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Responses of soil microarthropods to changes in soil water availability in tallgrass prairie

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Abstract Changes in precipitation and soil water availability predicted to accompany global climate change would impact grasslands, where many ecosystem processes are influenced by water availability. Soil biota, including microarthropods, also are affected by soil water content, although little is known about how climate change might affect their abundance and distribution. The goal of this study was to examine soil microarthropod responses to altered soil water availability in tallgrass prairie ecosystems. Two separate experiments were done. The first utilized control and irrigated plots along a topographic gradient to examine the effects of soil water content on microarthropod densities. Microarthropods, mainly Acari, were significantly less abundant in irrigated plots and were generally less abundant at the wetter lowland sites. The second study utilized reciprocal core transplants across an east-west regional precipitation gradient. Large, intact cores were transplanted between a more mesic tallgrass site (Konza Prairie) and a more arid mixed-grass site (Hays) to determine the effects of different soil water regimes on microarthropod abundance and vertical distribution. Data from non-transplanted cores indicated greater total microarthropod densities at the drier Hays site, relative to the wetter Konza Prairie site. Data from the transplanted cores indicated significant effects of location on Acari densities in cores originating from Hays, with higher densities in cores remaining at Hays, relative to those transplanted to Konza. Acari densities in cores originating from Konza were not affected by location; however, oribatid mite densities generally were greater in cores remaining at Konza Prairie. These results confirm the importance of soil water content in affecting microarthropod densities and distributions in grasslands, and suggest complex, non-linear responses to changes in water availability.

Key words Acari · Climate change · Grassland soils · Soil microarthropods · Soil water content

Introduction

The Central Plains region of the United States includes short-grass, mixed-grass and remnants of tallgrass prairie. The community composition and distribution of these prairie types depend on climate patterns and a regional east-west precipitation gradient (Risser et al. 1981). Ecosystem processes (e.g. decomposition, nutrient cycling and primary productivity) in these grasslands also are influenced greatly by water availability (Risser et al. 1981; Knapp 1984). Therefore, any changes in water availability resulting from global climate change would likely result in substantial ecological responses in these systems (Field et al. 1992). Although past climatic changes (i.e. droughts) altered both productivity and species composition of the Central Plains grasslands (Weaver 1954), the potential effects of predicted future climate changes are unclear.

The potential impacts of climate change on the soil biota of these grasslands are largely unknown. Soil fauna are important in processing detritus and regulating the availability of nutrients (Anderson 1988; Moore et al. 1988). While bacteria and fungi directly process the majority of organic matter inputs to the soil, their interactions with soil invertebrates dictate nutrient immobilization and mineralization patterns (Seastedt 1984a; Seastedt and Crossley 1988). Soil fauna are sensitive to environmental conditions in the soil and can move through the soil profile in response to changes in temperature and water availability in order to find suitable microhabitats (Coleman and Crossley 1996). Thus, any changes in soil water availability as a result of climate change will likely affect the abundances of soil organisms, where they reside in the soil, and how they influence ecosystem processes.

Microarthropods are one group of soil invertebrates that influence soil processes in a variety of fundamental

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ways. Microarthropods encompass a wide range of feeding behaviors and occupy a wide variety of habitats. Their abundance, community composition and effects on various soil processes have been studied in many terrestrial ecosystems and summarized in numerous reviews (Harding and Stuttard 1974; Peterson and Luxton 1982; Seastedt 1984a). A number of studies also have examined their feeding behaviors and interactions with other soil biota within the soil environment (Moore et al. 1988; Seastedt et al. 1988; Ingham et al. 1989). The indirect effects of microarthropods on ecosystem processes, especially decomposition and nutrient cycling, through interactions with other soil invertebrates and microbes (e.g. grazing on microbes), are important, but they also affect decomposition processes directly through comminution, fecal production and dissemination of propagules (Seastedt 1984a; Moore et al. 1988).

Microarthropod abundances and activities have been documented for some grasslands (Curry 1969, 1987), although there have been few studies done in North American tallgrass prairie (Lussenhop 1981; Seastedt 1984b). Studies of the vertical distribution of microarthropods in the soil profile also are few (Price and Benham 1977; Leatham and Milchunas 1985; Perdue and Crossley 1990), and we know of no such studies in tallgrass prairies. Research in other ecosystems has indicated seasonal and diurnal migrations throughout the soil profile in response to changes in temperature and water availability (Whitford et al. 1981). Studies of microarthropod vertical distribution may be important in determining potential responses of microarthropods to changes in temperature and soil water availability.

Here we present results from two studies designed to examine the effects of soil water availability on abundances and vertical distribution of microarthropods. Experiment 1 (the Irrigation Transect Experiment) was done at the Konza Prairie Research Natural Area and utilized natural differences in soil water availability resulting from topography, as well as induced differences in soil water availability through the use of an irrigation system. Experiment 2 (the Regional Core Transplant Experiment) was a regional-scale study that took advantage of the east-west precipitation gradient occurring across the Central Plains. The use of both local and regional scale studies was intended to provide a more broad-based understanding of how changes in soil water availability might affect microarthropod abundances and distributions.

Study sites and methods

Experiment 1 – Irrigation Transect Experiment

The Irrigation Transect Experiment was conducted at the Konza Prairie Research Natural Area, a 3487 ha tallgrass prairie located in the Flint Hills, about 15 km south of Manhattan, Kansas (39°05'N, 96°35'W). Konza Prairie is managed by the Division of

Biology at Kansas State University as a Long-Term Ecological Research (LTER) site, and substantial data are available on soils, vegetation and climate (Hulbert 1969; Abrams et al. 1986; Bark 1987). The vegetation is characteristic of tallgrass prairie and is dominated by *Andropogon gerardii* Vitman (big bluestem), *Sorghastrum nutans* (L.) Nash (indian grass), *Panicum virgatum* L. (switchgrass) and *Andropogon scoparius* Michx. (little bluestem). Mean annual precipitation is 835 mm but varies greatly, and droughts occur often (Brown and Bark 1971). Mean monthly air temperatures range from -3° to 27° C, and mean monthly soil temperatures range from 1.6° to 29.3° C.

