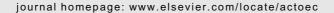


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# Original article

# Effects of water addition on soil arthropods and soil characteristics in a precipitation-limited environment

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#### ABSTRACT

We investigated the effect of water addition and season on soil arthropod abundance and soil characteristics (%C, %N, C:N, moisture, pH). The experimental design consisted of 24 groups of five boxes distributed within a small aspen stand in Saskatchewan, Canada. The boxes depressed the soil to create a habitat with suitable microclimate for soil arthropods, and by overturning boxes we counted soil arthropods during weekly surveys from April to September 1999. Soil samples were collected at two-month intervals and water was added once per week to half of the plots. Of the eleven recognizable taxonomic units identified, only mites (Acari) and springtails (Collembola) responded to water addition by increasing abundance, whereas ants decreased in abundance with water addition. During summer, springtail numbers increased with water addition, whereas pH was a stronger determinant of mite abundance. In autumn, springtails were positively correlated with water and negatively correlated with mites, whereas mite abundance was negatively correlated with increasing C:N ratio, positively correlated to water addition, and negatively correlated with springtail abundance. Although both mite and springtail numbers decreased in autumn with a decrease in soil moisture, mites became more abundant than springtails suggesting a predator-prey (mite-springtail) relationship. Water had a significant effect on both springtails and mites in summer and autumn supporting the assertion that prairie soil communities are water limited.

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# 1. Introduction

Primary productivity in both temperate and tropical regions is constrained by water availability (Deshmukh, 1984; Le Houerou et al., 1988; Silvertown et al., 1994; Knapp and Smith, 2001). Annual precipitation on the dry-climate prairies is highly variable (Sala and Lauenroth, 1982; Frank and Inouye, 1994; Wolanski et al., 1999) and at the regional scale, variation in annual precipitation accounts for most of the spatial variability in productivity ( $r^2 = 0.90$ ; Sala et al., 1988). Prairie organisms are adapted to the irregular spatial

tem productivity and decomposition rates (Whitford et al., 1981). Hence, prairie regions are quite responsive to changes in water availability (Knapp et al., 2001).

Within prairie ecosystems, spatial variation in habitat can

and temporal fluctuations in precipitation that affects their

distribution and abundance, and in turn, can affect ecosys-

Within prairie ecosystems, spatial variation in habitat can affect soil–arthropod relations (Ferguson, 2001). For example, grassland soils experience greater variation in soil moisture relative to forests and are subjected to a greater evapotranspiration rate because of higher temperatures, which in turn decreases soil moisture (Wilson and Kleb, 1996; Ferguson, 2004b). Soil microarthropods are found in many soils and are recognized as indicators of soil quality because they contribute to litter decomposition, nutrient cycling, and soil structure (Battigelli et al., 1994; Narula et al., 1996; Wilby and

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Brown, 2001). Mites and springtails make up a significant part of the belowground food web in many terrestrial ecosystems. Due to their sensitive organs both microarthropods actively seek dark microclimates (Hopkin, 1997; Salmon and Ponge, 1998). Therefore, different vegetation types (grass, shrub, forest) may provide distinct habitats for microarthropods because light penetration, moisture content, pH, and soil nutrients (N, Ca, K, S, Mg, P) are affected by vegetation and thereby influence species composition and abundance (Schaefer, 1995; Paquin and Coderre, 1997b; Ferguson, 2001).

Fluctuations in soil characteristics influence the abundance of microarthropods (Ponge, 1993). Changes in pH, for example, result in changes in mite (Acari) and springtail (Collembola) abundance as well as their interactions with other organisms (Verhoef and Dorel, 1988). Because microarthropods are concentrated in the litter layers and upper horizons of the soil, they are susceptible to abiotic changes. Consequently, their abundance and distribution is highly dependent on their individual tolerance limits to temperature and moisture conditions (Paquin and Coderre, 1997a; Jastrow, 1987; Faber and Verhoef, 1991; Narula et al., 1996; Brand and Dunn, 1998; Johnston, 2000).

In this study, we test whether water limits soil arthropod numbers in a prairie ecosystem (grass–shrub–forest transition) and describe the changes in soil characteristics associated with soil arthropod abundance over seasons and through experimental water addition. We address the question as to whether water addition results in an increase in abundance of soil arthropods and subsequently affects soil characteristics.

