Insect Diversity in Two Burned and Grazed Grasslands

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ABSTRACT This study examined insect diversity in two native grassland ecosystems undergoing burning and grazing by bison and cattle, the Niobrara Valley Preserve (Nebraska) and the Tallgrass Prairie Preserve (Oklahoma). Sweep-sampling for insects was conducted during July 1994 and 1995 along transects in management units that were grazed by bison and partially burned, grazed by cattle and either burned (Tallgrass) or unburned (Niobrara), or ungrazed and unburned. At both sites, species richness (S) and diversity (log series α) were higher and similarity (Sorensen's index) lower for bison than for cattle or ungrazed management units. High bison management unit diversity was associated with significantly higher S and α in burned (Tallgrass) and unburned (Niobrara) portions of bison units compared with their respective cattle units, suggesting that habitat heterogeneity in terms of plant productivity, composition, and structure were higher in bison versus cattle and ungrazed management units. Replicated factorial experiments and sampling of additional taxa and time points are needed to verify how fire and grazing management impacts insect diversity in these grasslands.

KEY WORDS insects, fire, grazing, sandhills prairie, tallgrass prairie

THE INFLUENCE OF LAND use and management practices on insect diversity is an important issue in the ecology and conservation of grassland ecosystems. Insects can significantly impact net primary production and fluxes of nutrients and energy (Seastedt and Crossley 1984, Tscharntke and Greiler 1995, Carson and Root 1999, Callaham et al. 2000), and they interact with nearly all other grassland organisms, because of their abundance, species richness, life history attributes, and diverse functional roles (Miller 1993; Siemann et al. 1997, 1998; Redak 2000).

Fire and grazing were historically important in presettlement grasslands (Axelrod 1985), and are now major land use practices throughout the North American Central Plains (Collins and Wallace 1990). Fire and ungulate grazers including bison and cattle, are primary drivers of grassland plant composition and productivity (Owensby and Anderson 1967, Pfeiffer and Steuter 1994, Coppedge and Shaw 1998). For example, spring burning increases dominance by warm season C_4 grasses and reduces species richness and abundance of herbaceous dicots ('forbs'; Gibson and Hulbert 1987), while grazing reduces grass dominance, encourages higher forb diversity, and causes diversity-enhancing disturbances including trails, wallows, and nutrient patches (Hartnett et al. 1997, Coppedge and Shaw 1998).

The impacts of fire and grazing on insect diversity would be expected to parallel their impacts on plant communities (Nagel 1973, Hunter and Price 1992, Evans and Seastedt 1995). For example, spring burning should reduce insect diversity because of increased grass dominance and reduced forb diversity (Gibson and Hulbert 1987). In contrast, grazing should increase insect diversity in concert with higher forb diversity and more frequent disturbance (Coppedge and Shaw 1998). Bison and cattle may differ in the extent of their impacts on insect diversity, with bison potentially stimulating diversity more than cattle because of bison's stronger propensity toward consumption of dominant grasses (Hartnett et al. 1997).

This study examines patterns in insect species diversity in two native grassland preserves subjected to bison and cattle grazing and prescribed burning. Cattle are a major influence on grassland communities because most native grasslands are in commercial cattle production. Previous studies have questioned how bison or cattle differ in their impacts, which grazing species may be more appropriate for use in grassland management (Plumb and Dodd 1993), and whether fire is appropriate for preserve management from an insect perspective (Swengel 1998). Until recently, relatively few datasets were available to address these questions (Siemann et al. 1997, 1998; Haddad et al. 2001; Jonas et al. 2002).

Materials and Methods

Study Sites. Grassland insect communities were sampled at the Niobrara Valley Preserve, a 21,000 hectare mixed-grass prairie in Brown County, NE

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(42.7° N, 99.8° W), and at the Tallgrass Prairie Preserve, a 14,800 hectare tallgrass prairie in Osage County, OK (36.5° N, 96.2° W). Both sites are former commercial cattle ranches acquired by the Nature Conservancy and managed to preserve native grassland ecosystems by restoring fire and bison grazing. The vegetation at the Niobrara Valley Preserve is dominated by grasses including *Andropogon hallii, Schizachyrium scoparius, Stipa comata,* and *Panicum virgatum,* accompanied by a diverse group of forbs (Churchill et al. 1988). The Tallgrass Prairie Preserve is in the southern Flint Hills tallgrass prairie. Dominant grasses include *Andropogon gerardii, Schizachyrium scoparius, Panicum virgatum,* and *Sorghastrum nutans,* accompanied by a similarly diverse forb assemblage (Great Plains Flora Association 1986).