The Irrigation Transect Experiment was established in an area subjected to annual spring burning, which spanned an upland to lowland topographic gradient. Upland soils belonged to the Clime-Sogn complex (fine, mixed mesic Udic Haplustolls), with soil texture (0–5 cm) of 22% sand, 44% silt and 34% clay; C content was 4.12% and N content was 0.40%. Lowland soils were Irwin silty clay loams (fine, mixed mesic Pachic Argiustolls), with a soil texture (0–5 cm) of 21% sand, 41% silt and 38% clay; C content was 3.26% and N content was 0.33%. This area included a natural gradient of soil water availability, resulting from topography (drier uplands and wetter lowlands), as well as soil water differences induced through the use of an irrigation system. Two replicate irrigation lines ran from upland to lowland topographic positions (approx. 140 m), along with two parallel, non-irrigated control transects. Irrigation occurred from May through September along the transects and was scheduled to offset any water deficit in plants near the irrigation line. The timing and amounts of supplemental water added were based on measured rainfall amounts and estimated evapotranspiration and, therefore, varied as a function of actual rainfall patterns and seasonal plant demands. In 1994, for example, May to September precipitation was 402 mm, and an average of 342 mm of additional irrigation water was added along the transect. A more complete description of the site and details of the irrigation treatment are presented in Knapp et al. (1994) and Lewis (1996). These localized differences in water availability were used to address the effects of soil water availability on microarthropod abundances and composition.

Sixteen sample plots (3 m diameter) were delineated along the Irrigation Transect Experiment, including four upland control plots, four upland irrigated plots, four lowland control plots and four lowland irrigated plots. The irrigated plots were 2–3 m on either side of the irrigation lines (approx. 80% of the water was distributed within 2–3 m from the irrigation pipe; J.K. Koelliker, personal communication). Control plots were located at least 7 m apart on opposite sides of the control transects. In the analysis and discussion of results from this experiment, the control and irrigated plots are referred to as “treatments,” while the upland and lowland areas are referred to as “sites.”

To quantify microarthropod abundances, two 5 cm diameter \times 5 cm deep cores were collected from each of the 16 plots in May (post-burn), July, and October of 1994 and 1995 ($n=8$ per treatment-site combination per date). Microarthropods were extracted from the cores over a 1-week period using high-gradient, Tullgren-type extractors (Crossley and Blair 1991). Gravimetric soil water content at the time of collection also was determined after drying at 60° C. In 1995, additional in situ measurements of volumetric soil water content were obtained using a time domain reflectometry (TDR) system (Campbell Scientific, Inc.). Microarthropods were identified to insect order and Acari suborder. A logarithmic transformation ($x+1$) was used to normalize abundance data prior to statistical analyses (Berthet and Gerard 1965). Effects of irrigation, topographic position and time (season) on microarthropod abundances and composition were assessed by ANOVA (SAS Institute 1989).

Experiment 2 – Reciprocal Core Transplant Experiment

The Reciprocal Core Transplant Experiment was part of a larger project examining how plants, soil organisms and key soil processes of grassland ecosystems respond to different soil water re-

gimes and to identify potential consequences of these responses for ecosystem function. It included two locations with different climates: Konza Prairie (see vegetation and climate description in Experiment 1) and Hays, Kansas. The Konza site for this experiment was located on a deep, nearly level (0–1% slope) Reading silt loam formed from alluvial sediments. Reading soils are fine, mixed mesic Typic Argiustolls with a silt loam A horizon (approximately 28 cm deep) overlaying light to heavy silty clay loam B1 and B2t horizons. The Hays site was located approximately 240 km west-southwest of Konza (38°75'N, 99°20'W). The vegetation was typical of a semi-arid mixed-grass prairie, and included *Bouteloua curtipendula* [Michx.] Torr. (side-oats grama), *A. scoparius*, *B. gracillis* [H.B.K.] Lag. ex Griffiths (blue grama), *Buchloe dactyloides* [Nutt.] Engelm. (buffalo grass) and *Agropyron smithii* Rybd. (western wheat grass). The area also contained patches of tallgrass species, such as *A. gerardii* and *P. virgatum*. The Hays site was located on a deep, nearly level (0–1% slope) Harney silt loam formed in calcareous, medium textured loess. The A1 and A3 horizons were silt loams and light silty clay loams, respectively, overlaying light to heavy silty clay loam B horizons. While the upper 30 cm of soil at the Konza and Hays sites were texturally similar, there was a notably higher clay content below approximately 30 cm in the soils of the Konza site. Mean annual precipitation at Hays is 580 mm, or approximately 30% less than the mean for Konza Prairie (835 mm). Mean monthly air and soil temperatures at Hays are similar to those at Konza. These regional scale differences in precipitation amounts were used to address the effects of altered soil water availability on microarthropod abundances and depth distribution.

Seventy large, intact soil cores (25 cm diameter × 70 cm deep) encased in open-ended polyvinylchloride cylinders were collected from the mesic, tallgrass Konza site and from the arid, mixed-grass Hays site using hydraulic coring equipment (Swallow et al. 1987). Cores at both sites were taken from areas dominated by *A. gerardii* to minimize variability among cores. Half the cores were placed back into holes at their site of origin, and half were transplanted into holes at the other site. The end result of this reciprocal transplant was a grid of 35 “native” and 35 “transplanted” cores, arranged in a randomized block design at each of the two sites. Native cores were used to compare microarthropod abundances, composition and vertical distributions in grassland sites developed under different annual precipitation regimes. Transplanted cores were used to study how microarthropod abundances, composition and vertical distributions respond to changes in soil water availability.