#### 2. Methods

# 2.1. Description of study area

The study area consisted of a 0.13 km² stand of undisturbed trembling aspen (*Populus tremuloides* Michx.) forest located within 1.5 km of the city of Saskatoon in the prairie region of south-central Saskatchewan, Canada (52°10′N, 106°41′W). Grassland prairies in this region include small patches of forest dominated by an aspen overstorey and an understorey of

serviceberry (Amelanchier sp.). The forest floor consists of a 3–7 cm O horizon. The mineral soil in the region consists primarily of silt and clay with some sand (Christiansen, 1970). Weekly precipitation and temperature during the April–September 1999 study period ranged from 0 to 49.4 mm and from 3.7 to 20.3 °C, respectively (Environment Canada, 2000). There was no evidence or known history of grazing or other agricultural use of the site.

#### 2.2. Experimental design

Twenty-four plots were randomly established along a grassshrub-forest gradient, approximately 5 m apart and consisted of five adjoining boxes (Fig. 1). For the water addition treatment, twelve plots were randomly selected from the total and 500 ml of water was added under each box once a week for 20 weeks. Boxes consisted of two 2-liter milk cartons (hereafter referred to as a box), one fitted inside the other (to create a solid box), and half filled with sand (ca. 2 kg). Cardboard milk cartons (i.e. boxes) had a plastic coating and were red and white in color. Boxes depressed the leaf litter an average of 1.3 cm (Ferguson, 2000) creating a footprint-sized depression 21 by 9.5 cm<sup>2</sup> by 1.3 cm for soil arthropods, similar to that beneath a rock resting on the forest floor. Humidity and temperature under boxes indicated an increase and decrease, respectively, compared to outside the boxes (Ferguson, 2001) that offered a home to a diverse soil fauna community.

#### 2.3. Arthropod sampling

During field surveys, boxes were overturned and the numbers and size of all macroarthropods (> 3 mm) and most microarthropods (< 3 mm) observed directly under the boxes were recorded without disturbing leaf litter. Leaf litter was not moved and only arthropods directly under the box and located on top of the litter at the moment when the box was lifted were recorded. The pattern of lifting boxes in each plot varied throughout surveys. Between April and September 1999, 20 weekly surveys were conducted between the hours of 1100–1700. The survey numbers do not reflect absolute abundance but rather a relative measure of abundance

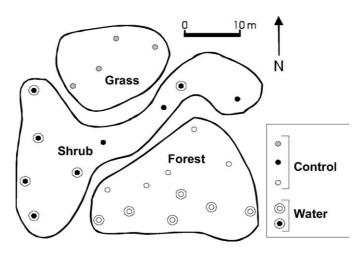


Fig. 1 - Landscape pattern of study site showing grass, shrub, and forested areas and water addition plots.

of surface-dwelling soil arthropods. Time spent watching of overturned box was not standardized but approximated 1–3 min.

Recognizable Taxonomic Units (RTU; Bolger et al., 2000; Ferguson and Berube, 2004) were used to group all observed arthropods based on differences in size and feeding habits. Springtails (Collembola) and predatory mites (Gamasides) were the most abundant microarthropods in this study (Ferguson and Joly, 2002). All springtail species, regardless of stages of development, were placed in one taxonomic group, as most species consume fungi (Hopkin, 1997). Surface-dwelling springtails were slow, small (length ranged from 0.2-2.6 mm), and soft-bodied. Predatory mites were identified according to their long legs and greater mobility (relative to phytophagous mites), and are non-specific predators that commonly feed on springtails (personal observations and Berg et al., 1998). All macroarthropods were counted but only data for the more abundant groups are considered here: spiders (Araneida), ants and their larvae (Formicoidae), beetles (Coleoptera and Staphylinidae) and their larvae, centipedes (Chilopoda), bugs (Hemiptera), adult flies (Diptera), and Diplurans. Other macroarthropod groups were identified but not analyzed due to low numbers included: phytophagous mites (Acari: Oribatida), Homoptera, Pseudoscorpionida, Lepidoptera (moth and butterfly larvae), Anoplura, Gastropoda, Isopoda, Thysanoptera (thrips), Psocoptera (barklice), and earthworms.

#### 2.4. Soil sampling

One hundred twenty-five milliliter of soil from the L horizon was sampled under one of the boxes from each of the 24 plots (five box patterns), on 20 April (spring), 22 July (summer), and 19 September (autumn) 1999 (N=72 samples) and were immediately frozen. Samples consisted of leaf litter, twigs, roots, and small amounts of mineral soil. Each soil sample was tested for moisture content, C, total N, pH level, and available water.

