

Aboveground Invertebrate Responses to Land Management Differences in a Central Kansas Grassland

JAYNE L. JONAS,¹ MATT R. WHILES,² AND RALPH E. CHARLTON

Kansas State University, Department of Entomology, 123 West Waters Hall, Manhattan, KS 66502

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ABSTRACT Macroinvertebrate communities in a central Kansas grassland were examined to assess their responses to differences in land management and explore their viability for biological assessment of grasslands. Canopy (drop-trap) and ground-dwelling (pitfall traps) communities were quantitatively sampled from June–September 1998 and 1999. The responses of the whole arthropod community and two focal groups, Coleopteran families and Orthopteran species, to three land use types (brome fields, old fields, and native prairies) were examined. Vegetation analyses reflected clear differences among land use types. *Bromus inermis* Leyss, an exotic grass, and *Andropogon gerardii* Vitman, a native grass, dominated brome fields and native prairie sites, respectively. Old fields were composed of a mixture of native and exotic plant species. Coleopteran family richness and diversity were significantly greater in native prairies than brome fields ($P < 0.05$), whereas orthopteran species richness and diversity peaked in brome fields. Diversity and richness of all arthropod groups examined were significantly, positively correlated with plant species diversity and richness in drop-trap samples ($P < 0.05$). Coleopteran family diversity and richness in pitfall samples were positively correlated with abundance of native plants, but orthopteran species diversity and richness were negatively correlated with native plant abundance. Coleopteran and orthopteran responses to land use appeared linked to differences in management practices. Whereas coleopterans appeared most influenced by plant community composition, orthopterans showed sensitivity to mechanical disturbance associated with haying on native prairie. Plant and arthropod group diversities were not consistently correlated, demonstrating that arthropod groups can reflect differences in a landscape that may not be apparent from examining plant communities alone.

KEY WORDS Coleoptera, Orthoptera, biological assessment, indicator species

BIOLOGICAL ASSESSMENT AND long-term monitoring programs have been developed by various agencies worldwide in response to an awareness of the adverse economic and ecological effects of habitat degradation (Crisp et al. 1998, Dickinson et al. 1998). Most terrestrial bioassessment programs are designed to assess ecological integrity of ecosystems and generally focus on plant or vertebrate groups. In freshwater systems, invertebrates have proved to be a valuable assessment tool and are widely used in biomonitoring programs (e.g., Hilsenhoff 1987, 1988; Barbour et al. 1999), but the use of invertebrate groups in terrestrial monitoring programs has progressed slowly (Kemp et al. 1990). However, there have been recent developments in the use of a variety of invertebrate groups for biomonitoring, including tiger beetles (Rodriguez et al. 1998), Lepidoptera (Erhardt and Thomas 1991),

soil-dwelling Diptera (Frouz 1999), and terrestrial snails (de Vaulfeyry and Pihan 2000).

Management practices that target vertebrate diversity at a regional scale can also benefit invertebrates, but there is also evidence that some forms of habitat degradation and fragmentation may negatively impact invertebrates without producing a marked effect on vertebrate assemblages (Murphy and Wilcox 1986, Kemp et al. 1990, Oliver and Beattie 1993, New 1997). For example, Murphy and Wilcox (1986) found that butterfly diversity on habitat "islands" in the Great Basin Desert was more sensitive to local fragmentation than bird diversity, even though the regional diversity patterns of both groups were correlated. Although Odum (1971) cautioned against the use of small organisms as ecological indicators because of their dynamic life cycles, Landres et al. (1988) argued that smaller organisms might be most appropriate for assessing small-scale and/or short-term disturbances. In agreement, Burke and Goulet (1998), in a study of forest-restricted beetles in Ontario, showed that insects, with their smaller area requirements, are more

¹ Present address: the Nature Conservancy, P.O. Box 1745, North Platte, NE 69101.

² Present address: Department of Zoology, Southern Illinois University, Carbondale, IL 62901–6501 (e-mail: mwiles@zoology.siu.edu).

likely to reflect effects of isolation and fragmentation than are birds or large mammals.

Invertebrate community diversity and dynamics are often tightly linked to plant communities. Although studies by Murdoch et al. (1972) and Knops et al. (1999) indicated that there is a positive correlation between plant and insect species richness, Oliver and Beattie (1993) asserted that invertebrates should be emphasized as much as plants and vertebrates in biodiversity assessment programs because of their abundance, diversity, and virtual omnipresence. Furthermore, the incorporation of invertebrate groups into assessment programs can enhance sensitivity at smaller spatial and temporal scales (Landres et al. 1988, Kremen et al. 1993). For example, changes in the habitat structure of European grasslands resulted in a decrease in the abundance of diurnal lepidopterans before noticeable changes in host plant communities (Erhardt and Thomas 1991).

Invertebrate diversity is often related to plant species diversity, structural diversity, patch size, and density (e.g., Smith et al. 1985, Tscharncke and Greiler 1995). However, specific mechanisms underlying these patterns are often difficult to identify, and it is not always evident whether insect species richness depends more on taxonomic composition or the physical structure of the plant community. The habitat heterogeneity hypothesis (Hart and Horowitz 1991) predicts that arthropod richness should be greater where there is higher structural heterogeneity in the form and species of vegetation present (Evans 1988, Tscharncke and Greiler 1995, Dennis et al. 1998).