Five native and five transplanted cores were collected from each site twice a year (May and October/November) in 1994 and 1995. The cores were sectioned into 0–10, 10–20, 20–40 and 40–60 cm depth increments. For this study, 5 cm diameter × 5 cm deep soil cores were taken from the upper surface of each depth increment. Microarthropods were extracted and identified as described above to establish composition, abundances and depth distributions. Because microarthropods were extracted from only the upper 5 cm of each depth increment, an averaging procedure was used to estimate densities of total microarthropods to a depth of 45 cm in the large soil cores. Mean densities in the depth increments for which we had no direct measurements (5–10, 15–20, and 35–40 cm) were estimated as the average of measured densities in the cores taken immediately above and below those increments. These values then were added to the densities of microarthropods in depth increments for which we had direct measurements (0–5, 10–15, 20–25, and 40–45 cm) to estimate total microarthropod densities to a depth of 45 cm. We did not extend these estimates to 60 cm, since we did not measure microarthropod densities below 45 cm. Log transformed ($x+1$) data for total microarthropod densities per core first were analyzed with a mixed-model analysis of variance ANOVA, using core origin, core location and date as fixed effects and block as a random effect. Subsequently, separate ANOVAs were done on cores originating from either Konza or Hays to assess the effects of present core location, depth and date (season) on microarthropod abundances and depth distributions.

Results

Experiment 1 – Irrigation Transect Experiment

The water content of soil cores collected along the Irrigation Transects for microarthropod extraction was affected by collection date ($P < 0.0001$), irrigation treatment ($P < 0.0001$) and a date-treatment interaction ($P < 0.001$). Soil cores from irrigated plots were significantly wetter than those from control plots on three of six dates (Fig. 1), and site (upland vs lowland) did not significantly affect soil water content in the 5 cm deep cores at the time of collection (data not shown). These results generally were consistent with more frequent in situ measurements of volumetric soil water content (0–15 cm) using TDR in 1995, although TDR measurements also indicated drier conditions at the upland sites on most dates (Fig. 2).

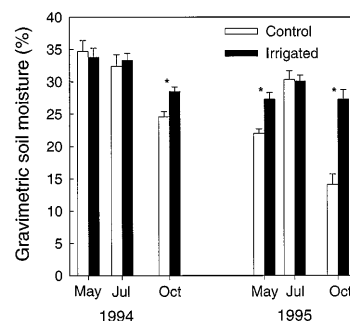


Fig. 1 Gravimetric soil water content in 0–5 cm deep cores collected for microarthropod extraction from control and irrigated plots (averaged across upland and lowland sites). Data are means of eight samples per treatment. Vertical lines are ± 1 SE

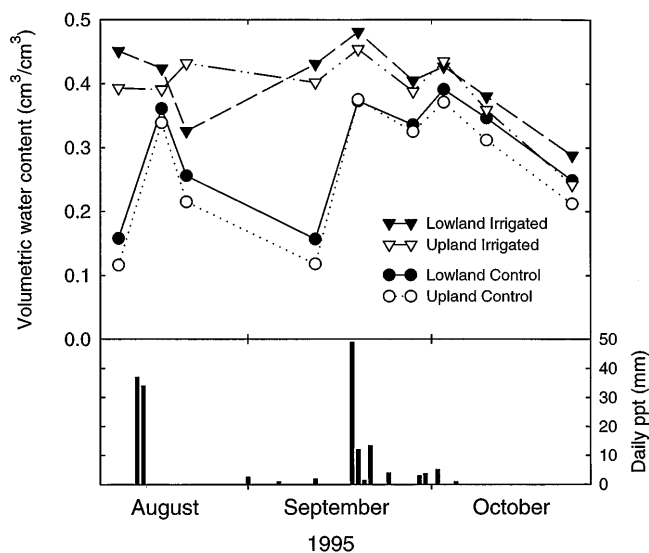
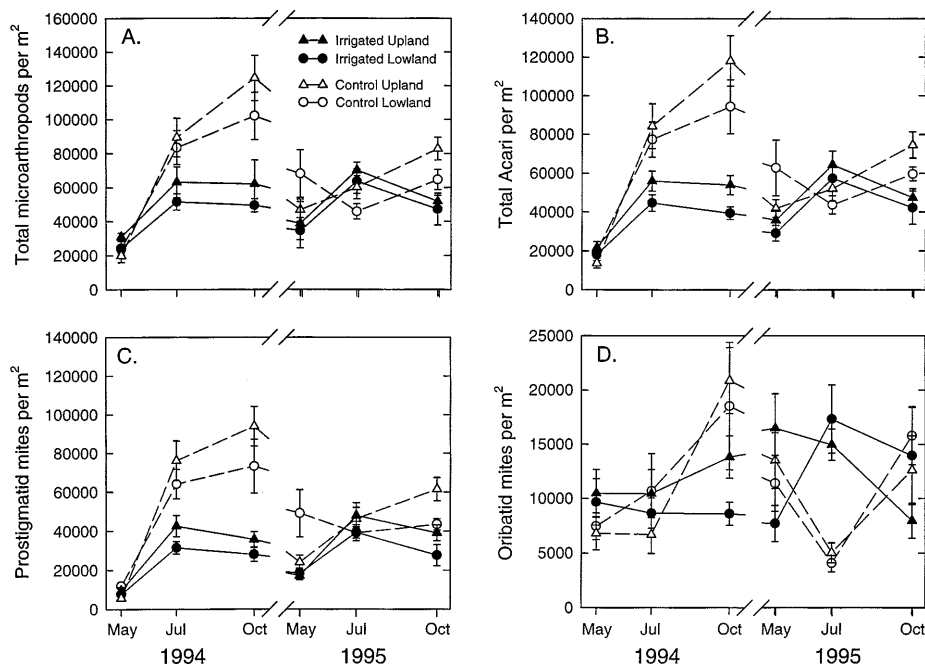


Fig. 2 Volumetric soil moisture content (0–15 cm) in upland and lowland irrigated and control plots in the Irrigation Transect Experiment as determined by time domain reflectometry (top panel), and daily precipitation (ppt) amounts (bottom panel) from August to October 1995

Fig. 3 Abundances of **A** total microarthropods, **B** total Acari, **C** prostigmatid mites and **D** oribatid mites in control and irrigated plots at upland and lowland sites. Data are means of eight samples per treatment. Vertical lines are ± 1 SE



Surprisingly, abundances of total microarthropods generally were greater at the drier upland sites and in control plots (Fig. 3A). A three-way ANOVA indicated that microarthropod abundances were affected by site (upland > lowland), treatment (control > irrigated), date and a date-treatment interaction (Table 1). Two-way ANOVAs (treatment and site) by date indicated significantly greater abundances of total microarthropods in control plots, relative to irrigated plots, on four of the six sample dates (July and October 1994, May and October 1995). Microarthropod densities were greater in the irrigated plots only in July 1995, and there were no effects of site or treatment in May 1994.