The amount of water (% moisture) retained in the soil after leaching, erosion, and runoff was estimated by drying 5 g of wet crushed soil from each sample in an oven at 110 °C for 48 hours. The samples were then re-weighed and the percent moisture content was calculated (Kalra and Maynard, 1991).

The principle of weight loss of soil by ignition was used to determine total C (Kalra and Maynard, 1991). The initial 5 g of soil used for the moisture content was additionally used to determine C content. Two grams of the oven-dried soil was burned in a muffle furnace at 600 °C for 24 hours. The samples were then placed into a desiccator to cool and then reweighed to determine weight loss. Each soil weight was multiplied by 58% as the estimated amount of carbon in soil (Kalra and Maynard, 1991). The final results are expressed as the percent carbon content.

Total nitrogen was measured by grinding each sample to <60 mm. A 0.5 mg sample was mixed in a 75 ml test tube with 2 or 3 boiling glass beads and 7.5 ml of sulfuric acid ( $H_2SO_4$ ). This resulted in the organic nitrogen being converted to ammonia (Kalra and Maynard, 1991). After 5 hours of digestion, the samples were boiled at 150 °C for one hour

or until a color change, and then further boiled at 200 °C. The test tubes were then heated at 380 °C until the solution became transparent. The samples were removed immediately after the clearing, then cooled, and the acid and the soil solution was mixed. Distilled water was added to fill each 75 ml test tube, and shaken and stored overnight. The samples were analyzed for total nitrogen on the Skalar autoanalyzer and completed within 36 hours of digestion. For quality control, three blanks were included with each batch of 40 samples and three duplicates were included for every batch of 20 samples. Carbon to nitrogen ratios were calculated using the results of the % N (mg/l) and the % carbon content.

Soil pH was determined by placing 1 g of each soil sample into plastic beakers and saturated with 10 ml of distilled water. The solution was left for one-half hour before the acidity was determined potentiometrically. One gram for each sample was then placed into a separate beaker with 10 ml of 0.01 M CaCl<sub>2</sub> solution. They were also left for one-half hour before reading to determine the reserve acidity. Between each reading, the glass bulb was washed with distilled water. Each sample was stirred to ensure that the soil was completely covered with the solution.

The soil available water, including both the moisture content at field capacity and moisture content at the permanent wilting point, was calculated using the available water method outlined in McKeague (1978). The available water fraction was determined only for the autumn samples as preliminary analyses determined that moisture content did not differ between treatment (water addition) and control (no water addition) for spring and summer samples (see Section 3).

# 2.5. Statistical analysis

Statistical tests that included ANOVA, multiple regressions, and path analyses (Sokal and Rohlf, 1981) were done using SAS (SAS Institute Inc., 1990) statistical software for microcomputers. Changes in soil arthropod abundance (RTU, dependent variables) over time (weekly surveys), vegetation type (grass, shrub, forest), and with/without water addition (independent variables) were conducted with analysis of variance (ANOVA) of ranked data (nonparametric test: Conover and Iman, 1981). Sample units were the five-box groups (N = 24) sampled every week (N = 20) (total = 480). Week of survey was a random variable whereas water addition and vegetation type were fixed variables. The dependent variables were square root transformed values of abundance of microarthropods (springtails and mites) and nine macroarthropod groups. Abundance measures included zero values, and were therefore coded by adding 0.5 (Sokal and Rohlf, 1981: 421). Results are given as untransformed means.

Differences in the five soil measurements were tested over season (spring, summer, autumn) and vegetation type using ANOVA of ranked data. Season was considered a random variable whereas vegetation type was fixed.

For the comparison between the effects of soil characteristics and arthropod (mite and springtail) abundance the soil variables were used as explanatory variables in a stepwise regression model of ranked data (Conover and Iman, 1981).

Independent explanatory variables included moisture content, pH, C %, N %, C:N ratio, and available water fraction (autumn only) and were removed from the model if P > 0.10. A forward selection of significant explanatory variables was used to find the best combination of the selected variables.

