DISTURBANCE BY FIRE FREQUENCY AND BISON GRAZING MODULATE GRASSHOPPER ASSEMBLAGES IN TALLGRASS PRAIRIE

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Abstract. Understanding determinants of local species diversity remains central to developing plans to preserve biodiversity. In the continental United States, climate, grazing by large mammals, fire, and topography are important ecosystem drivers that structure North American tallgrass prairie, with major impacts on plant community composition and vegetation structure. Frequency of fire and grazing by bison (*Bos bison*), through effects on plant community composition and altered spatial and structural heterogeneity of vegetation in tallgrass prairie, may act as bottom-up processes that modulate insect community species richness. As previously seen for plant species richness, I hypothesized that grazing had more impact than fire frequency in determining species richness of insect herbivore communities. I examined this prediction with grasshoppers at Konza Prairie, a representative tallgrass prairie site in which fire frequency and bison grazing are manipulated over long terms with landscape-level treatments.

Topographic position (upland vs. lowland) and fire frequency (1-, 2-, 4-year intervals, and unburned) did not significantly influence grasshopper species richness or indices of diversity, while grazing had significant effects. On average, I found ~45% more grasshopper species and significantly increased values of Shannon H' diversity at sites with bison grazing. Species abundances were more equally distributed (Shannon's Evenness Index) in grazed sites as well. No significant interactions among burning and grazing treatments explained variation in grasshopper species diversity. Grasshopper species richness responded positively to increased heterogeneity in vegetation structure and plant species richness, and negatively to average canopy height and total grass biomass. Variation in forb biomass did not influence grasshopper species richness. A significant positive relationship between grasshopper species richness and overall grasshopper density was observed. Species richness increased marginally as watershed area of treatments in grazed areas increased, but not in ungrazed areas. Disturbance from ecosystem drivers operating at watershed spatial scales exhibits strong effects on local arthropod species diversity, acting indirectly by mediating changes in the spatial heterogeneity of local vegetation structure and plant species diversity.

Key words: Acrididae; disturbance, habitat heterogeneity, Konza Prairie; long-term study; Phasmida; prescribed burning; Tettigoniidae.

INTRODUCTION

Specifying local determinants of species diversity is a grand challenge in ecology, one that requires an understanding of the interaction between the regional species pool and the ecological processes that filter this pool to facilitate establishment and ultimately determine local coexistence (Ricklefs and Schluter 1993, Huston 1994, Rosenzweig 1995, Mauer 1999, Gaston and Blackburn 2000, Collins et al. 2002). Large-scale processes can influence ecological responses at many scales (Rosenzweig 1995, Davidowitz and Rosenzweig 1999), and ecosystem drivers such as grazing, fire, and climate can have important consequences for understanding diversity at many levels (Collins and Steinauer 1998, Collins et al. 1998, 2002, Knapp et al. 1998a,

1999, 2002). Often left unresolved at local levels are the relative contributions of intermediate to larger scale factors acting over broad landscapes for understanding underlying mechanisms that determine local species richness, and how these processes interact (Frank et al. 1998, WallisDeVries et al. 1998, Keesing 2000, Fuhlendorf and Engle 2001). This study investigates effects of long-term, large-scale disturbance by fire and grazing to local species diversity of the Orthoptera, an abundant insect herbivore assemblage in grasslands.

Arthropods contribute significantly to grassland biodiversity (Miller 1993, Tscharntke and Greiler 1995, Arenz and Joern 1996, Jonas et al. 2002, Fay 2003), community-level trophic dynamics (Fagan and Hurd 1991, Moran et al. 1996, Moran and Hurd 1998, Fagan et al. 2002), and ecosystem function (Curry 1994, Belovsky and Slade 2000, Blair et al. 2000, Hunter 2001, Jones et al. 2002, Meyer et al. 2002). While contributing significantly to grassland structure and function, ecological assemblages of grassland invertebrates vary

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significantly in time and space in response to local biotic and abiotic conditions (Belovsky and Joern 1995, Collins and Steinauer 1998, Kaufman et al. 1998). These conditions are influenced by complex, large- and small-scale disturbances such as fire and grazing along with effects of climatic variability (Evans 1984, 1988a, b, Jonas et al. 2002, Fay 2003).

Fire and grazing by large mammals are large-scale disturbances that act as primary ecosystem drivers in North American tallgrass prairie (Axelrod 1985, Collins and Wallace 1990, Pfeiffer and Steuter 1994, Coppedge and Shaw 1998, Knapp et al. 1998b). Historically, tallgrass prairie burned regularly with an approximate return interval of 3–4 years (Knapp et al. 1998a). Frequency of burning influences vegetation structure, plant species diversity, and taxonomic composition, with grasses dominating after repeated annual burns, and increased forb diversity found at sites with longer intervals between fires (Gibson and Hulbert 1987, Knapp et al. 1998a). Nutrient cycling in tallgrass prairie can also be influenced by fire, which in turn determines host plant quality to herbivores (Ojima et al. 1994, Blair 1997, Turner et al. 1997, Blair et al. 1998).

Large vertebrate grazers also play significant roles in structuring North American grasslands (Vinton et al. 1993, Hartnett et al. 1996, 1997, Coppedge and Shaw 1998, Frank et al. 1998). In North American tallgrass prairie, bison (Bos bison L.) and now domesticated cattle are the most notable recent grazers, although a diverse grazing fauna populated the region as recent as 10 000 years ago (MacFadden 2000). Bison grazing leads to a dramatic increase in plant species diversity (especially forbs) in response to selective feeding on grasses (Vinton et al. 1993, Hartnett et al. 1996, Collins et al. 1998, Coppedge and Shaw 1998, Knapp et al. 1999). Moreover, structurally heterogeneous vegetation, variable plant nutritional quality, and altered nutrient cycling rates result from feeding and trampling by large mammalian grazers (Blair et al. 1998, Johnson and Matchett 2001).