The overwhelming abundance and diversity of arthropods, as well as the taxonomic instability of some groups, has limited development of assessment programs that include invertebrate communities (New 1997). This limitation can be overcome by focusing on a restricted suite of invertebrate groups. The Coleoptera and Orthoptera are two groups that are likely candidates for grassland monitoring programs. Orthopterans are present in almost all grassland habitats, accounting for a large proportion of arthropod biomass, and they can reach densities capable of devastating agricultural crops (Smith et al. 1985, Tscharncke and Greiler 1995, Baldi and Kisbenedek 1997). Coleopterans are a very speciose group, constituting approximately one-third of all known animal species (May 1978). Coleopterans influence, and are influenced by, their environment in numerous ways, having varied and complex feeding patterns, daily and seasonal activity patterns, and flight capabilities (Arnett 1968, White 1983, Borror et al. 1989). Furthermore, some coleopterans have declined with increasing human impacts on their habitats. For example, the American burying beetle, *Nicrophorus americanus* Oliver, is now a federally endangered species (USFWS 1991).

The overall objective of this research was to examine the responses of invertebrates to different land management practices in a Great Plains grassland system. In doing so, we also assessed the viability of using invertebrate communities in this region for biological

assessment and compared two commonly used sampling methods, drop-traps and pitfall traps. We explored patterns by examining plant communities and the entire aboveground macroinvertebrate community at a broad taxonomic level, as well as focusing on the Coleoptera and Orthoptera at finer taxonomic scales. In addition, we examined specific relationships between invertebrate groups and plant community composition. We hypothesized that invertebrates, as a whole community and at finer levels of taxonomic resolution, would respond predictably and similarly to the gradient of conditions available and that this response would be linked to changes in plant communities resulting from past and current management practices. Specifically, we predicted that invertebrate diversity would be positively correlated with the abundance of native plants.

Materials and Methods

Study Site. This study was conducted on a 1,411-ha tract of land that is operated by the Kansas Army National Guard as the Smoky Hills Army National Guard Training Facility (SHTF) (ANGCR 1997). This site is located at 38° 47' N, 97° 45' W, in Saline County, KS. The property lies on the eastern edge of the Smoky Hills physiographic province of the dissected High Plains and is composed of a mixture of tallgrass and mixed-grass prairie (Jonas 2000). The region has a continental climate with mean daily temperatures ranging from 0.14°C in winter to 27°C in summer. The bulk of annual precipitation (≈ 80 cm/yr average) falls between April and September.

Roughly 75% of the Army range was leased for haying, which occurred between 1 July and 15 August during each study year. A 324-ha portion ($\sim 24\%$) was designated as live fire impact area, and 1% was planted wildlife food plots (ANGCR 1997). Military uses of the land include short-range weapons training, bivouac, light infantry-training exercises, and tracked vehicle maneuvering. Tracked vehicle exercises are limited to a quarter section of the property and did not affect transects.

Portions of the range were planted with *Bromus inermis* Leys. in the mid 1970s. In 1996, the entire range received aerial application of Tordon*22K (Picloram; Dow Agro Sciences LLC, Indianapolis) at a rate of 0.057 liters active ingredient per acre to control the noxious weeds *Carduus nutans* L., and *Convolvulus arvensis* L.

Transect Establishment. Using land cover maps derived from Landsat Thematic Mapper images and visual surveys, the SHTF facility was divided into three broad categories of land use: native prairie, brome, and old field sites. Prairies were dominated by native vegetation and were hayed annually, whereas brome sites were hayed only occasionally and were dominated by exotic plants. Old fields were relatively undisturbed (not hayed), composed of a mixture of native and exotic plants, exhibited high aboveground plant biomass, and had a thick litter layer. Transects were established in areas that were representative of each

land use type and were located at least 25 m away from edges and roads. Within these areas, three 100-m line transects were randomly established in each land use type (Jonas 2000).

Vegetation Sampling. Vegetation was sampled at each transect using the step-point technique (Owensby 1973). One hundred random points were sampled within a 10 × 100 m area that was bisected by the transect line. For this technique, the plant closest to the nose pin on a sampling frame is identified and recorded at each point. Sampling occurred during late October–early November 1998, and in September 1999.

Invertebrate Sampling. Invertebrates were sampled using two collecting methods, a drop-trap and pitfall trap arrays, during the middle of each month from June–September 1998 and 1999. For the drop-trap, three randomly selected locations were sampled along each transect between 1000 and 1500 hours CST. The drop-trap consisted of a 0.25-m² plastic cylinder (≈0.5 m tall) with 0.5-mm mesh cloth covering the top to prevent arthropod escape. Two 6-m poles were used to suspend the trap so that it could be carried overhead between two people, thus minimizing disturbance to the sample area. The trap was quickly dropped and secured to avoid escape of invertebrates between the soil surface and trap bottom. The abundance of large and small invertebrate taxa in samples indicated that this technique was relatively efficient. A 24-cc gasoline powered blow-vac (model 358.797931, Craftsman, Hoffman Estates, IL), with a collecting bag secured in the intake tube, was inserted in the drop-trap through a slit in the mesh covering, and the vegetation and soil surface inside the trap were thoroughly vacuumed. The contents of the collection bag were then emptied into a plastic bag, placed on ice in the field, and frozen upon return to the laboratory.

For pitfall traps, five traps were set 5 m off of the transect line at the 10, 30, 50, 70, and 90 m points. Plastic cups (11 cm diameter × 14 cm depth) were placed in the ground so that the lip of the cup was flush with the soil surface. Traps were filled with 75% ethanol, and ≈75 ml of mineral oil was added to reduce evaporation. After 48 h, traps were collected and taken back to the laboratory where invertebrates were removed and placed in vials of fresh 85% ethanol.