Many important ecological and evolutionary processes are influenced by multiple interacting factors (Quinn and Dunham, 1983) that are best analyzed using path analysis and related techniques (Petraitis et al., 1996). Predictions are possible if models are based on causal relationships, not correlative, between the variables (Zmyslony and Gagnon, 2000). In path analysis, the model is formulated as a path diagram, in which arrows connecting variables represent regression coefficients. We compared two models using path analysis. Model 1 predicted that mite and springtail abundance were best explained by time (seasons), space (vegetation type), treatment (water addition or control), and predator or prey (mites as predators explained springtail abundance or springtails as prey explained mite abundance). In contrast, Model 2 used the same Model 1 variables with the additional four-soil variables moisture, C, N, and pH. The latter model tested whether adding soil characteristics improved the model fit. In both models, we assumed that season and vegetation type were not correlated (i.e. correlation coefficients set to 0.0 regardless of the observed correlation; Petraitis et al., 1996). Models were compared based on explanation power (R<sup>2</sup>). Here, we use the a priori path model approach that distinguishes formal hypothesis testing in the presentation of a formal path model that is derived from a testable idea rather than preliminary data analysis. In other words, the causal models are separate from the data that will be used to estimate strengths of paths in the model.

### 3. Results

# 3.1. Soil arthropod abundance

Differences occurred with water addition, time (2-week surveys), and vegetation type among the soil arthropod groups (Table 1). However, among the soil arthropod groups, only

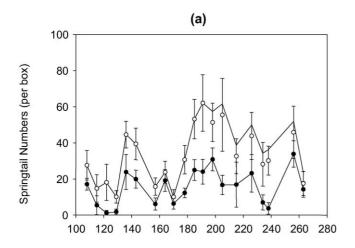
mites and springtails responded significantly to water treatment. Most arthropod groups showed seasonal differences in abundance with the exception of ants, ant larvae, and diplurans (Table 1). Springtail abundance differed with vegetation type: lower in grass habitat (3.35 individuals/plot) and greater in shrub (4.91) and forest (4.69). Also, springtail abundance was greater with water addition (5.58 versus 3.70). Mite abundance also increased with water addition (4.34 versus 3.40). However, mite abundance was greater in shrub (4.32) versus grass (3.44) and forest (3.41). Spider abundance did not differ with water or vegetation type. Ant abundance decreased with water addition (1.41 versus 1.11 with water) but did differ with vegetation type (higher in grass (1.86) versus shrub (1.21) and forest (1.09). Ant colonies did not differ with water addition or vegetation type. Also, beetle, bug, fly, and dipluran abundance did not differ with water addition or vegetation type.

Mites and springtails were the most abundant soil arthropods and they peaked in abundance in the summer with a higher overall number of mites than springtails. The abundance of springtails and mites were greater in watered versus non-watered plots (Fig. 2). For mites, the increase in the summer was similar in both the control and experimental plots but the abundance was significantly higher in the watered plots (mean = 64) compared to the non-watered plots (mean = 38). The further decrease in mite abundance in the fall in the non-watered plots (mean = 3) suggests that factors other than the water addition contributed to the change in the population of mites over summer. Mite abundance peaked in summer whereas springtail numbers were more variable over time.

As springtail and mite abundance both showed increases with water addition, we chose to analyze the effects of changes in abundance of these two groups relative to soil characteristics with and without water addition. Differences occurred in soil characteristics relative to water addition only for the September survey (Table 2). Likely, the effects of water addition on soil characteristics are cumulative and would be found most pronounced at the final sampling.

Table 1 – Results of analysis of variance to determine the effects of vegetation type, time, and water addition on abundance of soil arthropods (N = 480)

