

Dynamics of springtail and mite populations: the role of density dependence, predation, and weather

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Abstract. 1. Ecological theory suggests that density-dependent regulation of organism abundance will vary from exogenous to endogenous factors depending on trophic structure. Changes in abundance of soil arthropods were investigated at three trophic levels, springtails (Collembola), predaceous mites (Acari), and macro-arthropods (spider, adult and larval beetles, centipedes). Predictions were that springtails are predator regulated and mites are food limited according to the Hairston *et al.* (1960) model, which predicts alternating regulation by competition and predation from fungi to springtails to mites to macro-arthropods. The alternate hypothesis was based on the bottom-up model of trophic dynamics, which predicts that each trophic level is regulated by competition for resources.

2. The relative contributions to springtail and mite population dynamics of endogenous (i.e. density-dependent population growth related to food availability) and exogenous (i.e. predation and weather) factors were tested using time-series analysis and experimental manipulation of water conditions. Box patterns were distributed within an aspen forest habitat located in the Canadian prairies and surveyed weekly from May to September 1997–1999. Each box depressed the leaf litter, creating a microhabitat island for soil arthropods that provided counts of invertebrates located immediately beneath the boxes.

3. Strong evidence was found for endogenous control of springtail and mite numbers, indicated by a reduction in population growth related to density in the previous week. Contrary to predictions, no evidence was found for regulation of springtail numbers by mites, or for regulation of mite numbers by macro-arthropods. Springtail population growth rate was related positively to current springtail density (8 and 23% variation explained) and related negatively to 1-week lagged density (85 and 58%), and related negatively to temperature (5 and 5%) for time-series data and for experimental addition of water respectively. Mite population growth rate was related positively to current mite density (54%) and temperature (4%), and negatively to 1-week lagged mite density (20%) and precipitation (6%) for time-series analysis. For experimental addition of water, mite growth rate was related positively to current mite density (44%) and temperature (5%), and negatively to 1-week lagged density (11%). Results differed from the Hairston *et al.* (1960) model predictions but were consistent with a bottom-up view that springtail and mite populations were regulated intrinsically by competition for food and secondarily by temperature as a function of reproduction.

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Key words. Acari, Collembola, humidity, life cycle, macro-arthropods, numerical response, population dynamics, precipitation, regulation, reproduction, time-series analysis.

Introduction

A key question in soil biology and understanding the trophic structure of the biota in the soil-litter system is how populations are limited relative to trophic position (Pace *et al.*, 1999; Walker & Jones, 2001). Although there is recent theoretical evidence to suggest that soil food-web structure can influence population processes (Zheng *et al.*, 1997), there is a dearth of experimental data on the ecosystem-level consequences of soil food-web architecture, and much remains unknown about how soil food-web structure affects ecosystem productivity (Wardle, 1999). Some general patterns in the trophic organisation of soil animal communities have been observed despite a high degree of stochastic variation (Swift *et al.*, 1979; Petersen & Luxton, 1982; Schaefer, 1995; Mikola & Setälä, 1998; Ferguson, 2001): high species diversity within trophic groups, tendency to trophic generalism, high numbers and fluctuating mesofaunal predators, and continuity in litter decomposition.

An important question regarding soil community interactions among trophic levels is whether populations are regulated by competition for resource availability or by density-dependent predation. The Hairston *et al.* (1960) model predicts alternating regulation by predation and competition in the three-level chain such that micro-flora (i.e. fungi and algae) are regulated by competition for food; microphytophages, such as springtails (Collembola), are predator regulated; and predators (e.g. predaceous mites) are regulated by competition for prey (e.g. Schaefer, 1995). In contrast to the Hairston *et al.* (1960) model, however, the bottom-up view suggests that micro-phytophages (e.g. Collembola) and their predators (e.g. mites) are food controlled in detritivore communities (e.g. Laakso & Setälä, 1999).

In the work reported here, the Hairston *et al.* (1960) and bottom-up hypotheses were tested using time-series analysis and a field experiment of springtail and mite populations in a soil-leaf litter system. The experimental design to study trophic-level effects consisted of boxes distributed within an undisturbed aspen *Populus tremuloides* forest. The weight of the box depressed the litter layer similar to a rock on the forest floor. Microclimate differences under the box relative to exposed soil litter created a home to a diverse soil fauna community (Ferguson, 2000). Springtails are primarily fungivores or detritivores that play an important ecological role in preparing organic material for decomposition (Zinkler & Stecken, 1985). Populations of springtails are considered to be controlled by exogenous factors such as temperature and moisture (Klironomos & Kendrick, 1995; Hopkin, 1997) or predation (Hågvar, 1995; Schaefer, 1995), however the influences of endogenous factors that act in a density-dependent manner such as competition for limited

food are less well known (Theenhaus *et al.*, 1999). Predaceous mites commonly feed on springtails (Berg *et al.*, 1998; Ferguson, 2001) and both springtails and mites are common prey of macro-arthropods, including spiders, beetles, and centipedes (Eisenbeis & Wichard, 1987; Ferguson, 2001).