Grassland arthropod diversity is often linked to heterogeneity in vegetation structure, plant species composition and the general structure and physical complexity of the habitat (Lawton 1983, 1995, Evans 1984, 1988a, b, Heidorn and Joern 1987, Kemp et al. 1990, Andow 1991, Crisp et al. 1998, Dennis et al. 1998, Siemann 1998, Siemann et al. 1998, Knapp et al. 1999, Haddad et al. 2000, Kaspari 2000). Because disturbance from grazing and fire has such strong effects on vegetation characteristics, responses by arthropod communities to fire and grazing most likely result from indirect responses acting through changes in plant community composition and habitat structure (Tscharntke and Greiler 1995, Fay 2003). Consequently, understanding determinants of insect species diversity in a grassland landscape requires that one consider fire, grazing, and topography as well as the indirect means by which they affect arthropod species responses (Warren et al. 1987, Meyer et al. 2002).

The combined effects of large-scale, controlled burns of different frequency, bison grazing activity, and topography on the local diversity of grasshoppers (Orthoptera: Acrididae and Tettigoniidae) in a North American tallgrass prairie landscape are examined here. Long-term, landscape-level experimental manipulations of bison grazing and fire using controlled spring burns at the Konza Prairie provide an opportunity to investigate the importance of landscape-level disturbances on grasshopper species diversity. The primary hypothesis is that grasshopper diversity increases in response to disturbance from bison grazing and burning treatments to the degree that habitat heterogeneity is increased (Fuhlendorf and Smeins 1999, Fuhlendorf and Engle 2001). At issue here is the challenge to understand the origin and nature of the underlying mechanisms that promote local species richness of dominant insect herbivores in grassland, using North American tallgrass prairie as a model.

METHODS

Konza Prairie

The Konza Prairie (near Manhattan, Kansas, USA); 39°05′ N, 96°35′ W) is a tallgrass prairie typical of the Kansas Flint Hills, which exhibits a highly variable Midwestern United States continental climate consisting of wet summers and dry, cold winters (Knapp et al. 1998b). Konza Prairie is a large, protected research site (3487 ha) with long-term, watershed-level burning and bison-grazing experimental treatments (Knapp et al. 1998b). Mean annual precipitation is 835 mm, most of which occurs during the primary growing season. Precipitation and net primary productivity (NPP) are highly variable among years, and to a lesser degree among sites within years. Lower than average precipitation and NPP were seen in 2002. The flora is dominated by warm-season tallgrass species (e.g., Andropogon gerardii Vitman and Sorghastrum nutans (L.)); mid- and short-grass species can be common on sites with shallow soils. Over 300 forb species can be found, but grasses contribute ~80% to the total biomass.

Fire interval and grazing treatments applied at the watershed level comprise the long-term management of the site. Knapp et al. (1998b, 1999) describe in detail the Konza Prairie site and the long-term burning and grazing treatments (including a map of treatments). Watershed boundaries follow natural topographic boundaries, and range from an average of 44 ± 28.5 ha (mean ± 1 SD; range = 18.98–105.14 ha) for ungrazed sites to 97 ± 23.3 ha (range = 56.77 −135.45 ha) for grazed sites. Forty-two sites in 23 landscape units of different overall area and scattered throughout Konza Prairie were sampled in August 2002; sites included upland vs. lowland topography, different long-term burn intervals, and bison grazing vs. no grazing.

PLATE 1. Fire and grazing by large ungulates were historically important in tallgrass prairie, and the management of both has important ecological consequences for plant and invertebrate communities. To address the role of native grazers, and their interactions with fire, bison (*Bos bison*) were reintroduced in 1987 to a 1000-ha area of the Konza Prairie LTER site (pictured above) that includes replicate watersheds burned at 1-, 2-, 4-, and 20-year intervals and a range of topography and vegetation types. Photo credit: John Blair.

For sites sampled here, late-spring prescribed burning treatments are applied to replicate watersheds at scheduled intervals of 1, 2, 4, and 20 years. Burning treatments at Konza Prairie date from 1972 to the present, although treatments were initiated simultaneously at all sites; replications of treatments were added subsequently as additional land was acquired. Bison were introduced in 1987 and the herd increased until 1992 (see Plate 1). Since 1992, the herd has been maintained at approximately 200 individuals, with unrestricted access to a 1012-ha portion of the site, including 10 watersheds subjected to the above combination of burn frequencies of late-spring prescribed fire. On average, bison remove ~25% of the aboveground net production annually, and ~90% of bison diet consists of grasses (van Vuren and Bray 1983, Steuter et al. 1995, Hartnett et al. 1997). No water or supplemental food is provided to bison.

Long-term manipulations of disturbance to tallgrass prairie watersheds were used to assess overall community responses of grasshoppers as representative insect herbivores. Burn frequency and bison grazing are considered as categorical treatments in analyses, reflecting the cumulative, long-term effects of treatments on vegetation rather than just current year effects. Ad-

ditional comparisons into mechanisms resulting from recent effects of fire and recent grazing complement these analyses. Elapsed time since the last fire provides insights into responses by grasshopper assemblages to recentness of fire; responses to recent fire in longer term 2-, 4-, and 20-year treatments that are burned in different years can be assessed. Bison roam freely among all burn treatments throughout the grazed portion of Konza Prairie. All watersheds are visited throughout the year at irregular and currently unpredictable schedules, including during the growing season, when sites with highly palatable forage are present elsewhere. Bison do not graze indiscriminately across the landscape or in local areas at Konza Prairie, and use of watersheds and portions of watersheds is essentially independent over the long term (Hartnett et al. 1997, Knapp et al. 1999). I treated each sampling site as an independent event with respect to grazing because of these large-scale grazing patterns.

