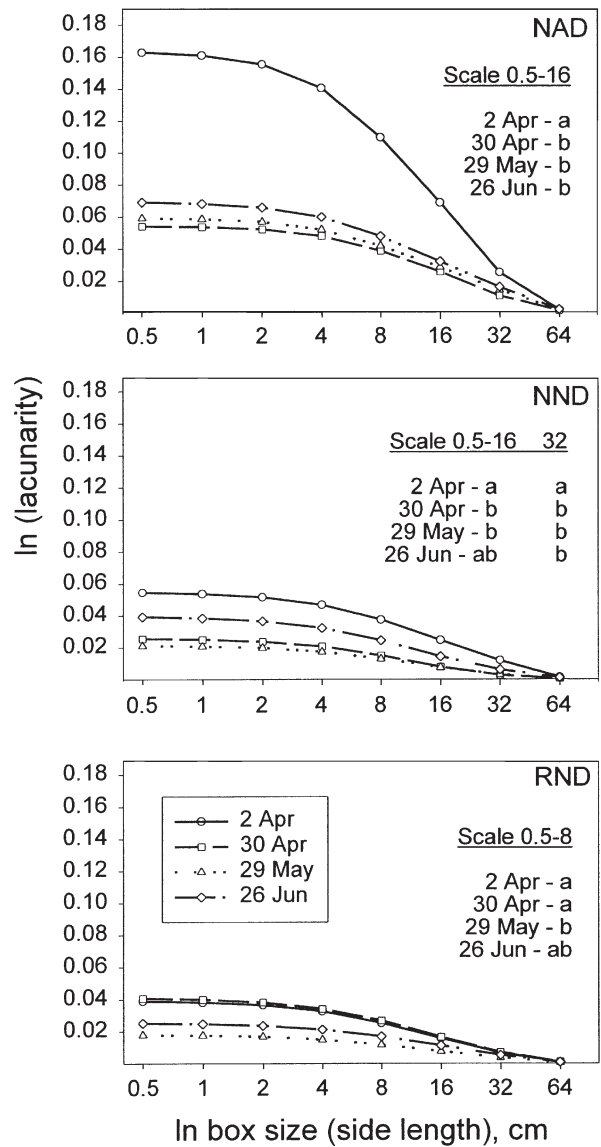


Fig. 3. Temporal dynamics of spatial heterogeneity of relative light intensity (RLI) at the soil surface for four dates in 1-m² plots ($n = 7$) in three mesic grasslands: NAD = native prairie with annual disturbance, NND = native prairie without annual disturbance since 1985 and RND = reverted prairie without annual disturbance since 1985. Letters indicate significant ($P < 0.05$) differences between sample dates.

spatial pattern of RLI in these grasslands. Differential spatial and temporal distribution of the development of species and growth forms during the growing season probably contributed to observed temporal differences in spatial heterogeneity of light distribution in these grasslands as it does in other grasslands (Kuppers 1994; Hikosaka & Hirose 1997; Skálová et al. 1999). In addition, morphology of the dominant species within grasslands substantially influences both the spatial patterns and temporal dynamics of light distribution (Anten & Hirose 1999). Because 'historical' and current disturbances differentially modified vegetation composition in the two non-disturbed grasslands, differences in spatial and temporal patterns of light distribution most likely resulted from differences in the dominant growth form. For example, early season (i.e. April) growth of forbs in NND grassland increased foliage cover resulting in a shift to lower RLI levels in the frequency distribution (Fig. 1). Germination and growth of forbs most likely occurred throughout the plots in gaps of all sizes as spatial heterogeneity decreased across all scales (Fig. 3). The dominance of forbs in this grassland, whose cover directly determines their effect on light levels (Skálová et al. 1999), contributed to the significant temporal dynamics in the spatial heterogeneity of light distribution. The observed increase in spatial heterogeneity in late June is attributable to the early senescence of these forbs. In contrast, growth of the dominant caespitose grass *S. scoparium* in RND grassland begins in mid-May; thus, there was little change in the RLI frequency distribution and spatial heterogeneity during the early growing season. Observed decreases in spatial heterogeneity at the 29 May sample date are attributable to the rapid growth of *S. scoparium* during this month. Because significant seasonal dynamics in spatial heterogeneity occurred only at small scales (box sizes 0.5 to 8 cm), this suggests that changes in canopy cover resulted from growth of individual perennial grass plants, rather than germination and growth of new individuals in gaps maintaining stability in larger scale spatial patterns (spatial configuration and arrangement of larger gaps).

Considerable early-season growth of the cool-season grass *N. leucotricha* in NAD grassland completely changed the frequency distribution of RLI from a high-RLI dominated to a low-RLI dominated light landscape from early to late April. Associated with these changes in RLI values, spatial heterogeneity of light distribution significantly decreased at small to intermediate scales (box size = 0.5 to 16 cm). Growth of warm-season grasses in May and June maintained these patterns of RLI frequency distribution and spatial heterogeneity.

Community structure, both dependent and independent of disturbance, can determine the invasibility of grassland (Smith & Knapp 1999). Because the frequency distributions of RLI values, species composition and standing crop dynamics differed between disturbed and non-disturbed grasslands, it should be expected that these mesic grasslands would differ in susceptibility to invasion and in the identity of successful invaders. Interference provided by existing standing crop (i.e. shading) in the non-disturbed grasslands may decrease invasion as few species can establish in dense shade (Thompson & Baster 1992). However, invasive species could still establish if they have characteristics commonly displayed in 'understorey', shade-tolerant species e.g. thin leaves and high shoot-to-root ratios. In contrast, species with adaptations to high light environments and relatively drier and warmer soils, with seeds that break dormancy and germinate under these conditions (Silvertown & Smith 1989) should be more invasive in annually disturbed grasslands.

Size distribution of gaps and the light intensity within gaps cannot be inferred directly from lacunarity analysis. Such information requires explicit cut-off levels to define gaps which may differ between species. Lacunarity analysis with continuous data, however, provides a parsimonious, multiple-scale measure of the spatial pattern of the light-landscape. It reflects not only the size distribution but also the spatial configuration and arrangement (not measured by the compositional measure of gap size distribution) of the light gaps. Lacunarity analysis is a true spatial measurement that can quantify the pattern of spatial heterogeneity and can also offer the opportunity of examining possible scale-dependence of ecological processes such as dispersal, establishment, survival and reproduction.

Using lacunarity analysis to characterize and compare magnitude and timing of seasonal dynamics in spatial heterogeneity of light distribution can be vital to understanding ecosystem function, as light is a key functional component of mesic grassland ecosystems (Burke et al. 1998). Integrating lacunarity analysis with the more traditional measurements of grassland ecosystems may be an effective way to assess functional consequences of structural changes (e.g. growth form changes) caused by different disturbance regimes in grassland ecosystems.

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