Acari (mites) were the most common major group of microarthropods, comprising 71–95% of total microarthropod numbers. Acari were generally more abundant in control plots than in irrigated plots (Fig. 3B), and a three-way ANOVA (date, treatment and site) indicated significant effects of treatment, date and date-treatment interactions on Acari abundances (Table 1). Two-way ANOVAs (treatment and site) by date indicated greater abundances of Acari in control plots on all dates except May 1994 (no treatment effect) and July 1995 (higher) in irrigated plots. Differences between upland and lowland sites were marginally significant ($P=0.07$), and there was a significant treatment-site interaction, with greater abundances of mites in the upland sites ($P<0.01$) in the irrigated treatment only.

Prostigmatid and oribatid mites were the most abundant Suborders of mites, comprising 89–99% of total Acari numbers in various site-treatment-date combinations. On average, prostigmatid mites were about 2.7 times more abundant than oribatid mites. Prostigmatid mites generally were more abundant in control plots

than in irrigated plots (Fig. 3C), and a three-way ANOVA (date, treatment and site) indicated significant effects of date, treatment, date-site interaction and date-treatment interaction (Table 1). No significant effect of site alone was indicated, although there was a significant treatment-site interaction with greater abundances of prostigmatid mites in the upland sites ($P<0.01$) in the irrigated treatment only. Two-way ANOVAs (treatment and site) by date revealed greater prostigmatid mite abundances in control plots on all collection dates, except May 1994 (no treatment effect) and July 1995 (higher in irrigated plots). Oribatid mite abundances (Fig. 3D) were significantly affected by date, a date-site interaction and a date-treatment interaction (Table 1). No significant main effects of site or treatment alone were indicated. Two-way ANOVAs by date indicated greater oribatid mite densities in control plots in October 1994, at upland sites in October 1994 and May 1995, and in the irrigated plots in July 1995.

Experiment 2 – Reciprocal Core Transplant Experiment

Annual amounts and seasonal patterns of precipitation at Hays and Konza Prairie for 1993, 1994 and 1995 are presented in Table 2. The majority of precipitation over the three years at both sites fell during the spring and summer seasons. As expected, Hays received significantly less precipitation than Konza Prairie in the year prior to, and the years of, the study. Annual precipitation amounts at Konza Prairie during the study (682–1061 mm) were consistently higher than at Hays (413–469 mm). The differences between annual precipitation amounts at Hays and Manhattan were consistently

Table 1 ANOVA of abundances of microarthropods from the Irrigation Transect Experiment at Konza Prairie

Dependent variable	Source of variation	df	SS	F	P
Total microarthropods	Date	5	29.0582	36.28	0.0001
	Treatment (trt)	1	2.8782	17.97	0.0001
	Site	1	0.6537	4.08	0.0450
	Date × trt	5	6.2509	7.80	0.0001
	Date × site	5	0.8656	1.08	0.3729
	Trt × site	1	0.4144	2.59	0.1096
	Date × trt × site	5	0.7393	0.92	0.4675
	Error	165	26.4304		
Total	188	68.0515			
Acari	Date	5	38.7003	45.76	0.0001
	Trt	1	3.9352	23.27	0.0001
	Site	1	0.5551	3.28	0.0719
	Date × trt	5	6.8011	8.04	0.0001
	Date × site	5	1.1138	1.32	0.2592
	Trt × site	1	0.7473	4.42	0.0371
	Date × trt × site	5	0.7266	0.86	0.5099
	Error	165	27.9072		
Total	188	81.3268			
Prostigmata	Date	5	76.3499	77.28	0.0001
	Trt	1	8.7343	44.20	0.0001
	Site	1	0.2442	1.24	0.2678
	Date × trt	5	6.2261	6.30	0.0001
	Date × site	5	4.2670	4.32	0.0010
	Trt × site	1	1.2390	6.27	0.0132
	Date × trt × site	5	1.7976	1.82	0.1117
	Error	165	32.6040		
Total	188	132.4439			
Oribatida	Date	5	7.5675	3.78	0.0029
	Trt	1	1.2021	3.00	0.0850
	Site	1	0.2178	0.54	0.4619
	Date × trt	5	17.4235	8.70	0.0001
	Date × site	5	4.6426	2.32	0.0456
	Trt × site	1	0.5631	1.41	0.2374
	Date × trt × site	5	1.4655	0.73	0.6004
	Error	165	66.0733		
Total	188	99.2377			

Table 2 Annual amounts (**bold**) and seasonal patterns of precipitation inputs (mm) at the Manhattan and Hays weather stations for 1993–1995. Seasonal precipitation inputs were grouped as follows – winter: Dec of the previous year, Jan, Feb; spring: Mar, Apr, May; summer: Jun, Jul, Aug; autumn: Sep, Oct, Nov

	Manhattan, Kansas	Hays, Kansas	% difference
1993 Annual precipitation	1416.8	965.0	32%
Spring	414.8	163.1	
Summer	787.4	593.3	
Autumn	136.9	81.0	
1994 Annual precipitation	681.7	412.5	39%
Winter	47.2	58.2	
Spring	195.1	97.5	
Summer	327.9	164.9	
Autumn	105.2	93.0	
1995 Annual precipitation	1061.0	469.1	56%
Winter	77.2	68.6	
Spring	569.2	290.0	
Summer	271.5	82.6	
Autumn	167.4	42.7	

greater (32–56%) than the predicted long-term difference of 30% (835 mm at Konza vs 580 mm at Hays).