Grasshopper sampling

I used sweep net sampling to assess grasshopper species richness (Acrididae and Tettigoniidae); I also included one species of walking stick (Phasmida), which is functionally similar although no longer included in

the order Orthoptera. Using a 30.5 cm diameter sweep net, four standardized 100-sweep transects ~10 m apart were made at each site in early August 2002, and combined for each site. All sampling was performed in an area approximately 50 × 100 m that was arbitrarily selected but representative of the watershed and topographic position in question. I sorted grasshoppers to species and calculated relative abundances for each site; both adults and nymphs were included in estimates. The Appendix lists species encountered in this study using this sampling protocol. Sweeping is the best method to estimate species richness and associated relative abundances of grasshoppers in tallgrass prairie vegetation (Evans et al. 1983). When possible, grasshopper densities (individuals per square meter) were estimated by counting the number of grasshoppers in a series of 30 0.1-m² rings at each of four transects per site (Onsager and Henry 1977). Individual species densities were estimated by combining relative abundances and total grasshopper densities, which allows responses among watersheds to be normalized by overall abundance in species ordinations. My results are based on 34 species and 12 042 individuals collected in the sweep-net transect samples from these 42 sites; density estimates were determined at 35 sites. All grasshopper samples were taken under sunny conditions with wind speed <10m/s.

Habitat attributes

Grasshopper communities are known to respond to various attributes of the vegetation (Otte 1976, Joern and Lawlor 1980, Joern 1982, Kemp et al. 1990). I characterized habitat attributes along a 30-m transect established arbitrarily at each grasshopper sampling site.

Grass and forb biomass.—Vegetation biomass (grams per square meter) was sampled at each site by clipping all vegetation along three, 0.1 × 3 m swathes randomly located along 30-m transects. Grasses and forbs were separated, dried, and weighed.

Vegetation canopy.—Height to the nearest centimeter was estimated by determining the height of the vegetation using a rod graduated in millimeters, a method that works well in grassland (Cody 1974, Wiens 1974, Joern 1982). Twenty measurements were made along a 30-m transect. Structural heterogeneity was estimated as the coefficient of variation (CV) based on these measurements.

Plant species richness.—Plant species richness at each site was estimated by counting the number of plant species in each of ten 0.25-m² quadrats, randomly located along a 30-m transect.

Recent grazing.—To gain a sense of the immediate impact of grazing on grasshopper assemblages, the influence of recent grazing activity on grasshopper diversity was assessed. Recent grazing intensity was classified using the level of vegetation grazing, and amount and freshness of dung within the immediate sample

site. Recent grazing activity at each site was classified based on an ordinal scale: 0 (nongrazed sites; no evidence of recent grazing because bison never present); 1 (no recent grazing but site located in grazed area); 2 (small amount of grazing evident, probably by one or two animals); 3 (moderate grazing from many animals; many grazed patches interspersed in ungrazed matrix, and evidence of relatively fresh dung); 4 (extensive grazing, but grazing lawn not yet developed; evidence of large herd grazing activity, including recent dung); and 5 (extensive grazing with much return grazing leaving a closely cropped site and little vertical structure). A grazing lawn develops when grazers repeatedly revisit a site, resulting in closely cropped vegetation of generally higher nutritional quality (McNaughton 1984).

Statistical analyses

I used general linear models (ANOVA and regression using the method of least squares) to evaluate hypotheses. SAS/STAT (Proc GLM; SAS Institute 1989) was used to analyze general linear models. Burn interval and grazing were treated as categorical variables in analyses. The effect of topography was nested within a fire × grazing interaction in an unbalanced design.

An index of species diversity was calculated using the Shannon diversity index ($H' = -\Sigma p_i \ln p_i$, where p_i is the proportion of individuals found in the ith species) (Magurran 1988). The Shannon diversity index is distributed normally and was used as a dependent variable in ANOVA (Magurran 1988) to determine how burning and grazing affect species diversity. Evenness indicates the relative contribution of all species to the calculation of the diversity index. Evenness (E) for each sample was calculated as: $E = H'/\ln S$ (Magurran 1988), where a value of 1.0 results when all species are equally abundant. All variables were transformed to assure normality and equal variances among treatments using square-root (species richness), natural log (H') and $\sin^{-1}$ square-root (evenness) transformations before analyses were performed; results are presented in their nontransformed states.