Both preserves are divided into three management units, one grazed by bison, a second grazed by cattle, and a third ungrazed/unburned unit. At the Tallgrass Preserve, bison were introduced in 1993 on a 2000 hectare area stocked at 1.2 AUM (animal unit months) ha^{-1} y^{-1}, with estimated consumption of 12.5% of annual aboveground net primary production. During this study cattle grazed from mid-April through mid-July on ≈9,000 hectares, at a stocking rate of 1.4 AUM ha^{-1}. Cattle grazing at Tallgrass before Nature Conservancy acquisition consisted of year-round cow-calf production and spring stocker cattle. Prescribed burning was conducted in both grazed management units beginning in 1993. Parts of the bison unit remained unburned or were burned in either spring, summer, or fall each year, without set boundaries, so that later burns partially overlapped earlier ones, creating a landscape-scale mosaic that mimicked presettlement fire patterns. The target fire return interval for a given parcel was 5 yr. In 1994, seven parcels burned for 450 hectares, and in 1995 eight parcels were burned totaling 440 hectares. The objective of prescribed burning in the cattle unit was maintenance of cattle forage quality, thus the entire unit was burned annually in spring (April). This is a typical management practice in the Flint Hills (Hulbert 1973).

Bison were reintroduced to the Niobrara Valley Preserve in fall of 1985, stocked year-round at 0.2 AUM ha^{-1} y^{-1}, or ≈25% consumption of annual ANPP. The cattle unit was stocked at 0.2 AUM ha^{-1} from May through October. Prescribed burning also was conducted in the Niobrara bison unit with the same objective as Tallgrass, with an average fire return interval of 7.5 yr, and ≈400 hectares burned in four parcels each year. The Niobrara cattle unit was not burned during this study, typical for Sandhills rangelands.

Insect Sampling. Insect communities were sweep-sampled during the last two weeks of July in 1994 and 1995 along 27 250 m transects at each preserve. Transects were placed randomly among the bison ($n = 12$ transects), cattle ($n = 12$), and ungrazed ($n = 3$) management units. Transects in the Tallgrass bison unit sometimes crossed burn boundaries, while Niobrara transects always fell within burned or unburned portions. Transects were randomly relocated within each management unit in the second year of sampling, maintaining the same number of transects per management unit.

Each transect consisted of five 5 m × 5 m plots spaced at 50 m intervals. Each plot was swept along a serpentine path so that the vegetation canopy throughout the entire plot was sampled. Sweeping was conducted at midday on cloud-free days with winds below 9 m s^{-1}. The material collected from each plot was individually bagged and kept on ice, then the sweeping sequence was repeated within 30 min of the first sampling, yielding two sweep samples per plot and 10 samples per transect. All samples were frozen for later sorting.

Insects were sorted to morphologically distinguishable species and counted. Morphospecies-level identification correlates strongly with taxonomic species counts (Oliver and Beattie 1996), and hereafter 'species' implies 'morphospecies.' Samples collected in 1994 were presorted to remove debris, and refrozen until final sorting. The 1995 samples were not presorted, but were passed through a #6 wire mesh sieve to separate debris from insects. Sievings were examined for insects. Certain taxa did not hold up well during collection and processing, notably spiders, aphids, and some Diptera. Also, some abundant grassland taxa were either not effectively sampled by sweeping or were not abundant during the sampling periods. Thus, the analysis is based on six orders consistently present across all management units at both sites. Voucher specimens were deposited in the Kansas State University Museum of Entomological and Prairie Arthropod Research.

Diversity Measures. Insect diversity was characterized by pooling the ten samples per transect and calculating species richness (S) and the log-series α. The α statistic was chosen because of its lack of sample size bias and insensitivity to the underlying species abundance distribution (Magurran 1988). Species similarity within management units was calculated for all pairwise combinations of transects within each management unit ($n = 66$ for bison and cattle, $n = 3$ for ungrazed) using the quantitative Sorensen's index (C_N), which measures transect-to-transect overlap in composition within each management unit. S, α, and C_N were also calculated with the samples pooled by plot. This allowed characterization of the burned and unburned portions within the bison management units.