In the laboratory, invertebrates were sorted into taxonomic groups, and all insects were identified to order using Borror et al. (1989). Identification of coleopteran families was based on Arnett (1968), White (1983), Borror et al. (1989), and the Kansas State University Museum of Entomological and Prairie Arthropod Research (KSU-MEPAR) collection. Hebard (1936), Coppock (1962), Blecha (1974), Otte (1981, 1984), Helfer (1987), and the KSU-MEPAR collection were used for Acrididae and adult Tetrigidae species identifications. Tettigoniidae and Gryllidae were identified as morphospecies because of the lack of adequate nymphal taxonomic keys. It has been shown that this approach can have an 86% correspondence to formal species identifications (Oliver and Beattie 1993). Noninsects were identified to the low-

Table 1. Plant species that ranked in the top five in abundance in brome ($n = 3$), old field ($n = 3$), or native prairie ($n = 3$) sites during 1998 and 1999 at Smoky Hills Training Facility

Plant species	Origin	Brome	Old field	Prairie
<i>Agrostis stolonifera</i> L.	Introduced	3 (3)	—	0.2 (0.2)
<i>Andropogon gerardii</i> Vitman	Native	0.2 (0.2)	13 (5)	57 (5)
<i>Aristida oligantha</i> Michaux	Native	8 (5)	—	1 (1)
<i>Bouteloua curtipendula</i> (Michaux) Torrey	Native	—	—	7 (3)
<i>Bromus inermis</i> Leyss.	Introduced	57 (10)	0.3 (0.2)	0.3 (0.3)
<i>Carex</i> spp.	Native	3 (1)	6 (2)	0.8 (0.4)
<i>Dichanthelium oligosanthos</i> (J.A. Schultes) Gould var. <i>scribnerianum</i> (Nash) Gould	Native	3 (1)	3 (1)	4 (1)
<i>Poa pratensis</i> L.	Introduced	3 (2)	23 (8)	2 (2)
<i>Schizachyrium scoparium</i> (Michaux) Nash	Native	2 (1)	5 (2)	17 (7)
<i>Sorghastrum nutans</i> (L.) Nash	Native	0.2 (0.2)	14 (4)	2 (1)
<i>Sporobolus asper</i> (Michaux) Kunth	Native	8 (3)	15 (5)	—

Values are average percent composition (± 1 SE).

est practical taxonomic unit. Coleoptera and Orthoptera voucher specimens were deposited at KSU-MEPAR (voucher collection 124).

Statistical Analyses. Shannon diversity (H'), richness (s), and abundance of plants, invertebrates, coleopteran families, and orthopteran species were calculated for each land use type ($n = 3$ of each) and analyzed with repeated measures analysis of variance (ANOVA) (PROC MIXED, SAS Institute 1996). Abundance of invertebrates from drop-trap samples was calculated as number of individuals per m², and abundance from pitfall samples was calculated as number of individuals per five traps. Where ANOVA tests for fixed effects were significant, the least square means procedure was used to examine relationships between individual means ($\alpha = 0.05$). Correlation analyses were used to examine relationships between invertebrate and plant communities. Because of the inherent variability associated with arthropods in the field, and the low number of replicates available for each land use type, we used an a priori alpha level of 0.10 for correlation analyses.

Results

Plant Communities. A total of 36 plant species were identified on transects at SHTF during 1998 and 1999. The dominant species in brome sites was *B. inermis* ($57 \pm 10\%$, mean \pm SE), whereas old fields were mostly composed of *Poa pratensis* L. ($23 \pm 8\%$) (Table 1). *Andropogon gerardii* Vitman ($57 \pm 5\%$) was the most common species in prairie sites (Table 1). Brome transects were considered biologically disturbed because they had a high proportion of introduced plant species. There were no species found exclusively in brome or old field sites, but *Bouteloua curtipendula* (Michaux) Torrey, a native grass, was unique to prairie

sites. Forb species accounted for 11 (± 9)%, 15 (± 11)%, and seven (± 3)% of plants identified in brome, old field, and prairie sites, respectively. Woody species were absent from brome fields, but were present in small numbers in old field ($0.3 \pm 0\%$; *Symphoricarpos orbiculatus* Moench and *Rosa arkansana* Porter) and prairie ($0.5 \pm 0.5\%$; *R. arkansana*) sites.

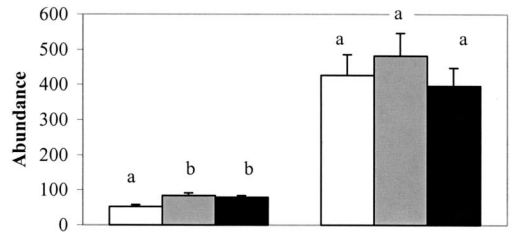
Patterns in plant species richness, Shannon diversity, and native species abundance were similar between 1998 and 1999. Over the course of the two years, there were no significant differences in Shannon diversity among brome, old field, or prairie sites ($F = 2.85$; $df = 2,6$; $P = 0.13$). However, old field sites had significantly higher plant species richness than brome or prairie sites ($F = 5.60$; $df = 2,6$; $P = 0.04$); whereas native species abundance was significantly lower at brome sites compared with old-fields and significantly higher at prairie sites compared with old fields ($F = 10.28$; $df = 2,6$; $P = 0.01$).

Invertebrate Communities. A total of 30,955 individual invertebrates were collected between June and September 1998 and 1999 in pitfall samples, and this was significantly greater than the number collected in drop-trap samples (3,875 individuals) during the same period ($F = 100.34$; $df = 1,24$; $P < 0.0001$). Pitfall trapping also resulted in significantly greater ordinal richness ($F = 672.89$; $df = 1,24$; $P = 0.0001$) and diversity ($F = 20.61$; $df = 1,24$; $P = 0.0001$), coleopteran family richness ($F = 222.01$; $df = 1,24$; $P = 0.0001$) and diversity ($F = 183.85$; $df = 1,24$; $P = 0.0001$), and orthopteran species richness ($F = 255.97$; $df = 1,24$; $P = 0.0001$) and diversity ($F = 246.45$; $df = 1,24$; $P = 0.0001$) compared with drop-trap sampling.