Ordination of taxonomic composition

Principal-components analysis (PCA), an eigenanalysis ordination technique that maximizes the variance explained by each successive orthogonal axis, was used to examine community-level taxonomic responses to treatment combination. Differences in site-specific scores indicate the degree to which grasshopper communities have different species or show differences in relative abundances of shared species based on the entire set of species. I used PC-Ord software (McCune and Mefford 1999) in the analyses to extract axes that summarize the taxonomic composition of each representative grasshopper community for each site. The first three PCA axes were assessed using ANOVA to determine how regional landscape factors, local factors
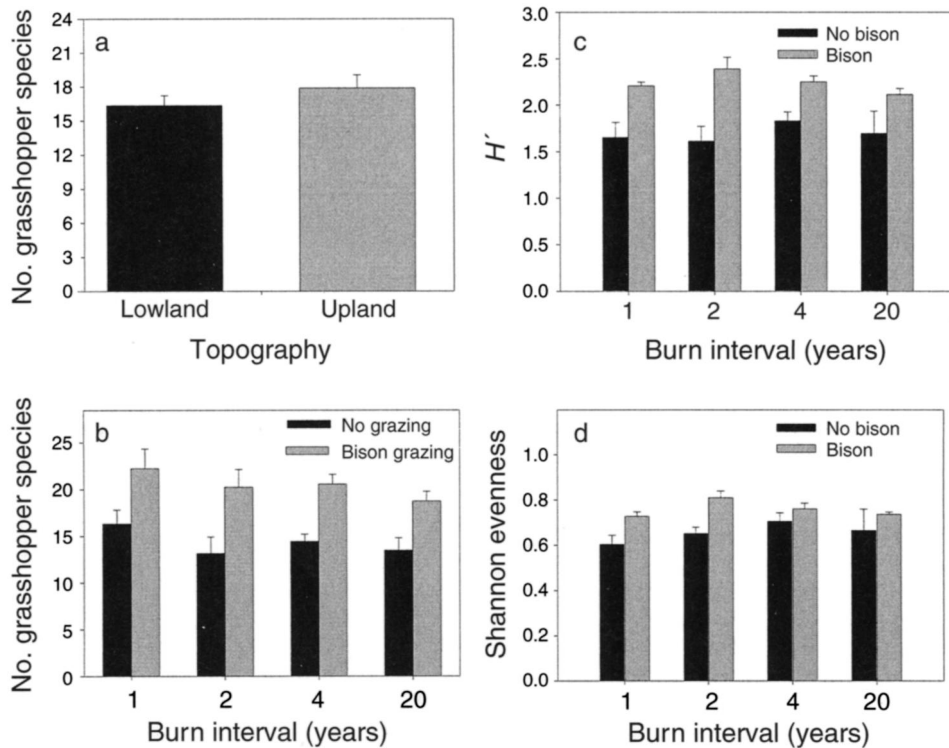
FIG. 1. Grasshopper species richness and diversity in response to major grassland system drivers are illustrated: (a) effects of topography on species richness, and (b–d) effects of fire frequency and grazing on (b) species richness, (c) species diversity (H'), and (d) Shannon evenness. Mean values + 1 SE are presented.

and management practices interact to explain the resulting grasshopper assemblage composition.

RESULTS

Grasshopper species diversity

Habitat responses to burn frequency and bison grazing.—Effects of fire and grazing on local vegetation was evaluated as grass and forb biomass, plant species richness, average canopy height, and the CV of canopy height and plant species richness. Grazing had a significant, positive influence on plant species richness ($R^2 = 0.19, P = 0.004$) and canopy height heterogeneity ($R^2 = 0.49, P < 0.001$), and significant negative effects on canopy height ($R^2 = 0.64, P < 0.001$) and grass biomass ($R^2 = 0.24, P < 0.005$). The total number of fires since treatments began showed a negative effect on plant species richness ($R^2 = 0.47, P < 0.0001$), and time since last fire showed a significant but weak positive influence on canopy height ($R^2 = 0.12, P = 0.025$). All other possible responses by the six plant community attributes specified above showed no statistically significant responses to recent grazing, time since last fire, or total number of fires.

Grasshopper species responses.—Over all sites sampled, average species richness was 16.2 ± 7.8 species (mean $\pm$ 1 SD, range 6–24 species), Shannon H' averaged 1.95 ± 0.8 (range 0.96–2.56), and the average

Shannon Evenness Component (E) was 0.7 ± 0.18 (range 0.42–0.89). I observed no significant difference in grasshopper species richness between upland and lowland sites (Fig. 1a; $F_{1,26} = 1.25, P > 0.3$), or in response to fire among sites with different burn intervals (Fig. 1b, $F_{3,26} = 1.73, P = 0.19$; Fig. 1c, $F_{3,26} = 0.61, P = 0.62$). No significant difference in grasshopper species richness ($F_{2,14} = 1.36, P = 0.29$) was detected among burn treatments when comparing only ungrazed sites. Grasshopper species richness did not vary with the total number of fires at a site since treatments were begun in a watershed ($R^2 = 0.006, P = 0.64$) or with the time elapsed since the last fire ($R^2 = 0.04, P = 0.17$).