Data Analysis. The study was based on sampling in the unreplicated management units. Thus, the objective of the analysis was to compare the management strategies applied to these units, using transect-level calculations of diversity measures, and to compare the burned and unburned portions of the bison units to each other and to the other units, using plot-level calculations of diversity measures. Tallgrass Preserve insect assemblages were analyzed separately from Niobrara assemblages because of site differences in climate, vegetation, and management, but the two sample years were analyzed together because the transects were randomly relocated in the second year and preliminary analysis suggest similar diversity re-

Table 1. Species richness (S) and abundance (n) of the major insect orders in sweep samples from the Tallgrass Prairie and Niobrara Valley Preserves, July 1994 and 1995

	Tallgrass prairie				Niobrara valley				Total	
	1994		1995		1994		1995			
	S	n	S	n	S	n	S	n	S	n
Coleoptera	70	439	104	1,545	54	598	126	5,203	206	7,785
Hymenoptera	75	926	71	1,215	75	1,454	135	2,457	186	6,052
Diptera	55	755	67	1,125	45	335	72	424	122	2,639
Homoptera	47	2,304	58	4,678	54	2,797	91	4,846	116	14,625
Hemiptera	31	142	49	795	39	313	78	1,230	101	2,480
Orthoptera	27	1,182	22	186	30	935	21	164	46	2,467
Other[a]	10	59	8	48	13	153	20	161	29	421
Total	315	5,807	379	9,592	310	6,585	543	14,485	806	36,469

[a] Other orders encountered rarely in the samples: Ephemeroptera, Lepidoptera, Mantodea, Neuroptera, Odonata, Phasmida, Thysaneura.

sponses in both years. Statistical comparison of S, α, and C_N were conducted using one-way analysis of variance (ANOVA) (Proc GLM; SAS Institute Inc 2000) with transect as the observational unit for management unit (bison[b+ub], cattle[b] or [ub], ungrazed[ub]) comparisons, and plot as the observational unit when separating the bison units into bison[b] and bison[ub] portions. Means separations were based on Bonferroni-adjusted *t*-tests among all possible pairwise means comparisons.

Results

Sampling yielded nearly 36,500 insects representing 806 species from 15 orders for the two sites combined (Table 1). Sampling efficiency estimated from species accumulation curves averaged ≈82% (data not shown). 95% sampling efficiency would have required 5 to 10 more samples per transect. Over 95% of the species encountered belonged to Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, and Orthoptera, with Coleoptera and Hymenoptera consistently the most speciose, and Homoptera (primarily Cicadellidae) and Hymenoptera (Formicidae) consistently the most abundant.

Transects in the Tallgrass bison[b+ub] unit had the highest S ($F_{2,51}$ = 3.37, P = 0.0422; Fig. 1A) and α values ($F_{2,51}$ = 11.53, P = 0.0001; Fig. 1B). Cattle[b] transects had intermediate S and the lowest α values, while the ungrazed[ub] transects had the lowest S and intermediate α. The bison[b+ub] transects had the lowest C_N ($F_{2,267}$ = 26.99, $P < 0.0001$; Fig. 1C), while cattle[b] and ungrazed[ub] transects had higher and nearly equal C_N.

The Niobrara bison[b+ub] transects also had the highest S ($F_{2,51}$ = 3.17, P = 0.0504; Fig. 1D) and α ($F_{2,51}$ = 4.50, P = 0.0159; Fig. 1E), with ungrazed[ub] transects intermediate, and cattle[ub] transects lowest. C_N was lowest for bison[b+ub] transects, intermediate for cattle[ub], and markedly higher in ungrazed[ub] ($F_{2,267}$ = 29.68, $P < 0.0001$; Fig. 1E).

When the Tallgrass bison unit was reanalyzed by plot to separate the burned and unburned portions, the bison[b] plots had higher S than cattle[b], bison[ub], or ungrazed[ub] plots ($F_{3,259}$ = 18.96, P = 0.0001; Fig. 2A). α in bison[b] and bison[ub] plots was