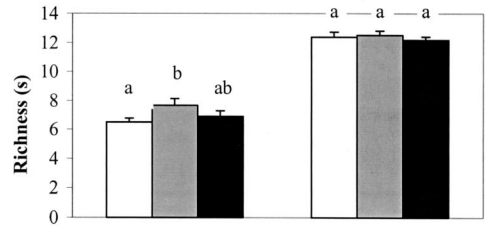
Twenty-six invertebrate orders/groups were collected from combined drop-trap and pitfall samples during the study period. Pseudoscorpiones, Diplura, and Isoptera were found only in brome sites, while Microcoryphia were only in old fields. There were no orders unique to native prairie sites. Invertebrate abundance ($F = 11.10$; $df = 2,12$; $P = 0.01$) and richness ($F = 3.75$; $df = 2,12$; $P = 0.05$) values from drop-traps were higher in old fields than brome fields (Fig. 1 A and B). Drop-trap samples from prairie sites also harbored significantly greater abundance of invertebrates than brome fields ($F = 11.10$; $df = 2,12$; $P = 0.01$), but richness in prairie site drop-traps did not differ from old field or brome sites. Pitfall trap invertebrate abundance ($F = 0.89$; $df = 2,12$; $P = 0.44$) and richness ($F = 0.86$; $df = 2,12$; $P = 0.45$) did not differ significantly with land use, and Shannon diversity from drop-traps ($F = 1.73$; $df = 2,12$; $P = 0.22$) or pitfall traps ($F = 1.01$; $df = 2,12$; $P = 0.39$) did not differ among land use types (Fig. 1).

Coleopteran Families. Forty coleopteran families were collected from drop-trap and pitfall trap samples in 1998 and 1999 (Table 2). Abundance ($F = 6.87$; $df = 2,12$; $P = 0.01$) and richness ($F = 12.21$; $df = 2,12$; $P = 0.001$) of coleopterans collected in drop-trap samples was greater in old field and native prairie land use types than in brome fields (Fig. 2 A and B). Although coleopteran abundance ($F = 10.35$; $df = 2,12$; $P = 0.002$) from pitfall samples was greatest in brome

A. Total invertebrate abundance



B. Ordinal richness



C. Ordinal diversity

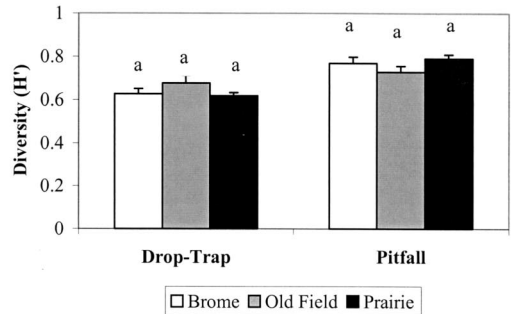


Fig. 1. Mean \pm 1 SE (A) total abundance, (B) ordinal richness, and (C) ordinal diversity (H') from drop-trap and pitfall samples in brome, old field, and prairie ($n = 3$ for all sites at Smoky Hills Training Facility during 1998 and 1999. Drop-trap abundance is given as no. of individuals per m^2 and abundance from pitfall traps is expressed as number of individuals per five pitfalls. Bars with different letters are significantly different ($P < 0.05$).

fields, Shannon diversity ($F = 4.67$; $df = 2,12$; $P = 0.03$) was significantly lower in brome fields compared with native prairie or old field sites (Fig. 2C).

Orthopteran Species. There were 27 species of acridids, and one species each of Gryllacrididae, Tetrigidae, and Tridactylidae identified from combined pitfall and drop-trap samples taken in 1998 and 1999. Fourteen Gryllidae and 15 Tettigoniidae morphospecies were also collected (Table 3). Drop-trap samples did not show any differences in abundance ($F = 1.98$; $df = 2,12$; $P = 0.18$) or Shannon diversity ($F = 2.09$; $df = 2,12$; $P = 0.21$) among land use types (Fig. 3 A and C). However, orthopteran species richness in drop-traps ($F = 4.04$; $df = 2,12$; $P = 0.05$) was significantly greater in brome and old field sites than native prairie

Table 2. Total number of Coleoptera collected in pitfall (360 traps) and drop-trap (216 traps) samples in brome, old field, and prairie sites at Smoky Hills Training Facility during 1998 and 1999

Feeding group/family	Pitfall traps			Drop-traps		
	Brome	Old Field	Prairie	Brome	Old Field	Prairie
Phytophagous						
Scarabaeidae	921	17	109	0	0	1
Anthracidae	124	118	28	0	7	2
Elateridae	61	55	41	2	3	2
Buprestidae	10	10	9	—	—	—
Phalacridae ^a	0	0	1	0	8	8
Bruchidae ^a	—	—	—	0	1	0
Chrysomelidae	52	22	31	10	9	18
Cerambycidae	0	0	2	0	0	1
Apionidae ^b	—	—	—	0	0	1
Curculionidae	4	9	5	1	14	6
Meloidae	70	23	14	—	—	—
Hydrophilidae ^a	0	1	0	—	—	—
Lathridiidae	5	8	5	4	4	4
Mordellidae	4	0	4	0	0	1
Alleculidae ^a	0	0	0	0	0	1
Nitidulidae	0	1	3	—	—	—
Predaceous						
Carabidae	366	199	195	1	18	7
Cicindelidae	39	38	19	—	—	—
Cucujidae	0	0	6	—	—	—
Coccinellidae	3	3	0	3	6	4
Cleridae	0	1	0	0	1	0
Histeridae	10	4	6	—	—	—
Melyridae	2	0	2	1	1	0
Rhizophagidae	8	11	10	—	—	—
Staphylinidae	109	319	112	1	9	4
Other						
Corylophidae (fungivore)	0	8	6	0	0	1
Silphidae (scavenger) ^a	10	3	15	—	—	—
Tenebrionidae (scavenger)	4	11	6	—	—	—
Leiodidae (scavenger)	5	2	8	—	—	—
Dermestidae (scavenger)	3	2	1	4	0	0
Cryptophagidae (scavenger) ^a	1	3	0	—	—	—
Pselaphidae (fungivore)	4	1	2	—	—	—
Mycetophagidae (fungivore)	6	8	29	—	—	—
Scolytidae (fungivore) ^a	1	0	1	—	—	—
Scaphidiidae (fungivore) ^a	0	0	1	—	—	—
Scydmaenidae (fungivore) ^b	10	0	2	—	—	—
Anobiidae (scavenger) ^b	1	0	0	—	—	—
Endomychidae (fungivore) ^b	0	0	1	—	—	—
Limnichidae (gatherer) ^a	—	—	—	1	0	0
Total	1839	877	673	28	81	61