Grazing by bison resulted in a significant 42% increase in grasshopper species richness (Fig. 1b, $F_{1,26} = 35.2, P < 0.0001$) and increased H' (Fig. 1c, $F_{1,26} = 30.36, P < 0.001$). No significant interactions were observed among any of the long-term treatment combinations. Over a short time scale, grasshopper species richness increased with increased level of recent grazing ($Y = 14.43 + 3.43X - 0.42X^2; R^2 = 0.5, P < 0.0001$). A strong positive relationship between grasshopper species richness and overall grasshopper density for the site also resulted (Fig. 2a). Moreover, grazing affected the species richness–area relationship (Fig. 2b), where species richness increased with the area in grazed watersheds, but not in ungrazed ones.
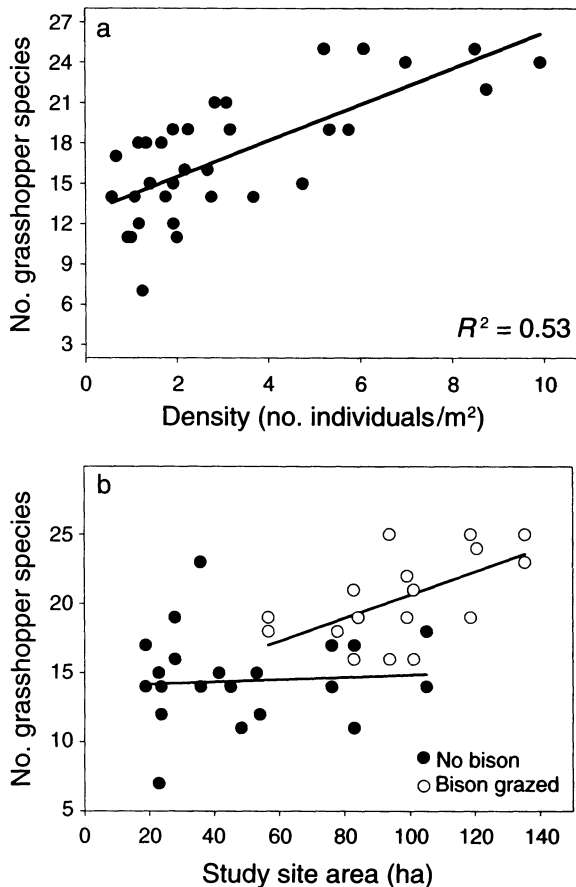
FIG. 2. (a) Grasshopper species richness varies positively with overall grasshopper density (all species at a site) ($Y = 1.28 + 1.34X$, $R^2 = 0.53$, $P < 0.001$). Grasshopper density was only sampled for 35 of the 42 sites for which grasshopper species richness was determined. (b) Grasshopper species richness increases with the area of the watershed grazed by bison ($Y = 12.247 + 0.0838$; $R^2 = 0.33$, $P = 0.006$), but no relationship between watershed area and grasshopper species richness is observed in ungrazed areas ($R^2 = 0.000$, $P = 0.75$). Data are from the Konza Prairie, Kansas, USA.

Shannon evenness was similarly affected by bison grazing (Fig. 1d), where a significant increase in E for grasshopper assemblages was detected with bison grazing ($F_{1,26} = 14.4$, $P < 0.0008$). No significant response by E to burn frequency ($F_{3,26} = 1.8$, P $= 0.17$) was detected, and no interaction between burning and grazing ($F_{3,26} = 1.27$, $P = 0.31$) was found. Topographic differences in evenness were significant ($F_{8,26} = 2.3$, $P = 0.049$), where E varied among grazing $\times$ burn frequency combinations in somewhat idiosyncratic ways that defy generalization. A significant decreasing quadratic relationship exists between species richness and Shannon Evenness (Fig. 3) (Adjusted $R^2 = 0.25$; $F_{2,41} = 7.73$, $P = 0.0015$), indicating that local assemblages with smaller number of species have a small number of dominant species, compared to more diverse assemblages which are somewhat more evenly distributed.

Moreover, E increased marginally with species richness in ungrazed sites, but no relationship between species richness and E was observed for grazed watersheds (Fig. 3).

Grasshopper species richness responded significantly to habitat characteristics described by vegetation (Fig. 4): negatively with grass biomass, negatively with canopy height, positively with heterogeneity in canopy height, and positively with plant species richness. No significant relationships existed between grasshopper species richness and either forb biomass or the variability in plant species richness.

Taxonomic composition of grasshopper communities

Species composition of grasshopper communities varied among sites in response to influences of grazing and burning. In a PCA ordination of grasshopper communities among sites, Axis 1 explained 28.3%, Axis 2 explained 24.1%, and Axis 3 explained 20.0% of the total variation in species composition, a total of 72% of the total variation in grasshopper community assembly among sites. Variation in PCA scores among sites for each combination of burn intervals and grazing treatments for each of the first three PCA axes is presented in Fig. 5. Average PCA scores across treatments indicate that taxonomic shifts in grasshopper community composition occur in response to grazing and burning schedules. ANOVA was performed with the main factors of topography, grazing treatment, and controlled burn intervals (1, 2, 4, 20 years) and all interactions. No significant effects to species composition from burn frequency and grazing were observed for PCA Axis 1 (fire: $F_{3,25} = 2.1$, $P = 0.13$; grazing: $F_{1,25} = 3.0$, $P = 0.096$). A strong effect of burn interval ($F_{3,25} = 10.7$, $P < 0.001$) and a weaker effect from grazing ($F_{1,25} = 5.1$, $P = 0.03$) on grasshopper species