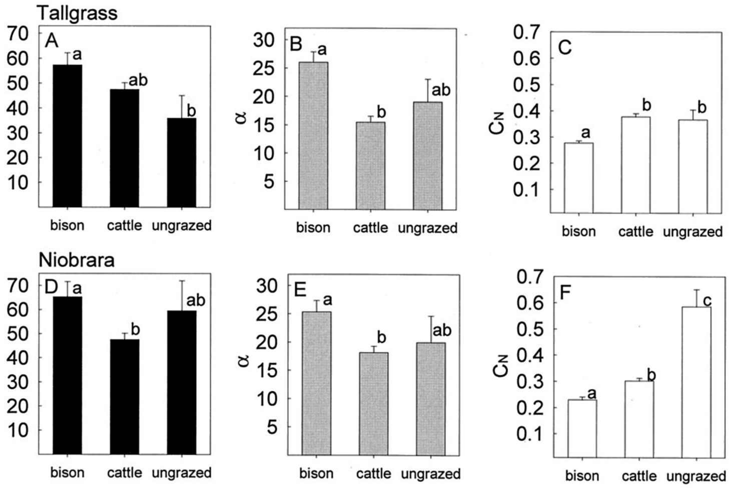

Fig. 1. Insect species richness (S, mean number of species per transect), species diversity (log series α), and within-management unit similarity (C_N, quantitative Sorensen's index) for management unit transects at the Tallgrass Prairie (Oklahoma) and Niobrara Valley (Nebraska) preserves. Letters denote significant differences among means.

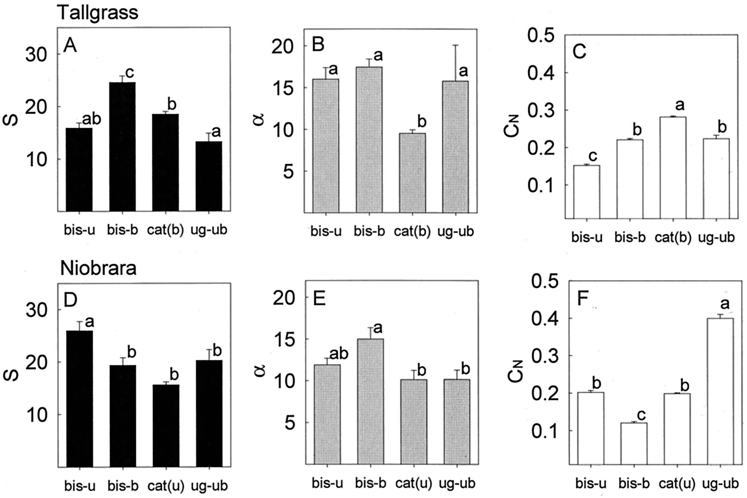

Fig. 2. Diversity indices for management unit sample plots at Tallgrass and Niobrara. Means ± 1 SE. S, α, C_N, and means separations as in Fig. 1.

higher than in cattle[b] plots, but equal to ungrazed[ub] plots ($F_{3,259} = 12.15$, $P = 0.0001$; Fig. 2B). Bison[ub] plots had the lowest C_N, bison[b] and ungrazed[ub] were intermediate, and cattle[b] plots highest ($F_{3,5522} = 286.62$, $P < 0.0001$; Fig. 2C).

At Niobrara, S was highest in bison[ub] plots ($F_{3,258} = 14.36$, $P = 0.0001$; Fig. 2D). α values were highest for bison[b], intermediate in bison[ub], and lowest in cattle[ub] and ungrazed[ub] plots ($F_{3,258} = 3.20$, $P = 0.0239$; Fig. 2E). C_N was lowest for bison[b], intermediate for bison[ub] and cattle[ub], and highest in ungrazed[ub] ($F_{3,5389} = 267.21$, $P < 0.0001$; Fig. 2F).

Discussion

This analysis found both sites to have higher S and α, and lower C_N on bison management unit transects compared with cattle and ungrazed units. Both bison units underwent the same burning protocol of partial, overlapping burns, creating a mosaic of habitat patches differing in frequency, season, and time since last burning. This likely created a more heterogeneous landscape in terms of plant productivity, composition, structure, and microclimate than cattle and ungrazed management units, which experienced uniform application or withholding of fire. Bison units always contained the most diverse sample plots (Fig. 2) in terms of S, α, and C_N, and these high diversity plots were likely responsible for the high overall bison unit diversity.

There was also evidence suggesting that high bison unit diversity was in part caused by bison grazing per *se*. Bison unit plots always had greater S and α than cattle unit plots when both were burned (at Tallgrass) and when both were unburned (at Niobrara; Fig. 2). At Tallgrass, the bison[b]-cattle[b] comparison is confounded by varying fire season in the bison unit, versus spring burning in the cattle unit. However, the comparison was not confounded under unburned conditions at Niobrara. The only evidence that cattle per se increased insect diversity was seen at Niobrara, where C_N in cattle[u] was substantially less than in ungrazed[u] (Fig. 2F), suggesting greater compositional variability among cattle[u] plots. The lack of evidence for cattle effects may reflect the shorter duration of cattle grazing compared with year-round bison grazing.