^a 1998 only^b 1999 only

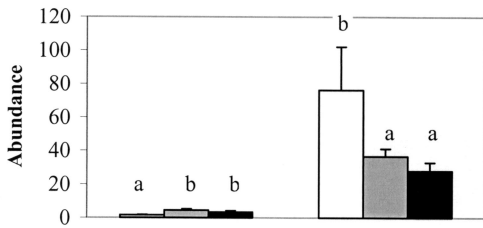
sites (Fig. 3B). Pitfall samples yielded greater orthopteran species richness ($F = 15.62$; $df = 2,12$; $P = 0.0005$) and Shannon diversity ($F = 14.16$; $df = 2,12$; $P = 0.0007$) in brome fields than native prairies or old fields (Fig. 3).

Seasonal Patterns. Sampling through the summer months resulted in a gradual decline in number of individual invertebrates, but this trend was not significant due to variability between 1998 and 1999 (Fig. 4). Ordinal richness ($F = 29.81$; $df = 3,72$; $P = 0.0001$) and diversity ($F = 11.17$; $df = 3,72$; $P = 0.0001$), coleopteran family diversity ($F = 9.80$; $df = 3,72$; $P = 0.0001$), and orthopteran species richness ($F = 22.80$; $df = 3,72$; $P = 0.0001$) and diversity ($F = 10.42$; $df = 3,72$; $P = 0.0001$) were all greater in June than July, August, or September, with the lowest values generally occurring in either August or September. Coleopteran family

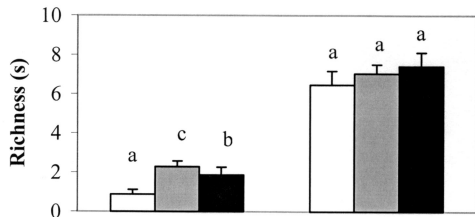
richness differed in that June and July had similar values, both of which were significantly greater than richness in August or September ($F = 23.65$; $df = 3,72$; $P = 0.0001$).

Vegetation and Invertebrate Relationships. Richness and Shannon diversity of invertebrate orders, coleopteran families, and orthopteran species from drop-trap samples were positively correlated with Shannon diversity and richness of plant species (Table 4). Total invertebrate density and coleopteran family diversity and richness from drop-traps were positively correlated with native plant abundance. Abundance of native vegetation was positively correlated with Shannon diversity and richness of coleopteran families from pitfall traps, but negatively correlated to Shannon diversity and richness of orthopteran species from pitfall samples (Table 4).

A. Coleopteran abundance



B. Coleopteran family richness



C. Coleopteran family diversity

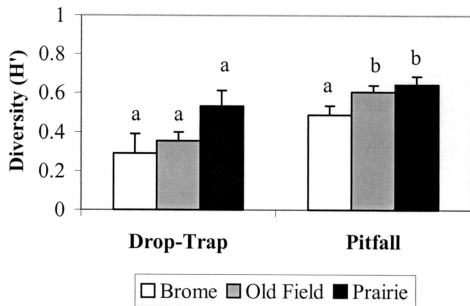


Fig. 2. Mean \pm 1 SE (A) abundance, (B) richness, and (C) diversity (H') of coleopteran families collected from drop-trap and pitfall samples in brome, old field, and prairie sites ($n = 3$ for each) at Smoky Hills Training Facility during 1998 and 1999. Drop-trap abundance is given as number of individuals per m^2 , and abundance from pitfall traps is expressed as number of individuals per five pitfalls. Bars with different letters are significantly different ($P < 0.05$).

Discussion

The vegetation of the nine transects studied at SHTF represented three distinct communities, based on species composition and proportion of native species, that reflected past and present management practices. During a concurrent study using the same study sites, two-way indicator species analysis (TWINSPAN; Hill 1994) of plant species abundance data also delineated transects into brome field, old field, and native prairie groupings, with *B. inermis* and *A. gerardii* identified as indicators separating brome fields and native prairies, respectively (Jonas 2000). The brome sites differed from old field and prairies in that they were dominated by introduced species and had

the highest abundance of annual plants. Similar patterns were noted when transects characterized by *B. inermis* were compared with those dominated by *A. gerardii* and *Sorghastrum nutans* (L.) Nash at nearby Fort Riley, KS (P. Fay, Kansas State University Division of Biology, unpublished data).

The prairie transects at SHTF had relatively low forb diversity compared with other native prairie sites in the region (e.g., Konza Prairie Biological Station, Knapp et al. 1998), and this was likely related to management practices. Although brome sites were hayed in some years, consistent annual haying of prairie sites may have contributed to the lower abundance of forbs on prairie transects (e.g., Anderson et al. 1989, Knapp et al. 1998). However, the rangewide application of the herbicide Tordon 22*K just 2 yr before this study makes it difficult to speculate on factors responsible for this trend.