FIG. 3. Relationship between Shannon evenness and species richness for the 42 local grasshopper assemblages that were sampled in response to bison-grazed vs. ungrazed sites. No significant relationship was observed for grazed sites ($R^2 = 0.03$, $P = 0.23$). Evenness increased marginally with species richness in ungrazed sites ($R^2 = 0.12$, $P = 0.059$; $Y = 0.48 + 0.13X$).
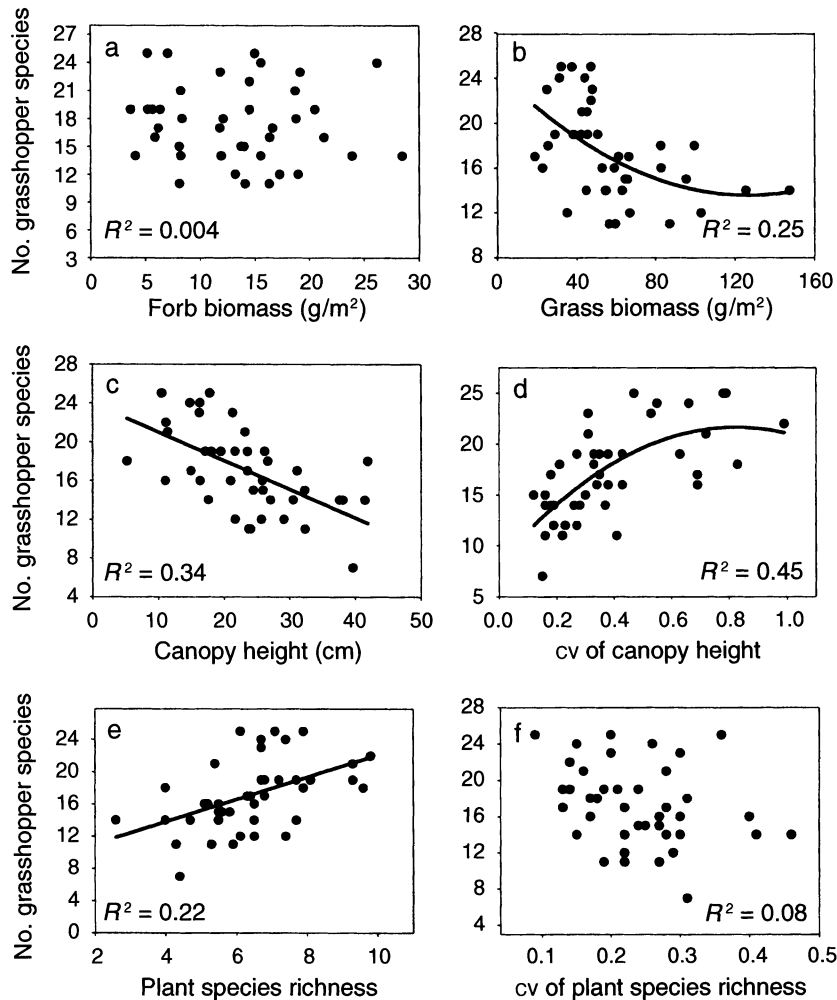
Fig. 4.   Relationship between grasshopper species richness and habitat characteristics hypothesized to be important factors. No significant relationship is observed between grasshopper species richness and (a) forb biomass or (f) the cv of plant species richness at a site. Significant regressions are seen for (b) grass biomass, (c) average canopy height, (d) cv of canopy height (local-scale structural heterogeneity), and (e) plant species richness.

composition was observed for PCA Axis 2. For PCA Axis 3, only controlled burn treatments had a significant effect ($F_{3,25}$ = 3.4, P = 0.03) on the responses, but one that was very different than that seen for PCA Axis 2. The main response along PCA Axis 3 indicates that assemblages in sites with annual burns differed greatly from the other burn treatments, which do not differ from one another. No significant interactions were observed for any treatment combinations.

The most common species at Konza Prairie (acridids: *Phoetaliotes nebrascensis, Melanoplus keeleri, Orphullela speciosa, Melanoplus scudderi, Hypochlora alba,* and *Melanoplus bivittatus*; tettigoniids: *Conocephalus* sp.; Phasmida: *Diapheromera femorata*) were dominant in both grazed and ungrazed sites, with only small shifts in rank order. The biggest shifts in species were large drops in relative abundance of the less abundant *Syrbula admirabilis, Hesperotettix viridis,* and *Ageneotettix deorum* in grazed vs. ungrazed sites. Oth-

erwise, shifts in combinations of mostly uncommon species are responsible for the different PCA scores at sites with different treatment combinations. Also, uncommon species dropped out of sites with low species richness. Because of big differences in overall density in grazed vs. ungrazed sites, uncommon species were found at even lower densities in ungrazed sites than for grazed sites (Joern 2004).

DISCUSSION

Repeated large- and small-scale disturbances result in grasslands that are highly variable in time and space and have important consequences for the maintenance of local species diversity (Coppock et al. 1983, Detling 1987, Evans 1988a, Collins and Glenn 1991, 1997, Collins et al. 1998, Kaufman et al. 1998, Knapp et al. 1999, Fuhlendorf and Engle 2001). Responses by plant communities to fire and large-animal grazing are seen in many community types worldwide, and other sources
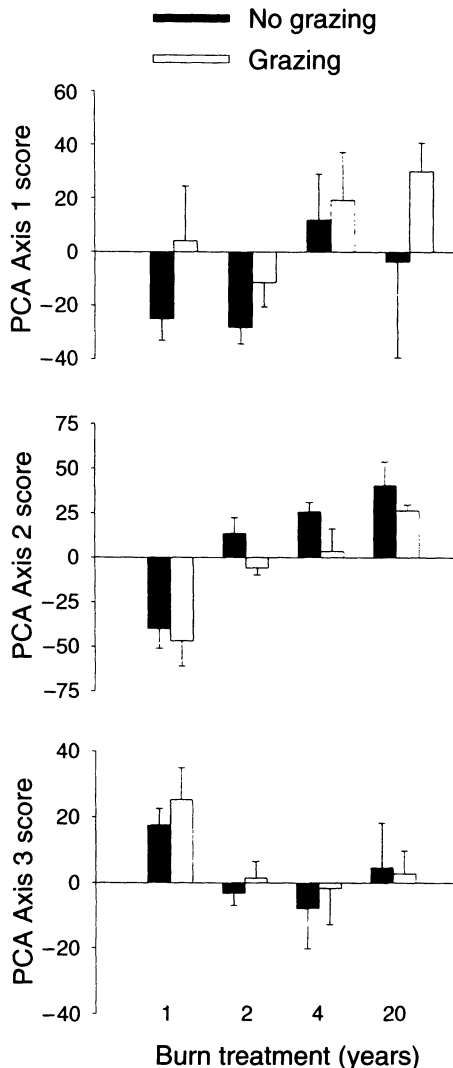
No grazing