Recognizable	Recognizable					Vegetation		Water addition		Arthropod abundance			
											(inc	dividuals	/plot)
Taxonomic	M	odel	T	ime	W	ater (	T	ype	No	Yes	Grass	Shrub	Forest
unit	F	P	F	P	F	P	F	P					
Microarthropods	3												
Springtails	26.3	0.001	20.4	0.001	126.4	0.001	3.35	0.04	a 3.70	b 5.58	a 3.35	b 4.91	b 4.69
Mites	100.4	0.001	111.9	0.001	32.7	0.001	13.9	0.001	a 3.40	b 4.34	a 3.44	b 4.32	a 3.41
Macroarthropod	s												
Spiders	1.91	0.008	2.06	0.006	0.28	0.59	0.87	0.42	a 0.84	a 082	a 0.86	a 0.81	a 0.85
Ants	2.04	0.004	0.89	0.59	1.26	0.26	9.73	0.001	a 1.41	b 1.11	a 1.86	b 1.21	b 1.09
Ant colonies	1.12	0.32	1.09	0.35	0.99	0.32	1.67	0.18	a 0.77	a 0.74	a 0.76	a 0.78	a 0.72
Beetles	1.65	0.03	1.87	0.01	0.34	0.55	0.21	0.81	a 0.81	a 0.83	a 0.81	a 0.82	a 0.83
Centipedes	2.33	0.001	2.19	0.003	1.72	0.19	2.77	0.06	a 0.86	b 0.91	a 0.80	ab 0.88	b 0.91
Bugs	1.85	0.01	1.62	0.049	0.62	0.43	4.80	0.009	a 0.83	a 0.82	a 0.90	b 0.81	b 0.81
Flies	3.28	0.001	3.63	0.001	0.01	0.91	1.49	0.23	a 0.82	a 0.83	a 0.79	a 0.82	a 0.85
Beetle Larvae	2.68	0.001	3.00	0.001	0.00	0.96	0.79	0.45	a 0.79	a 0.80	a 0.77	a 0.80	a 0.78
Diplurans	24.2	0.001	27.4	0.001	0.52		0.473	01 0.05	a 1.13	b 1.28	a 0.970	b 1.28	b 1.2
* Means with the same letter are not significantly different.													



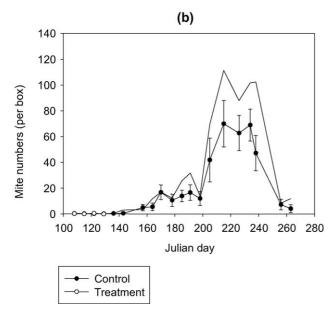


Fig. 2 - Springtail and mite numbers under treatment (250 ml water added after each survey) and control boxes.

#### 3.2. Soil characteristics

No differences occurred in the soil characteristics (C, N, C:N, MC, FC, PWP, AW) between water addition and control plots (Table 2). There was no rain 10 days prior to spring sampling

and 9.6 mm of rain fell 3 days before the summer sampling, which would have affected the amount of moisture in the soil at the time of sampling.

However, among the soil measurements, differences occurred over seasons. Carbon and C:N increased from a low in spring, to a high in summer and autumn. In contrast, N decreased from spring to summer.

# 3.3. Soil characteristics and mite and springtail abundance

Although springtail abundance was not correlated with soil characteristics during any of the three seasons, mite abundance was related to soil characteristics in summer and autumn. In summer, only mite abundance and pH were correlated with greater mite abundance in more acidic soils (r = -0.76, P = 0.001). During autumn, mite abundance was positively correlated with nitrogen (r = -0.76, P = 0.001) and negatively correlated with C (r = -0.36, P = 0.02) and C:N (r = -0.50, P = 0.01).

Partial correlations analysis determined the relative contribution of soil characteristics to mite and springtail abundance over the three seasons. Water was added to plots during the first field survey (20 April, 1999), therefore no relationships were evident during the spring season. During summer, higher water content and lower pH were correlated with greater mite abundance, whereas no significant relationships were evident for springtails (Table 3). In autumn, greater springtail abundance was related to water addition and fewer mites. For mites, greater abundance occurred with lower C:N, with water addition, and in plots with fewer springtails (Table 3).

# 3.4. Comparison of models

We compared two models explaining changes in mite and springtail abundance (Fig. 3). The first model (Model 1) assumed that together water addition, season, and vegetation type best explained changes in abundance of mites and springtails. The second model (Model 2) included the same assumptions as the first model (Model 1) with the addition of soil characteristics as explanatory variables describing changes in mite and springtail abundance (Table 4). For springtails, Model 2 explained more variation in springtail abundance than Model 1 (F = 3.3, P = 0.003,  $R_{adj}^2 = 0.21$  versus F = 5.3, P = 0.001,  $R_{adj}^2 = 0.19$ ). For mites, Model 2 explained more variation in abundance than Model 1 (F = 2.6, P = 0.01,  $R_{adj}^2 = 0.16$  versus F = 2.3, P = 0.07,  $R_{adj}^2 = 0.07$ ). Adding soil

Table 2 – Results of analysis of variance to determine the effects of vegetation type, season, and water addition on soil characteristics