Plant diversity, richness, and percent nativity analyses reflected different patterns during this study. Although not consistently more diverse than brome or prairie sites, old fields had greater plant species richness. Qualitatively, old fields also had higher canopy height and structural heterogeneity than prairie and brome sites. Hence, diversity values alone did not reflect some differences in plant communities associated with land management practices. Furthermore, neither plant species diversity nor richness values reflected differences in the nativity of the plant communities, an important correlate with invertebrate communities in this study. In an examination of lepidopterans and plant communities, New (1997) also noted that land management practices could result in shifts from native and/or specialist taxa to generalist and/or exotic taxa without changes in overall diversity.

Temporal Patterns. Of the months we sampled, June consistently yielded the greatest abundance, richness, and diversity of invertebrates, and these values generally decreased through the summer. In a study of beetles in forests of eastern North America, Burke and Goulet (1998) also found that richness was greatest during mid- to late-June. These results suggest that studies of invertebrate communities in temperate regions of the United States should target June sampling, particularly if resources limit the temporal extent of sampling. Furthermore, bioassessment techniques, which are often designed for rapid, cost effective sampling (e.g., rapid bioassessment based on limited sampling periods that maximize information), should focus on early summer months when terrestrial invertebrate communities are the focus. However, it is also important to recognize that although some periods might produce maximum abundance and diversity, there are substantial differences in the phenology of individual taxa, and some taxa may go undetected or be underrepresented by limited sampling periods. For example, during our study, Pseudoscorpiones and Microcoryphia were only collected in August samples, and Cicindellidae (Coleoptera) were captured in July, August, and September. Furthermore, July was the only month when Tridactylidae (Orthoptera) were

Table 3. Total number of Orthoptera individuals collected in pitfall (360 traps) and drop-trap (216 traps) samples from brome, old field, and prairie sites at Smoky Hills Training Facility during 1998 and 1999

Taxa	Pitfall traps			Drop-traps		
	Brome	Old Field	Prairie	Brome	Old Field	Prairie
Acrididae						
<i>Arphia simplex</i> Scudder	9	11	26	—	—	—
<i>Eritettix simplex</i> (Scudder) ^a	1	1	6	0	0	4
<i>Orphulella speciosa</i> (Scudder)	39	9	36	4	2	4
<i>Phoetaliotes nebrascensis</i> (Thomas)	26	37	5	16	16	2
<i>Opeia obscura</i> (Thomas) ^a	0	1	0	—	—	—
<i>Boopedon auriventris</i> McNeill ^a	1	0	0	—	—	—
<i>Syrbula admirabilis</i> (Uhler)	38	4	1	2	0	0
<i>Agenotettix deorum</i> (Scudder)	50	0	0	1	0	0
<i>Boopedon gracile</i> Rehn	45	4	0	2	0	0
<i>Melanoplus differentialis</i> (Thomas)	6	11	0	—	—	—
<i>Pardalophora</i> sp.	3	0	1	—	—	—
<i>Dissostaria carolina</i> L. ^a	0	1	0	—	—	—
<i>Campylacantha olivacea olivacea</i> (Scudder) ^a	3	2	0	—	—	—
<i>Hesperotettix speciosus</i> (Scudder)	5	6	0	2	1	0
<i>Hypochlora alba</i> (Dodge)	1	14	1	1	1	4
<i>Melanoplus packardii</i> Scudder	11	0	0	—	—	—
<i>Schistocera lineata</i> Scudder ^a	1	0	0	—	—	—
<i>Hippiscus ocelote</i> (Saussure) ^a	13	0	0	—	—	—
<i>Arphia</i> sp.	5	0	1	1	0	0
<i>Melanoplus femurrubrum femurrubrum</i> (DeGeer)	79	53	2	16	4	0
<i>Melanoplus bivittatus</i> (Say)	36	39	2	1	1	0
<i>Hadrotettix</i> sp.	13	1	0	—	—	—
<i>Melanoplus sanguinipes</i> (F.) ^a	1	0	0	—	—	—
<i>Melanoplus confusus</i> Scudder ^a	0	1	0	—	—	—
<i>Chortophaga virtisilata</i> (DeGeer) ^a	0	0	1	—	—	—
<i>Arphia xanthoptera</i> (Burmeister)	5	3	4	—	—	—
Unknown Acrididae	—	—	—	1	1	2
Gryllidae	356	268	486	13	29	19
Tettigoniidae	63	87	8	29	29	30
Gryllacrididae	0	1	4	—	—	—
Tetrigidae	1	7	2	0	1	0
Tridactylidae ^b	0	0	1	—	—	—
Total	797	513	637	89	85	65

^a 1998 only

^b 1999 only

present. Had we sampled only in June, these taxa would not have been accounted for in this study.

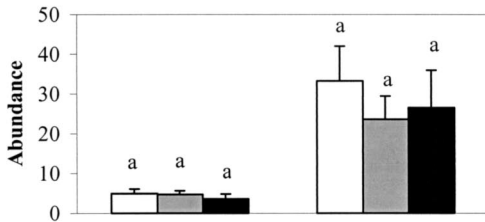
Drop-trap versus Pitfall Sampling. Despite differences between the two sampling methods we used, general trends of ordinal abundance and richness, coleopteran family diversity, and orthopteran species diversity among land use types were similar for drop-trap and pitfall trap collections. However, pitfall traps did collect a significantly greater number of individual invertebrates and produced higher richness and diversity values than drop-trap samples, and each method was biased toward somewhat different assemblages. Drop-trap samples were dominated by mostly diurnal taxa and canopy-dwellers, whereas pitfall traps were more efficient at capturing nocturnal and epigeal species.