Grazing

FIG. 5. Principal-components analysis of species composition of grasshopper communities in response to fire and grazing management treatments. The x-axis indicates the burn-interval treatment categories (1, 2, 4, and 20 years). The PCA is based on species abundances for each site. Values presented are the means ± 1 SE of site scores for each burn-interval treatment category.

of disturbance (e.g., wind, flooding, landslides) often play similar roles with profound impacts on community structure as well (Huston 1994). In North American tallgrass prairie, grazing interacting with fire, topography, and climate are key drivers responsible for modulating vegetation characteristics, including plant species richness and structure (Vinton et al. 1993, Hartnett et al. 1997, Collins et al. 1998, Knapp et al. 1999). As shown here, these same key grassland drivers also play important roles in modulating species richness and taxonomic composition of grasshopper communities, which are key insect herbivores in many types of grassland. Such relationships are also important for understanding poorly studied interactions between vertebrate

and invertebrate consumers in natural communities worldwide (Tscharntke and Greiler 1995, Tscharntke 1997, WallisDeVries et al. 1998, Keesing 2000), making it important to characterize such responses, because grazing is ubiquitous worldwide in grasslands.

Available studies illustrate the sometimes contradictory responses observed when attempting to assess the roles of disturbance from fire and grazing on arthropod communities (Warren et al. 1987, Kemp et al. 1990, Tscharntke and Greiler 1995, Harper et al. 2000, Swengel 2001, Panzer 2002, Tscharntke et al. 2002, Stoner and Joern 2004). Insect population responses to burning in grasslands can be both positive (Tester and Marshall 1961, Nagel 1973, Evans 1984, Anderson et al. 1989, Panzer 2002) and negative (Anderson et al. 1989, Bock and Bock 1991). In the absence of recent grazing, different fire frequencies in Kansas Flint Hills tallgrass prairie resulted in increased arthropod abundance and species richness, with clear shifts as to which individual species dominate (Nagel 1973, Evans 1984, 1988a, b, Meyer et al. 2002). Obviously it matters to insects when fire occurs in relation to critical exposed life history stages, as well as the impact of fire in limiting resources (Warren et al. 1987, Swengel 2001).

Arthropod responses to grazing from a variety of grasslands are perhaps less well understood (Morris 1967, Plumb and Dodd 1993, Tscharntke and Greiler 1995, Onsager 2000, Gebeyehu and Samways 2003), with effects on insect communities as variable as those seen for fire. Light or intermediate grazing intensities often lead to increased richness of insect species, including grasshoppers (Holmes et al. 1979, Roberts and Morton 1985, Onsager 2000, WallisDeVries and Reamakers 2001, Kruess and Tscharntke 2002, Gebeyehu and Samways 2003), but not always (Holmes et al. 1979, Kruess and Tscharntke 2002). While maximum species richness may be found at intermediate grazing levels, this notion is currently difficult to assess rigorously among sites that differ in potential primary productivity and plant species diversity.

Modulating insect diversity through habitat modification from landscape-scale disturbance

In this study, grasshopper communities from North American tallgrass prairie responded strongly to effects of bison grazing and spring burning, results consistent with related studies (Evans 1984, 1988a, b, Fay 2003). Fire had its greatest impact on the taxonomic composition of grasshopper communities, whereas grazing more strongly influenced both overall species richness and evenness as well as actual species composition. Grasshopper community responses result primarily from indirect effects of disturbance from fire and grazing on habitat characteristics, including both plant species composition and resulting structural attributes of vegetation.

Fire and grazing caused strong and consistent responses affecting habit characteristics, which in turn

influenced insect community responses. Based on this study, habitat characteristics that maximize grasshopper diversity at Konza Prairie include spatially heterogeneous habitat with open structure, a wide range of food plants, heterogeneous structure that provides enemy-free space and a range of sites to facilitate thermoregulation, and plant tissue of high nutritional quality. Here, grasshopper species richness showed positive relationships with plant species richness and heterogeneity in canopy height, and negative relationships with average canopy height and grass biomass, which tend to homogenize habitats in this system (Collins et al. 1998, Knapp et al. 1998b, 1999). Similar responses were seen between density and the habitat attributes of grass biomass, average canopy height, and the CV of canopy height (Joern 2004).

Although grasshopper species richness varies with increased burn interval in ungrazed grassland in association with greater forb species richness (Evans 1984, 1988a, b), grazing apparently has a much stronger influence on grasshopper communities than burning at Konza Prairie. A similar result was found for plant species richness (Collins et al. 1998) at this site. Final grasshopper species richness, H', or evenness was little affected by burn frequency in this study. There is clear evidence that the underlying dynamics of fire effects are relevant for understanding variability of grasshopper communities in time and space as described by Evans (1984, 1988a, b), and in the obvious shift in taxonomic composition of grasshopper species assemblages.

Two complementary processes act to facilitate both increased overall population size and species richness—factors that affect the likelihood of local extinction and those that promote more species because of increased numbers of resources as expected in a heterogeneous habitat. Here, a positive relationship was observed between overall grasshopper density and species richness. While interpretations linking overall density and species richness are potentially tautological, the relationship suggests that factors favorable for supporting increased abundances of populations of individual species (thus increasing total grasshopper numbers) in turn contribute to increased local species richness as an independent assembly. This relationship is reinforced by an area effect influencing species richness. Without additional information, it is not known whether or not species interactions play an important role in determining species richness or patterns of species coexistence in this context. Results presented here are consistent with the idea that local conditions permit populations to achieve sufficient size to become self-sustaining rather than act as sink populations susceptible to repeated local extinction. In an independent assembly of species model, increased species richness then follows as more populations become self-sustainable because of a good match between habitat conditions and species needs.