Within the bison units, fire had opposite effects on insect species richness and similarity between the two sites (Fig. 2), with greater S and C_N in burned portions of the Tallgrass bison unit, but lower S and C_N in burned portions of the Niobrara bison unit. Bison preferentially graze burned areas over unburned (Hartnett et al. 1997), and Niobrara bison had a higher stocking rate than Tallgrass bison. Thus, lower Niobrara bison[b] richness might result from relatively greater bison grazing pressure in burned patches, and higher Tallgrass bison[b] insect richness from relatively lighter bison grazing pressure.

Fire and grazing alter several aspects of insect habitat quality. Increased forb diversity after grazing likely results in more host plant species for herbivorous and host-specialized taxa. Grazing also increases N availability to specialist and generalist insects by increasing the availability of N to the vegetation (Blair et al. 1998). N is an important limiting resource, especially for herbivore taxa (Mattson 1980, Prestidge and McNeill 1983). In contrast, burning reduces plant species richness (Gibson and Hulbert 1987) and alters grazing patterns, increasing spatial heterogeneity in vegetation composition, quality, and probability of future fire and grazing (Hartnett et al. 1997, Coppedge and Shaw 1998). This likely leads to habitat patches within a management unit supporting relatively dissimilar insect assemblages, increasing overall management unit diversity. Several studies have linked these ecosystem traits with insect diversity (Murdoch et al.

1972, Root 1973, Evans 1988, Knops et al. 1999, Haddad et al. 2001, Jonas et al. 2002).

While these results reflect general trends in the assemblage sampled in this study, individual taxa are likely to show varying responses to management practices (Warren et al. 1987, Anderson et al. 1989). For example, Coleopteran and Orthopteran families showed contrasting diversity responses among old-field versus native prairie land-use types (Jonas et al. 2002). Fire and grazing can also cause direct mortality in some groups (Hayes 1927, Fay and Samenus 1993), especially internal feeders, whereas more vagile forms may avoid direct impacts.

Several factors limit the generalizations that can be drawn from this analysis. This study lacked true replication of the management units, and inherent site differences in vegetation, climate, soils, land use history, stocking rate, and fire season precluded direct statistical comparison of the sites. However, extensive sampling was conducted on widely separated transects, which were relocated for the second sampling, providing adequate representation of the management units. Additional sampling periods would give a more complete assessment of the canopy assemblage. Also, sampling of other faunal components such as detritivores, soil fauna, and species of conservation interest would broaden the interpretation of fire and grazing impact on insect diversity in these systems.

Conclusions

Management units at these two sites significantly differed in the diversity of their insect assemblages, with higher insect richness and diversity at both sites in management units grazed by bison in combination with a temporal and spatial mosaic of prescribed burning. Future studies should assess whether cattle combined with a similar mosaic of burns would produce similar levels of diversity as with bison. Additional replicated factorial experiments involving cattle, bison, and fire will also refine our understanding of the effects of these widespread grassland management practices on insect diversity.

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References Cited

Anderson, R. C., T. Leahy, and S. S. Dhillion. 1989. Numbers and biomass of selected insect groups on burned and unburned sand prairie. Am. Midl. Nat. 122: 151–162.

Axelrod, D. I. 1985. Rise of the grassland biome, central North America. Bot. Rev. 51: 163–201.

Blair, J. M., T. R. Seastedt, C. W. Rice, and R. A. Ramundo. 1998. Terrestrial Nutrient Cycling in Tallgrass Prairie, pp. 222–243. *In* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins [eds.], Grassl. Dynamics: Long-term Ecological Research in Tallgrass Prairie. Oxford University Press, New York.

Callaham, M. A., Jr., M. R. Whiles, C. K. Meyer, and B. L. Brock. 2000. Feeding ecology and emergence production of annual cicadas (Homoptera: Cicadadae) in tallgrass prairie. Oecologia (Berl.). 123: 535–542.

Carson, W. P., and R. B. Root. 1999. Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. Oecologia (Berl.). 121: 260–272.