Estimates of mean total microarthropod abundances to a depth of 45 cm in “native” cores at Konza and Hays ranged from about 95 000 to 362 000 per m² (Fig. 4). Surprisingly, mean abundances were significantly

greater ($P < 0.05$) in the non-transplanted Hays cores (the more arid site) than in non-transplanted Konza cores (the more mesic site). An ANOVA of microarthropod abundance data across all core origin, location and date combinations indicated significant effects of collection date ($P < 0.0001$), core origin (Hays > Konza;

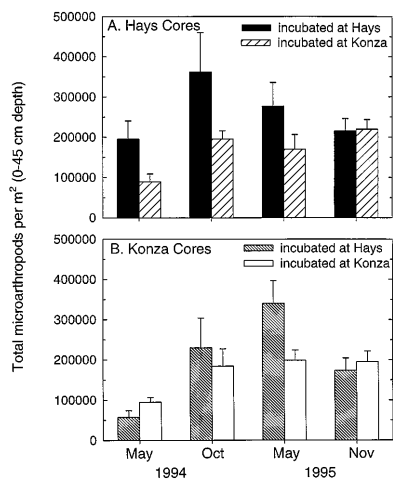


Fig. 4 Abundances of total microarthropods to a depth of 45 cm in soil cores originating from the more arid Hays site (A) or the more mesic Konza Prairie site (B). Soil cores either remained at their site of origin until sampling (*solid bars*) or were transplanted to the alternate site (*hatched bars*). Vertical lines are 1 SE

$P < 0.05$) and a core origin-location interaction ($P < 0.05$). Separate ANOVAs on cores originating from Hays and from Konza indicated a significant effect of location ($P < 0.01$) in the cores originating from Hays, with lower microarthropod abundances in cores transplanted to the more mesic Konza site, relative to cores remaining at Hays. There was no significant effect

of location on total microarthropod abundances in cores originating from Konza. Subsequent analyses focused on the mean abundances and depth distributions of the major groups of microarthropods (Acari, prostigmatid mites, and oribatid mites), and their responses to transplantation to sites with a different climatic regime.

Abundances of total Acari in cores originating from Hays were marginally affected by a date-location interaction (Table 3) and were greater in cores remaining at Hays than in cores transplanted to Konza on most dates (Fig. 5A and B). Acari densities in cores originating from Konza were not significantly different between cores transplanted to Hays and cores remaining at Konza (Fig. 5C, D); however, abundances differed with sample date (Table 4). Acari abundances varied with depth in both Konza and Hays cores. There were significant differences in Acari abundances at different sample depths in cores originating from both Hays (Table 3) and Konza (Table 4), as well as significant date-depth interactions (Tables 3 and 4). A Tukey's Studentized Range test indicated that abundances of total Acari in cores from both Konza and Hays (averaged over all dates and locations) were greatest at the 20–25 cm sample depth, lowest at a depth of 10–15 cm, and intermediate at depths of 0–5 and 40–45 cm.

In cores originating from Hays, abundances of prostigmatid mites (Fig. 6A, B) but not oribatid mites (Fig. 7A, B) were significantly affected by incubation location, and were greater in cores remaining at Hays

Table 3 ANOVA of microarthropod abundances in cores originating from Hays

Dependent variable	Source of variation	df	SS	F	P
Acari	Date	3	21.1646	9.08	0.0001
	Depth	3	20.1929	8.66	0.0001
	Location (loc)	1	1.7788	2.29	0.1328
	Date × depth	9	53.3605	7.63	0.0001
	Date × loc	3	5.4628	2.34	0.0762
	Depth × loc	3	1.7696	0.76	0.5191
	Date × depth × loc	9	8.7055	1.24	2.2739
	Error	126	97.9104		
	Total	157	211.5493		
Prostigmata	Date	3	44.6342	17.90	0.0001
	Depth	3	17.8223	7.15	0.0002
	Loc	1	3.5488	4.27	0.0408
	Date × depth	9	49.6986	6.65	0.0001
	Date × loc	3	7.3498	2.95	0.0354
	Depth × loc	3	1.3454	0.54	0.6560
	Date × depth × loc	9	10.3059	1.38	2.2049
	Error	126	104.7056		
	Total	157	239.4123		
Oribatida	Date	3	11.2442	5.06	0.0024
	Depth	3	22.2810	10.02	0.0001
	Loc	1	0.1880	0.25	0.6153
	Date × depth	9	65.8755	9.88	0.0001
	Date × loc	3	0.6464	0.29	0.8320
	Depth × loc	3	2.6318	1.18	0.3186
	Date × depth × loc	9	4.7782	0.72	0.6930
	Error	126	93.3649		
	Total	157	210.4629		

Fig. 5 Abundances of total Acari by depth increment in soil cores originating from Hays (A, B) or from Konza (C, D), and incubated at either Hays or Konza prior to sampling. Means are based on five samples per depth per collection date. Vertical lines are 1 SE