The spatial extent of disturbance at landscape levels may often act to increase diversity of consumers (especially arthropods) at local scales, but interactions with disturbance may be necessary for landscape effects to operate. Area effects on species diversity are well known for many taxa (Rosenzweig 1995). Here, for example, no effect of watershed area on species richness was observed without disturbance from grazing, but was detectable when grazing was operating. In part, this may reflect responses of local populations and their ability to persist based on population size as indicated above. Extinction is more likely in small populations. Bison grazing treatments at Konza Prairie result in higher grasshopper abundance overall with positive consequences to almost all species (Joern 2004). As seen here, more species are found on average at sites that support higher overall grasshopper densities, and the accompanying evenness component of diversity is higher at these sites. This suggests that disturbance accompanying grazing redistributes the quality and quantity of resources to support increased population sizes of many species, which in turn leads to the buildup of greater species diversity.

As habitat conditions and resources diversify in response to fire and grazing, more taxa can coexist at the local scale. Variable grassland vegetation structure coupled to increased plant species richness increases the availability of both resources and suitability of conditions necessary to support a variety of grasshopper populations because of effects on individual grasshoppers and their habitat. Increased structural heterogeneity resulting from recent grazing leads to more open habitat structure and an increased number of potential food plant species. The generally higher degree of the evenness component associated with grazed sites that supports higher species richness shown here suggests the importance of this link. For example, increased evenness of vegetation in a plant community with the same species richness resulted in higher densities of spittlebug (Wilsey and Polley 2002).

Several plausible mechanisms that follow directly from the above analyses can lead to increased grasshopper species richness. (1) The strong positive relationship between insect herbivore species richness and plant species suggests that an increase in available food types increases the number of species that exist locally (Joern 1979, 1983, Lawton 1983), even in largely generalist forb-feeding grasshoppers. Increased insect species richness in many systems worldwide is typically associated with increased plant species richness (Otte 1976, Evans 1984, 1988b, Collinge et al. 2003, Gebeyehu and Samways 2003), heterogeneity in local vegetation structure (Anderson et al. 1979, Holmes et al. 1979, Bock and Bock 1991, Bergman and Chaplin 1992, WallisDeVries and Reamakers 2001, Kruess and Tscharntke 2002), and in some cases responses to disturbance corresponding to the availability of specific host plants needed by insect herbivores. (2) Insect pop-

ulations often respond dramatically to thermal characteristics of their habitats (Kemp 1986, Kemp and Onsager 1986, Coxwell and Bock 1995). Spatially heterogeneous habitat with much open microhabitat may facilitate thermoregulation by grasshoppers without exposing them to predators as much as in closed canopy habitats. Thermoregulation is important for many individual activities and is especially important for maintaining digestion efficiency and resource acquisition (Yang and Joern 1994a, b). (3) Food plant quality often varies directly in response to grazing and fire, from affects on nutrient cycling rates, redistribution of soil nutrients, leaf regrowth after loss to grazers, and stress effects from trampling and soil compaction on leaf quality (Frank and Evans 1997, Frank et al. 1998). Ultimately, increased food quality could have big effects on population abundances and facilitate retention of more species. (4) Altered habitat structure may also affect the availability of enemy-free space in some fashion that affects grasshopper species richness (Lawton 1979, Joern 2002). Combined, relationships such as these implicate the importance of landscape-level disturbance from large herbivores and fire for determining local patterns of species richness of important insect herbivores in grasslands. Future studies focusing on these underlying mechanisms will further reveal dynamic relationships explaining grasshopper species richness.

General significance

Results from this study are consistent with an emerging paradigm that emphasizes the importance of increasing disturbance and heterogeneity to promote biodiversity (Biondini et al. 1989, Huston 1994, Fuhlendorf and Engle 2001). Natural grassland drivers act to develop a disturbance hierarchy resulting in significant amounts of structural heterogeneity in units ranging from small-scale patches to large-scale landscapes. Fire influences bison grazing patterns, which in turn determine grassland structure and plant species richness (Vinton et al. 1993, Pfeiffer and Steuter 1994, Hartnett et al. 1996, 1997, van de Koppel et al. 1998), and recent grazing activities determine the extent and patchiness of subsequent burns. In this sense, diversity can beget diversity, although in an indirect fashion. Additional studies are needed to work out specific details of these responses. Nonetheless, it is clear that the same large-scale system drivers that result in increased plant species richness often alter habitats to facilitate arthropod existence and increase species diversity. In addition to providing insights into the nature of species interactions that promote diversity at the local scale, results of this study indicate the need to develop conservation management plans for grasslands that include arthropod diversity as a goal. Disturbances from fire and especially large mammalian grazing are essential for maintaining arthropod diversity, and vegetation responses to disturbances can be easily monitored to accomplish management goals.

Perhaps more important is the likelihood that results described here are general and reflect responses to disturbance and habitat heterogeneity in a variety of ecosystems worldwide (Huston 1994). The importance of habitat heterogeneity and disturbance is known for other organisms besides Orthoptera for grasslands as well as other systems (Wiens 1974, 1984, Lawton 1983, Tscharntke 1997, Crisp et al. 1998, Dennis et al. 1998, WallisDeVries et al. 1998, Kaspari 2000). The next challenge is to examine responses of consumers to disturbance in more systems to better understand how disturbance to vegetation works its way up food webs. Disturbance at large scales greatly influences local community assemblages.

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APPENDIX

A table showing average relative abundances of species considered in the study over sites in watersheds grazed by bison and sites in ungrazed watersheds is available in ESA's Electronic Data Archive: *Ecological Archives* E086-045-A1.