Soil	Season				Vegetation type				Water addition		
Characteristic	P	April	July	Sept	P	Grass	Shrub	Forest	P	None	Water
Carbon	0.001	a 27.8	b 45.9	b 32.9	0.27	a 41.2	a 35.1	a 33.5	0.92	a 35.4	a 35.6
Nitrogen (× 10 <sup>3</sup> )	0.006	a 17.2	b 13.6	ab 14.9	0.85	a 15.6	a 15.3	a 14.8	0.65	a 15.1	a 15.2
C:N ratio	0.001	a 16.4	b 27.1	b 24.4	0.87	a 21.3	a 20.4	a 25.9	0.27	a 22.4	a 22.8
Moisture	0.001	a 136.2	b 105.2	c 83.6	0.16	a 135.7	a 106.4	a 98.5	0.25	a 114.3	a 102.3
pН	0.007	a 6.47	b 6.37	b 8.58	0.001	ab 6.41	a 7.92	b 6.51	0.23	a 6.42	a 7.85
Available water				232.8					0.20	a 267.6	a 209.6
FC				289					0.17	a 325	a 265.1
PWP				56.2					0.20	a 57.3	a 55.4
* Means with the same letter are not significantly different.											

Table 3 – Seasonal multiple regression model for springtail and mite abundance using the following independent variables: C:N ratio, C, nitrogen, moisture, pH, and two dummy variables (water addition: 0 = none, 1 = water; vegetation type: 1 = grass, 2 = shrub, 3 = forest)

Season	Dependent variable	Independent variable	Coefficient value	Partials	R <sup>2</sup>	P
Spring	Springtails	None				
	Mites	none				
Summer	Springtails	water	3.98	0.468	0.468	0.0002
	Mites	рН	-0.306	0.632	0.632	0.0001
Autumn	Springtails	water	1.567	0.178	0.178	0.04
		mites	-0.415	0.248	0.426	0.007
	Mites	C:N ratio	-0.0891	0.248	0.248	0.013
		water	1.831	0.139	0.387	0.041
		Springtails	-0.588	0.156	0.543	0.017

# Model 2

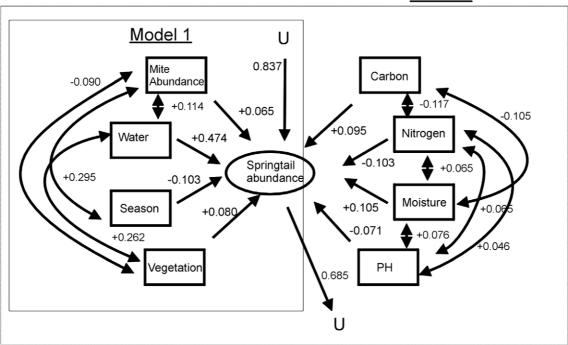


Fig. 3 – Path diagram comparing two models that describe the direct and indirect effects of soil characteristics and environmental variables on abundance of springtails: Model 1 predicts that mite abundance, water, season, and vegetation adequately explain variation in springtail abundance; whereas Model 2 combines the same predictions of Model 1 with the additional explanatory variables of soil characteristics (C, nitrogen, moisture, and pH). Correlation coefficients are compared (multiple regression models in Table 4). Double-headed arrows represent the correlations among the predictor variables and single-headed arrows are the correlations directly affecting springtail abundance. Sample size is 24 plots sampled over three seasons (N = 72 plots of five boxes) located within a poplar stand in the North American prairies. U represents the unexplained variance in the complete models.

characteristics improved the explanatory power of the first model that used seasonal and water-addition to explain changes in microarthropod abundance.

#### 4. Discussion

The amount of precipitation during the 1999 study period from spring to summer was above average (Ferguson, 2001). As a result water addition likely did not considerably increase the soil moisture content and soil and arthropod changes were minimal compared to plots without water

addition. Soil moisture storage varies between soil textures. Dry sites usually have rapid drainage and poor storage capacity and coarse soils are drier in summer than loam or clay (Brady, 1974). The parent material and geomorphology and thus drainage characteristics of our site was only generally known (Christiansen, 1970). Drainage characteristics may partly explain why the soil moisture continually decreased as water was added. Soil samples were comprised of sand, with rapid drainage, whereas more poorly drained soils are expected to have higher organic matter and N accumulation (Brady, 1974). Although no differences were found between water addition and soil characteristics, differences were