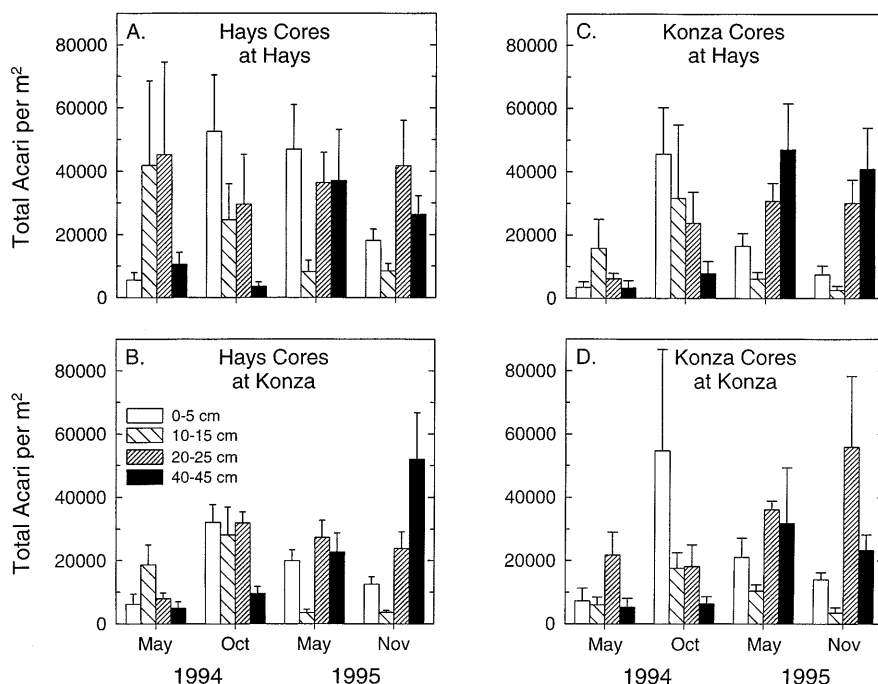
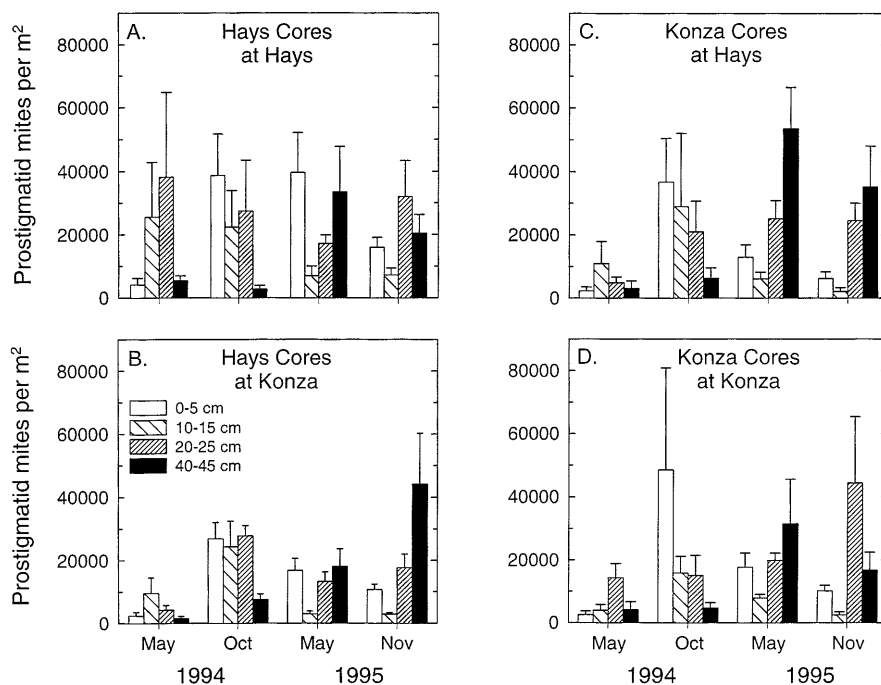


Fig. 6 Abundances of prostigmatid mites by depth increment in soil cores originating from Hays (A, B) or from Konza (C, D), and incubated at either Hays or Konza prior to sampling. Means are based on five samples per depth per collection date. Vertical lines are 1 SE



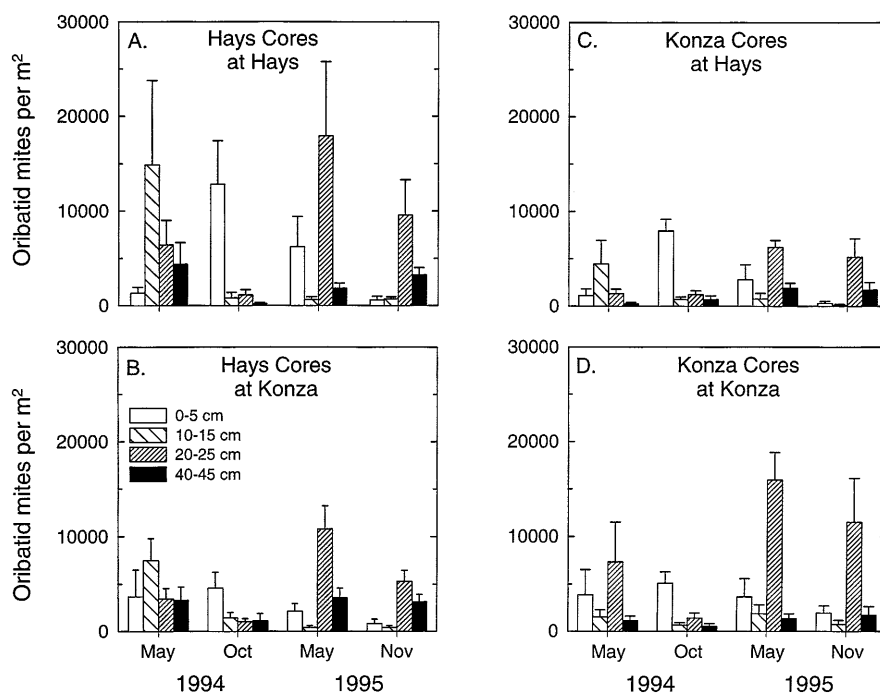
compared to cores transplanted to Konza. A three-way ANOVA (date, depth and location) indicated that prostigmatid mites in Hays cores were affected by location (Hays>Konza) and by a date-location interaction (Table 3). There also were significant effects of depth and date on prostigmatid mite abundances in cores from Hays. Oribatid mite densities in cores originating from Hays also were affected by depth, sample date and a date-depth interaction (Table 3). A Tukey's Studentized Range test revealed that oribatid mites in Hays cores (averaged over all dates and locations) were

significantly more abundant samples from 20–25 cm deep, relative to samples from 10–15 and 40–45 cm.