Comparison of the two collecting methods that we used also showed different patterns regarding relationships between invertebrate and plant communities. Using pitfall trap and vacuum sampling techniques, Webb and Hopkins (1984) found that heathland insect and plant diversities were not correlated. In our study, however, correlations between plant and invertebrate communities were dependent upon the sampling method. When compared with

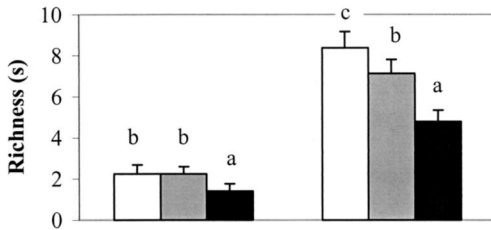
abundance of native plants, plant species diversity, and plant species richness, drop-trap samples consistently showed significant relationships. In contrast, there were only three relationships detected between invertebrates from pitfall samples and vegetation parameters, and they were negative correlations between native plant abundance and orthopteran species diversity, orthopteran taxa richness, and overall abundance of coleopterans. These differences are likely linked to the bias of each collecting method (canopy dwellers versus ground dwellers), and it is reasonable to assume that canopy dwelling invertebrates are more likely to respond to differences in plant species composition than ground dwelling groups.

There are potential limitations associated with the drop-trap and pitfall trap methods. For example, it appeared during this study that larger invertebrates (e.g., some adult grasshoppers and large carabid beetles) were sometimes difficult to capture with the vacuum of the drop-trap method. However, Johnson et al. (1957), working in grasslands of Great Britain, found that vacuum sampling typically removed over 95% of adult insects representing the major insect groups in a sampling area. In contrast, it has been

A. Orthopteran abundance



B. Orthopteran species richness



C. Orthopteran species diversity

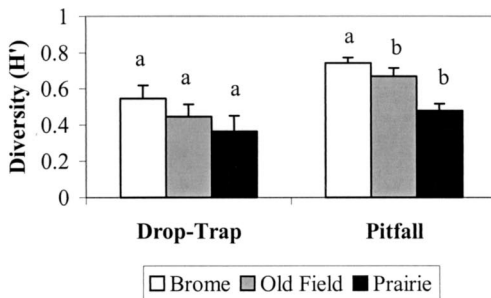


Fig. 3. Mean \pm 1 SE (A) abundance, (B) richness, and (C) diversity (H') of orthopteran species collected from drop-trap and pitfall samples in brome, old field, and prairie ($n = 3$ for each) sites at Smoky Hills Training Facility during 1998 and 1999. Drop-trap abundance is given as number of individuals per m^2 , and abundance from pitfall traps is expressed as number of individuals per five pitfalls. Bars with different letters are significantly different ($P < 0.05$).

found that pitfall traps are biased toward larger, more active species (Greenslade 1964). Pitfall trap data are also more difficult to quantify and standardize because this method relies on activity of the invertebrates and is therefore heavily influenced by prevailing weather conditions (Greenslade 1964, Halsall and Wratten 1988). Furthermore, it is difficult to interpret the spatial representation of a pitfall sample.

Because they target somewhat different assemblages and habitats, using both drop-trap and pitfall sampling methods might be best for inventory and assessment programs, but limited resources may not always allow for such an effort. Given that we ob-

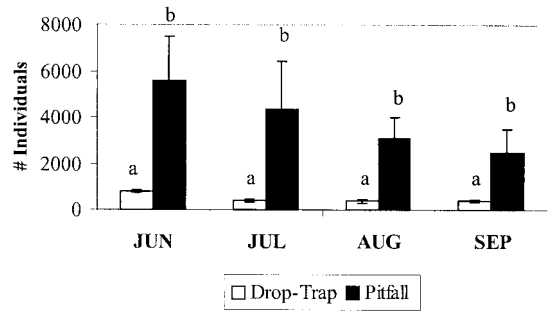


Fig. 4. Monthly mean \pm 1 SE number of individual invertebrates captured in drop-trap and pitfall trap samples at Smoky Hills Training Facility during 1998 and 1999. Bars with different letters are significantly different ($P < 0.05$).

served similar trends among land use types with both methods, that pitfall samples have more limitations associated with interpreting the data, and that relationships with plant communities were most evident with drop-trap samples, the drop-trap technique may be the best alternative for assessing land management influences on invertebrate communities in our region. However, the effectiveness of each method could vary substantially with location, habitat, and management or disturbance regimes.

Effects of Disturbance. Invertebrates in general and our focal groups, coleopteran families and orthopteran species, responded to differential land use at SHTF, and this response appeared most related to differences in plant structural heterogeneity and native plant species abundance. The habitat heterogeneity hypothesis predicts increased arthropod richness where there is heightened structural complexity in the form and species of vegetation (Evans 1988, Tscharrntke and Greiler 1995, Crisp et al. 1998, Dennis et al. 1998). Qualitatively, old fields appeared most structurally complex of the sites we examined, and they were also free of mechanical disturbance (hay) and were not dominated by exotic plant species. In agreement with tenets of the habitat heterogeneity hypothesis, old field drop-trap samples, which sampled the aboveground invertebrate community most closely associated with plants, produced highest to moderate richness for all groups examined. Old field drop-trap samples also had higher to moderate abundance and diversity values for all invertebrate groups that we examined.