Dependent variable	S	Springtails		Mites
Statistic	Model 1	Model 2	Model 1	Model 2
Degrees of freedom	4,71	8,71	4,71	8,71
F value	5.34	3.29	2.25	2.64
Probability	0.001	0.003	0.07	0.01
$R^2$	0.239	0.291	0.117	0.248
R <sup>2</sup> adjusted	0.194	0.203	0.065	0.155
Parameter estimate:				
Mite/springtail abundance	$+0.0414 \pm 0.117$	$-0.0415 \pm 0.124$	$+0.0449 \pm 0.127$	$-0.0415 \pm 0.126$
Water	$+0.555 \pm 0.129$	+0.589 ± 0.134	$+0.140 \pm 0.151$	$+0.140 \pm 0.151$
Season	$-0.121 \pm 0.118$	$-0.258 \pm 0.186$	$+0.307 \pm 0.119$	$+0.0496 \pm 0.188$
Vegetation	-0.0463 ± 0.121	$-0.0373 \pm 0.135$	-0.133 ± 0.125	$+0.0021 \pm 0.135$
Carbon		$+0.184 \pm 0.118$		$+0.230 \pm 0.116$
Nitrogen		$-0.170 \pm 0.113$		$-0.169 \pm 0.113$
Moisture		$-0.0686 \pm 0.161$		$-0.0646 \pm 0.161$
рН		$-0.0226 \pm 0.130$		$-0.262 \pm 0.125$

found between water addition and arthropods among the three seasons.

Although soil characteristics changed over seasons, no direct change was detected due to artificial water addition. During summer, water addition and pH affected mite abundance but no significant relationship was evident for springtails. In autumn, springtails and mites were negatively correlated, suggesting predator-prey relationships (Ferguson and Joly, 2002), and water addition increased the abundance of springtails. Path analysis indicated that inclusion of soil characteristics improved understanding (i.e. greater explained variation) of changes in soil arthropod abundance.

Mites and springtails and ants showed a significant response to the water addition. Their abundance was the highest in summer even with the decrease in soil moisture from spring through autumn. Similar seasonal patterns in abundance that related to the availability of water have been reported (Block, 1985; Reddy and Venkataiah, 1990; Ferguson, 2004b). The variation in abundance of mites and springtails followed similar patterns observed by Narula et al. (1996) and vertical migrations have been found to occur as a response to changes in soil moisture in grassland soils (Hassal et al., 1986). Thus, changes in mites and springtails over time may be explained by changes in distribution as well as mortality. The lower abundance of springtails in the spring is typically a response to low moisture, whereas maximum numbers occurred in the summer (Reddy and Venkataiah, 1990). Mites were almost absent in the spring as their populations decreased before winter and increased again following their one temperature-dependent reproductive period between spring and autumn (Reddy and Venkataiah, 1990). This peak in abundance was evident from our results and the increased abundance of mites and springtails in the summer agree with Narula et al. (1996) that maximum populations are reached during summer months or rainy seasons. Also, low numbers of mites and springtails occur during warmer temperatures and with low moisture during summer months (Johnston, 2000).

Springtails have higher reproductive rates than mites but are less protective, whereas mites possess scleritized exoskeletons (Schaefer, 1995). Adult mites are long-lived with an average lifespan of several months to 2 years from egg to adult (Bilgrami, 1997), whereas springtails have short lifecycles and produce many generations over a year (Schaefer,

1995). Springtail reproductive rate is highly dependent on optimal habitat and the largest densities occur following rainfall in undisturbed soil (Schaefer, 1995; Badejo et al., 1998). This can explain the increase in summer following a peak in reproductive rate in spring. Both mites and springtails decreased in autumn, which is a common seasonal pattern (Reddy and Venkataiah, 1990).

We found no direct relations between any of the soil characteristics (C, N, C:N, moisture, pH, available water, field capacity, and permanent wilting point) and water addition. However, seasonal patterns suggest an influence of the soil and path analysis indicated a significant contribution of soil characteristics to microarthropod abundance. Although no direct causal relationships were determined by our study methodology, the results indicate that the chemistry of organic matter has an effect on trophic relationships and community structure of soil arthropod communities (e.g. Berg et al., 1998).