Churchill, S. P., C. C. Freeman, and G. E. Kantak. 1988. The vascular flora of the Niobrara Valley Preserve and adjacent areas in Nebraska. Trans. Nebr. Acad. Sci. 16: 1–16.

Collins, S. L., and L. L. Wallace. 1990. Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman, OK.

Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. J. Range Manage. 51: 258–264.

Evans, E. W. 1988. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie. Can. J. Zool. 66: 1495–1501.

Evans, E. W., and T. R. Seastedt. 1995. The relations of phytophagous invertebrates and rangeland plants, pp. 580–634. *In* D. J. Bedunah and R. E. Sosebee [eds.], Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO.

Fay, P. A., and R. J. Samenus. 1993. Gall wasp (Hymenoptera: Cynipidae) mortality in a spring tallgrass prairie fire. Environ. Entomol. 22: 1333–1337.

Gibson, D. J., and L. C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72: 175–186.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence, KS.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. Knops. 2001. Contrasting effects of plant richness and compositionon insect communities: a field experiment. Am. Nat. 158: 17–35.

Hartnett, D. C., A. A. Steuter, and K. R. Hickman. 1997. Comparative ecology of native and introduced ungulates, pp. 72–101. *In* F. L. Knopf and F. B. Samson [eds.], Ecology and conservation of Great Plains vertebrates. Springer, New York.

Hayes, W. P. 1927. Prairie insects. Ecology 8: 486–492.

Hulbert, L. C. 1973. Management of Konza Prairie to approximate pre-white-man fire influences, pp. 14–17. *In* Proceedings, Third Midwest Prairie Conference, 22 September 1972, Manhattan, KS. Kansas State University, Manhattan, KS.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724–732.

Jonas, J. L., M. R. Whiles, and R. E. Charlton. 2002. Aboveground invertebrate responses to land management differences in a central Kansas grassland. Environ. Entomol. 61:1142–1152.

Knops, J., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. Ritchie, K. M. Howe, P. Reich, E. Siemann, and J. Groth. 1999. Effets of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol. Lett. 2: 286–293.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annu. Rev. Ecol. Sys. 11: 119–161.

Miller, J. C. 1993. Insect natural history, multispecies interactions and biodiversity in ecosystems. Biodiv. Consv. 2: 233–241.

Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and pattern in plants and insects. Ecology 53: 819–829.

Nagel, H. 1973. Effect of spring prairie burning on herbivorous and non-herbivorous arthropod populations. J. Kans. Entomol. Soc. 46: 485–496.

Oliver, I., and A. J. Beattie. 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. Ecol. Applic. 6: 594–607.

Owensby, C. E., and K. L. Anderson. 1967. Yield responses to time of burning in the Kansas Flint Hills. J. Range Manage. 20: 12–16.

Pfeiffer, K. E., and A. A. Steuter. 1994. Preliminary response of Sandhills prairie to fire and bison grazing. J. Range Manage. 47: 395–397.

Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecol. Applic. 3: 631–643.

Prestidge, R. A. and S. McNeill. 1983. The role of nitrogen in the ecology of grassland Auchenorryncha, pp. 257–281. *In* J. A. Lee, S. McNeill, and I. H. Rorison [eds.], Nitrogen as an ecological factor. Blackwell, Oxford, United Kingdom.

Redak, R. A. 2000. Arthropods and multispecies habitat conservation plans: are we missing something? Environ. Manage. 26:-S107.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol. Monogr. 43: 95–124.

SAS Institute. 2000. The SAS System for Windows, 8.01. SAS Institute, Cary, NC.

Seastedt, T. R., and D. A. Crossley. 1984. The influence of arthropods on ecosystems. Bioscience 34: 157–161.

Siemann, E., J. Haarstad, and D. Tilman. 1997. Short-term and long-term effects of burning on oak savanna arthropods. Am. Midl. Nat. 137: 349–361.

Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. Am. Nat. 152: 738–750.

Swengel, A. B. 1998. Effects of management on butterfly abundance in tallgrass prairie and pine barrens. Biol. Consv. 83: 77–89.

Tscharntke, T., and H. J. Greiler. 1995. Insect communities, grasses, and grasslands. Annu. Rev. Entomol. 40: 535–558.

Warren, S. D., C. J. Scifres, and P. D. Teel. 1987. Response of grassland arthropods to burning: a review. Agric. Ecosys. Environ. 19: 105–130.

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