In contrast to cores originating from Hays, prostigmatid mite abundances in cores originating from Konza were not affected by core location (Fig. 6C, D) but were affected by collection date, depth and a date-depth interaction (Table 4). There was a marginally significant effect ($P=0.08$) of incubation location on oribatid abundances in cores originating from Konza, but in this case greater oribatid mite abundances occurred in cores remaining at Konza compared to cores trans-

Table 4 ANOVA of microarthropod abundances in cores originating from Konza

Dependent variable	Source of variation	df	SS	F	P
Acari	Date	3	45.8946	16.22	0.0001
	Depth	3	30.1612	10.66	0.0001
	Location (loc)	1	1.3645	1.45	0.2314
	Date × depth	9	55.3747	6.52	0.0001
	Date × loc	3	0.6736	0.24	0.8697
	Depth × loc	3	1.7539	0.62	0.6034
	Date × depth × loc	9	4.3713	0.51	0.8614
	Error	123	116.0052		
	Total	154	258.2639		
Prostigmatid	Date	3	51.5219	17.62	0.0001
	Depth	3	28.8053	9.85	0.0001
	Loc	1	0.5611	0.58	0.4494
	Date × depth	9	52.6107	6.00	0.0001
	Date × loc	3	0.3284	0.11	0.9528
	Depth × loc	3	1.7902	0.61	0.6082
	Date × depth × loc	9	4.7223	0.54	0.8441
	Error	123	119.8589		
	Total	154	262.5062		
Oribatid	Date	3	5.1525	2.47	0.0647
	Depth	3	34.8492	16.74	0.0001
	Loc	1	2.1794	3.14	0.0789
	Date × depth	9	39.1107	6.26	0.0001
	Date × loc	3	2.5849	1.24	0.2976
	Depth × loc	3	2.3145	1.11	0.3471
	Date × depth × loc	9	5.6928	0.91	0.5177
	Error	123	85.3608		
	Total	154	178.9579		

Fig. 7 Abundances of oribatid mites by depth increment in soil cores originating from Hays (A, B) or from Konza (C, D), and incubated at either Hays or Konza prior to sampling. Means are based on five samples per depth per collection date. Vertical lines are 1 SE

planted to Hays (Fig. 7C, D). A three-way ANOVA (date, depth and location) of oribatid mite data from Konza cores revealed marginally significant effects of date and location (Konza>Hays), a significant effect of depth, and a significant date–depth interaction (Table

4). A Tukey's Studentized Range test revealed significantly greater abundances of oribatid mites in Konza cores (averaged over all dates and locations) at 20–25 cm deep, relative to all other sample depths.

Discussion

Experiment 1 – Irrigation Transect Experiment

This study examined the influence of soil water on one component of the soil biota—soil microarthropods. Soil water content typically is greater in lowlands than uplands in Flint Hills grasslands, and patterns of plant productivity usually reflect these gradients (Schimel et al. 1991; Knapp et al. 1993). Measurement of gravimetric soil water in 0–5 cm deep cores indicated no significant differences between upland and lowland sites on the dates sampled. This may be related to greater than normal precipitation during the study period. It also is likely that occasional measurements of gravimetric soil water content were insufficient to detect longer-term average differences between upland and lowland sites, as suggested by TDR measurements in 1995 (Fig. 2). Differences in soil water between irrigated and control plots were as expected, with higher soil water in irrigated plots.

Mean abundances of total microarthropods in the Irrigation Transect Study ranged from about 20000 to 120000/m² to a depth of 5 cm. A previous study at Konza Prairie (Seastedt 1984b) indicated mean total microarthropod densities of about 60000/m² in the top 5 cm of soil on annually burned upland sites, and significantly lower densities at annually burned lowland sites (46000/m²). We also found microarthropods to be more abundant at the generally drier upland sites. Although microarthropods in these studies were identified only to coarse taxonomic levels, the data provide a general overview of composition, function and densities of microarthropods in tallgrass prairie. As expected, Acari constituted the majority of total microarthropods, with prostigmatid mites and oribatid mites being the dominant suborders. Oribatid mites found in these studies are generally chewing detritivores. In contrast to many other terrestrial ecosystems where oribatid mites dominate, prostigmatid mites appear to be the dominant Acari in tallgrass prairie. The feeding habits of prostigmatid mites are more difficult to categorize since they include species representing a variety of trophic habits. The prostigmatid mite families Tydeidae and Eupodidae, which include piercing fungivores, were common in our study, as were species of Rhagidiidae, which are predators.

As noted, total microarthropods were more abundant at the drier upland sites. Abundances of total Acari were not affected by site alone, although oribatid mites were more abundant at upland sites, at least in October 1994 and May 1995. Thus, it appears that that differences in total microarthropod abundances between upland and lowland sites were driven by responses of other groups, including Collembola, Diplura, Protura, Symphyla, Formicidae and Coleoptera larvae. Irrigation significantly reduced abundances of both total microarthropods and total Acari. Reductions in

prostigmatid mite abundance contributed the most to this result, with greater numbers of prostigmatid mites in control plots on all but two collection dates. Oribatid mites were significantly more abundant in control plots only in October 1994.

Across biomes and ecosystem types, microarthropod abundances generally are greatest in areas of moderate soil water content and lowest in dry and extremely wet areas (Petersen and Luxton 1982), although organic matter distribution can be as important as water availability in extremely arid environments (Steinberger et al. 1984; Whitford 1989). Given that grassland soils are subject to periodic droughts and seasonal drying, we expected microarthropod abundances to be positively correlated with soil water content. However, results from this study indicated lower abundances of total microarthropods, total Acari and prostigmatid mites in areas where soil water content was greatest (i.e. lowland sites and irrigated plots). This was surprising and opposite to our initial expectations. The lower microarthropod densities at the lowland sites, noted in this and previous studies in tallgrass prairie (Seastedt 1984b), may be partly due to the higher clay content at lower catenary positions. In this study, clay content of the lowland soils was 38%, relative to 34% for upland soils. Finer textured soils would provide limited pore space and more restricted movement of microarthropods. However, this would not explain the negative responses to supplemental water. It is possible that microarthropod responses to soil water levels are non-linear and the irrigated plots may have been too wet, causing conditions that were not suitable for microarthropods (e.g. anaerobic conditions or a greater proportion of water-filled pore spaces). This suggests that increased soil water in this grassland may negatively impact soil microarthropod communities. However, caution must be used in extrapolating to long-term changes in soil water availability. First, these results were obtained in years having greater than average precipitation, and so control plots already were wetter than normal. Second, these results indicate only short-term responses to increased water availability. Microarthropod densities might recover, or even increase, with longer-term increases in soil water content (e.g. due to climate change) as a result of acclimation or shifts in community composition.