Coleopteran family richness and diversity were generally lowest in brome fields, which were dominated by exotic plant species, and this suggests there may be a relationship between native versus exotic plants and coleopterans in this region. Crisp et al. (1998) found that the abundance of native beetles in New Zealand was positively related to that of native plant species. Although we did not discriminate between native and exotic beetles during our study, we did find a significant positive correlation between native plant species abundance and coleopteran richness and diversity in drop-trap samples. Furthermore, of the beetles captured by either method, brome and old

Table 4. Pearson correlation coefficients (r) of mean 1998 and 1999 plant and invertebrate (from pitfall and drop-traps) community measures at Smoky Hills Training Facility ($n = 9$ for each comparison)

Invertebrate group	Invertebrate variable	Native plant species abundance		Species plant diversity (H')		Species plant richness (s)	
		Pitfall	Drop-traps	Pitfall	Drop-traps	Pitfall	Drop-traps
Arthropod (order)	Diversity (H')	0.10	0.22	-0.44	0.76 ^a	-0.46	0.72 ^a
	Richness (s)	-0.27	0.47	-0.44	0.71 ^a	0.17	0.71 ^a
	Density (n/m^2)	—	0.71 ^a	—	0.42	—	0.48
	Abundance ($n/5$ traps)	-0.25	—	0.14	—	0.14	—
Coleoptera (family)	Diversity (H')	0.45	0.67 ^b	-0.24	0.73 ^a	-0.17	0.74 ^a
	Richness (s)	0.06	0.69 ^b	-0.24	0.62 ^b	-0.42	0.63 ^b
	Density ($\#/m^2$)	—	0.58	—	0.40	—	0.50
	Abundance ($\#/5$ traps)	0.86 ^c	—	-0.16	—	-0.16	—
Orthoptera (family)	Diversity (H')	-0.18	-0.17	0.15	0.52	0.27	0.67 ^b
	Richness (s)	-0.20	-0.16	-0.04	0.58	0.12	0.65 ^b
	Density ($\#/m^2$)	—	-0.40	—	0.52	—	0.54
	Abundance ($\#/5$ traps)	-0.41	—	-0.59	—	-0.59	—
Orthoptera (species)	Diversity (H')	-0.86 ^c	-0.40	-0.18	0.69 ^a	0.02	0.76 ^a
	Richness (s)	-0.93 ^d	-0.40	0.29	0.67 ^b	0.41	0.62 ^b

^a $P < 0.05$, ^b $P < 0.10$, ^c $P < 0.01$, ^d $P < 0.001$

field sites harbored two or three unique families, respectively, whereas five families were found only in prairie sites, where native plants were most abundant (Table 2).

In contrast to coleopteran families, diversity and richness of orthopteran species was generally lowest in native prairies. As a result, unlike coleopterans, native plant species abundance was negatively correlated to orthopteran diversity and richness. This pattern may be related to food preferences by orthopteran species at our site. Feeding studies by Chu and Knutson (1970), Lambley et al. (1972), and Campbell et al. (1974) indicate many acridids prefer exotic grasses such as *B. inermis* and *P. pratensis* over native species. For example, *Agenotettix deorum* (Scudder) shows a strong preference for *B. inermis* as a food plant, and we collected this species exclusively from brome fields. It is also possible that the pattern with orthopterans that we observed may have been a negative response to mechanical disturbance. Evans (1988), in a study on a nearby site in Kansas, concluded that the distribution of grasshoppers in tallgrass prairie might be more related to differences in accumulated soil surface and standing plant litter than to plant species composition, presumably because of differences in microhabitats for eggs and early instar nymphs. All prairies sites at SHTF were hayed annually, and haying greatly reduces litter accumulation. However, brome fields and old fields, where orthopteran values were highest, were not hayed regularly (only brome site 3 was hayed, and only in 1998). Furthermore, brome site 3 was hayed in early July 1998, and orthopterans were present in drop-trap samples from that site only in June 1998. Likewise, orthopteran abundance in pitfall samples during 1998 dropped 81% between June and July (before and after haying, respectively), versus an average 55% decline in abundance in brome sites that were not hayed during the same period.

Regardless of the mechanisms, the response of orthopterans to differential land management at SHTF

has relevance to pest management in this region. For example, *Melanoplus* spp., which are notorious for their destructive potential (Woodruff 1937, Wilbur and Fritz 1940, Campbell et al. 1974), were most common in brome and old fields. In fact, of 263 *Melanoplus* individuals captured throughout this study, only 4 were found in native prairie sites. Woodruff (1937) noted that although a serious grasshopper outbreak occurred in the Great Plains during 1936, damaging grasshopper species were scarce in native prairies and caused little damage to native grass species. Hence, it may be best to manage nonagricultural sites, such as SHTF, as native prairies so that they do not serve as source areas for pest species and are buffered from damage during outbreaks.

Orthopteran species that are typically considered indicators of native prairie, such as *Orphulella speciosa* (Scudder) and *Syrbula admirabilis* (Uhler) (Woodruff 1937, Wilbur and Fritz 1940, Campbell et al. 1974), were more abundant in brome and old field sites than prairies at SHTF, suggesting they may not be useful as indicators in this region. However, one acridid species, *Eritettix simplex* (Scudder), did demonstrate potential as an indicator of native prairie during this study. Because of its ability to garner nutrition from plants unsuitable for other grasshopper species, Mulhern (1967) labeled *E. simplex* a "restricted feeder." Studies by Anderson (1964), Lambley et al. (1972), and Campbell et al. (1974) found that *Bouteloua* spp. were the preferred food plants of *E. simplex*. These grasses were found only in native prairie sites at SHTF, where *E. simplex* was found almost exclusively.

Indicator taxa are often used to assess biological responses on a larger scale (e.g., responses of entire communities), and an important consideration for selecting indicators is their ability to reflect these responses (Oliver and Beattie 1996). Our results suggest that *E. simplex* may be a valuable indicator of native prairie in this region, but orthopterans as a group may not be the best choice for reflecting large-scale patterns. Alternatively, coleopterans show promise be-

cause patterns of coleopteran abundance and family richness from drop-trap samples were similar to trends in overall invertebrate richness and abundance across the gradient of conditions that we examined, and the response trajectory was logical, based on plant communities and disturbance regimes of each land use type. Additionally, given the differential response of coleopterans and orthopterans during this study, metrics that account for the relative proportion of each, similar to many fish and invertebrate metrics that are currently used in freshwater bioassessments (e.g., Barbour et al. 1999), might serve best for biological assessments in this region.

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