Carbons to nitrogen ratios vary with climatic conditions, primarily temperature and the amount and distribution of rainfall (Brady, 1974). Therefore, it is not surprising that our results showed a change in C:N from the water addition because rainfall exerts a direct influence on the accumulation of N and organic matter (Brady, 1974). Hence, N increase with greater soil moisture agrees with our findings of highest N concentration occurring in spring with the highest soil moisture. Composition of soil arthropod communities changes across shrub-forest cover (Paquin and Coderre, 1997b; Ferguson, 2001) as predicted by C and N linkages with the quantity and quality of litterfall from vegetation. Precipitation amounts (April-June) significantly affected the rate of decomposition, particularly during extreme drought or excessive rainfall (Knutson, 1997). Litter and vegetation play a role in C:N as leaves that decompose slowly have the ability to store greater moisture and N changes are associated with shifts in species composition (Currie, 1999).

Although carbon is continually present in soil, C % in autumn was not significantly different from C% in summer. Arthropods require more N than C for development and the N decrease in summer suggests mineral uptake by arthropods and also possibly by tree roots. Soil microorganisms will draw upon the inorganic nitrogen pool to meet their requirements (Brady, 1974). Because greater N mineralization occurs in prairie soils when there is an abundance of organ-

isms (Wilson and Kleb, 1997; Rustad et al., 2001) the decrease in N in summer is likely related to the increase in abundance of mites and springtails.

Springtail fecundity and longevity is optimal with appropriate N and C consumption (Johnston, 2000). Springtails tend to concentrate around habitats high in N, as they are fungivorous feeders (Maclean et al., 1996). Springtails require large amounts of N for egg production, molting, and continued growth (Leonard and Anderson, 1991), whereas C is needed to build their body structure (Johnston, 2000). Springtails help regulate the N cycle and their distribution is related to the quality and quantity of food available and the type of vegetation and litterfall in an area (Leonard, 1984). The highest abundance of springtails was in the summer and the recorded decrease in N may have resulted from N being used for reproduction. In contrast, the highest amount of  $\ensuremath{\mathsf{C}}$ was recorded in summer indicating that carbon may not be required for effective reproduction by springtails (Leonard and Anderson, 1991).

Soil pH was the only soil characteristic influenced by different vegetation types (grass, shrub, forest). Water treatment did not have a significant effect on the pH in spring and summer; however, pH increased significantly in autumn. Apparently water addition raised the soil pH possibly due to the use of more basic tap water.

Although water treatment did not affect soil moisture, soil moisture content was high in spring and decreased over summer and autumn. Significantly higher amounts of soil moisture occurred in spring when there was little rain (April, 15 mm) relative to summer when there was abundant rain (July, 167 mm; see also Wilson and Kleb, 1996). Soil moisture may not have been a limiting resource for soil arthropods in 1999 due to higher than average rainfall (Ferguson, 2001) and in turn, water may have enhanced N uptake causing N to be the limiting resource to both organisms and plants. This may explain the fluctuations in both C and N concentrations (e.g. Wilson and Kleb, 1997). A significant decrease in moisture occurred from spring to autumn accompanied by a decrease in N in summer and an insignificant increase in N during autumn.

Mite abundance was more related to changes in soil characteristics than springtails, possibly due to narrower habitat requirements and longer lifecycles. Although pH was similar between spring and summer, the pH had a negative correlation with the mite abundance in summer. These results contrast with Van Straalen and Verhoef (1997) who found no response from mites when pH was near neutral. The pH was slightly basic in autumn and the mite populations decreased in combination with low soil moisture. Hagvar and Amundsen (1981) discovered the same results when mites significantly decreased as a result of lime being added to a site. Since there was no significant relationship between springtails and pH, the spring and summer results concur with Van Straalen and Verhoef (1997) findings of optimal pH levels for springtail reproduction of 6.5; the decrease in springtail abundance occurred with a further increase in pH.

Ultimately, litterfall type and quantity has an influence on abundance and distribution of soil arthropods. This is because arthropods require nutrients for growth and survival, although a lack of soil moisture restricts the movement and availability of nutrients (Brady and Weil, 1998). In sum, our assessment of the effect of water limitation on soil arthropods located on a prairie site found a relationship between soil characteristics and community effects. The overall manipulation of water availability in this mesic prairie habitat predicts that changes due to water addition (e.g. irrigation) or climate change (i.e. temperature warming and decreased precipitation; Knapp et al., 2001) will have a direct measurable impact on the soil arthropod community. Temporal and spatial differences in arthropod abundance and soil characteristics, such as carbon-nitrogen levels, suggest that trophic interactions will change with irrigation practices and climate change on mesic temperate grasslands. Further research is required to discern the trophic relations related to soil biota in energy and nutrient dynamic changes associated with climate change.

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