Experiment 2 – Reciprocal Core Transplant Experiment

Data from the Reciprocal Core Transplant Experiment suggested both long- and short-term effects of climate on grassland microarthropod abundances and distributions. Microarthropods were most abundant in “native” cores from the drier Hays site. There were significant changes associated with transplanting cores to sites with different climates. Transplanting cores originating from Hays to the wetter Konza environment resulted in significant reductions in abundances of microarthro-

pods and prostigmatid mites in particular, both of which maintained greater numbers in cores remaining at Hays. These results were unexpected. We anticipated that transplanting drier Hays cores to the potentially more favorable environment at Konza (e.g. increased soil water) would result in increased microarthropod densities. The simplest explanation is that Acari communities (in particular, prostigmatid mites) in cores originating from Hays were better adapted to the drier environment and were negatively impacted by the change in environmental conditions (e.g. increased soil water). Although unexpected, this is consistent with results of the Irrigation Transect Experiment and provides additional evidence for the non-linear responses of microarthropods to soil water in grassland ecosystems. This may be related to changes in survival and/or reproductive rates, although the specific mechanisms underlying these responses were not investigated.

Cores originating from Konza showed no significant effects of core location on total Acari and prostigmatid mite abundances, although oribatid mite densities were generally reduced in cores transplanted to the drier Hays site. Initially, we expected that Acari in cores originating from Konza would be negatively impacted by drier conditions occurring at Hays, resulting in lower densities in cores transplanted to Hays. However, abundances of total Acari (and of prostigmatid mites in particular) in Konza cores remaining at Konza were no greater than abundances in cores transplanted to Hays. This indicates that the drier environmental conditions at Hays did not negatively affect numbers of total Acari, or prostigmatid mites from Konza, and suggests that, in general, Acari communities in more mesic areas may be more tolerant of some environmental changes and may adjust to drier conditions. This is consistent with results from desert ecosystems, where microarthropods are frequently the only group of soil fauna that remain active in dry soils (Whitford 1989). In contrast, abundances of oribatid mite in cores originating from Konza were generally lower in cores transplanted to Hays, suggesting that oribatid mites may be not cope as well with environmental changes, especially drier conditions. This is consistent with studies in temperate forest ecosystems, showing that oribatids are very sensitive to climatic alterations (i.e. drier, warmer conditions) associated with forest canopy removal (Seastedt and Crossley 1981; Blair and Crossley 1988). These results suggest that reduced soil water availability may negatively impact some specific components of soil microarthropod communities (i.e. oribatid mites).

Patterns of microarthropod abundance as a function of sample depth in this study demonstrate the importance of sampling to depths greater than are usually sampled in grasslands. There have been very few studies of the vertical distribution of microarthropods, especially to great depths, and we know of no previous studies done in tallgrass prairie ecosystems. Studies of vertical distribution may be more important in grasslands, especially tallgrass prairie, than in other ecosystems

since the majority of plant biomass in grasslands is belowground, and microarthropods can occur abundantly throughout the soil profile. Most microarthropod studies examine only the upper 5–10 cm of soil, where the majority of microarthropods generally are thought to reside (Coleman and Crossley 1996). However, our sampling of microarthropods to a depth of 45 cm indicated that the top 5–10 cm of soil may not be representative of actual microarthropod densities and communities throughout that soil profile. Therefore, it appears that sampling the upper 5–10 cm of soil to quantify microarthropods, or their responses to experimental treatments, may not be sufficient, at least in tallgrass prairie. For example, we found significantly higher abundances of microarthropods in 20–25 cm deep samples in this study. This is consistent with the results of Leatham and Milchunas (1985) which indicated maximum mite abundances at both the soil surface and at a 25–40 cm depth in shortgrass steppe. The abundance of microarthropods throughout the upper soil profile may be related to the high amount of primary productivity that occurs belowground in grasslands. However, the depth distribution of microarthropods in our study was not correlated with root biomass or soil organic matter content, both of which were greatest in the upper 10 cm and declined with depth (data not shown). Instead, the vertical distribution of microarthropods in grasslands is likely a function of both resource availability and abiotic factors, including soil water availability (Leatham and Milchunas 1985). Droughts, a common occurrence in grasslands, can result in a drier surface soil, and microarthropods may migrate down the soil profile to areas of higher soil water content in grassland soils.

Conclusion

These studies provided new information on microarthropod densities and distributions in tallgrass prairie, and also indicated the importance of sampling to greater depths in order to sufficiently quantify microarthropod communities. The effects of varying water availability on soil invertebrates, both locally and regionally, provided some new insights into how potential climate change may affect grassland ecosystem functioning and productivity. Microarthropod responses to soil water availability are complex. Depth distributions of microarthropods suggest positive responses to water availability in the soil profile. However, increasing soil water content may, in fact, negatively impact soil microarthropod abundances and alter microarthropod composition. Increasing water availability, through the use of irrigation or by transporting cores to wetter environments, resulted in a decrease in total and/or specific groups of microarthropods. This suggests adaptation to current environmental conditions and a number of additional factors, such as soil depth, texture and organic matter content may regulate microarthropod densities and distributions in grasslands. Further research will be

necessary to better understand the factors controlling soil communities and processes in tallgrass prairie, and how this ecosystem might respond to climate changes.

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