This research was designed to investigate whether, and by what means, springtail and mite numbers are regulated. A regulatory factor is any density-dependent process that keeps populations within predictable density ranges by affecting population growth quantifiably (Murray, 1982; Fowler, 1987; Sinclair, 1989; Sinclair & Pech, 1996). First, springtail and mite time-series data were examined for density-dependent population growth to determine whether past densities regulate population growth rate. Population regulation could result from a number of factors, including density-dependent predation by mites on springtails (or macro-arthropods on mites) and intra-guild competition for resources via weather conditions (e.g. temperature and precipitation). For example, determining whether mites exert a negative influence on springtail population growth rate tested mite predation as a regulatory factor of springtails. If mites or macro-arthropods are shown not to be regulated by predation, then density dependence in springtail and mite population growth arises from intra-guild competition for resources. Finally, time-series analysis and experimental manipulation were used to evaluate the limiting effect of precipitation and temperature on springtail and mite numbers. The experimental manipulation increased moisture by water addition, resulting in an increase in litter decomposition. Water addition should lead to no consistent change in springtail biomass (Hairston *et al.*, 1960) or lead to an increase of springtail and mite biomass if populations are food limited (bottom-up model).

Materials and methods

Study organisms

In this analysis, micro-arthropods included groups of springtails (Insecta: Collembola) and mites (Acari: Oribatida; family Gamasides). In contrast, macro-arthropods included spiders, beetle larvae and adults, and centipedes. Evidence of macro-arthropod groups capturing and handling micro-arthropods, probably as food, was gathered over the field research. Due to small numbers, spiders, beetles, and centipedes were combined as one group. Other arthropods were counted; these data are presented elsewhere (Ferguson, 2001). Approximately five surface-dwelling springtail species are characteristically found on xeric prairie (Jensen *et al.*, 1973) and were placed in one group as they occupy a similar niche, consuming detritus, fungi,

and algae (Wolters, 1991; Hopkin, 1997). Surface-dwelling springtails are soft-bodied *plankton of the soil* (Aoki, 1973; Johnston, 2000). Springtails are parthenogenetic; sexual maturity generally occurs at the sixth instar and oviposition generally occurs within 12–48 h after moulting at 21 °C (Joosse, 1981; Axelsen *et al.*, 1997). The size of springtails averaged 1.5 mm (range: 0.2–2.6 mm, $n=20$) or 0.67 mg (range: 0.09–7.13 mg); mites averaged 1.7 mm including legs (range: 1.1–2.9 mm) or 0.49 mg (range: 0.32–6.10 mg; S. H. Ferguson, unpublished). Predatory mites were represented by the genus *Labidostomma* and were placed in one taxonomic group. Mites are protected by an exoskeleton and are non-specific predators that commonly feed on springtails (Berg *et al.*, 1998; S. H. Ferguson, pers. obs.). The life cycle of the mite is comparatively simple, consisting of four gamasid stages: larva, protonymph, deutonymph, adult. The length of the life cycle of mites is related indirectly to temperature within the range 15–28 °C (Wright & Chambers, 1994).

Study site

The study area consisted of a 0.13-km² stand of undisturbed trembling aspen in the prairie region of south-central Saskatchewan, Canada (52°10'N, 106°41'W). Mean monthly daily temperature (1961–1990) varied from 3.9 °C in April to 18.6 °C in July (annual mean = 2.0 °C) and precipitation varied from 19.7 mm in April to 63.4 mm in June (annual mean = 28.9 mm) (Environment Canada, 2000).

Survey design

Factors determining micro-arthropod population dynamics were examined by counting springtails, mites, and macro-arthropods under artificial microhabitats ($n=24$), created using contiguous sets of five 2-l plastic-coated cardboard milk cartons (soil surface area 200 cm²). Boxes were filled with sand to weigh ≈ 2 kg, and depressed the soil on average 1.3 cm. These boxes simulated a microhabitat island for soil arthropods similar to a rock on the forest floor (Ferguson, 2000). Boxes were overturned and the numbers and size of springtails and mites were counted. An effort was made to lift individual boxes without disturbing adjacent boxes and the pattern of lifting each of the five boxes varied among surveys. Twenty-three, 24, and 20 weekly surveys were conducted from May to October 1997, 1998, and 1999 respectively. For 1997, the first six survey results were excluded from data analysis due to a colonisation effect whereby few soil arthropods were observed initially. Therefore, 17 surveys in 1997 were included in the time-series analyses for a total of 61 surveys across 3 years. Surveys began when the ground was no longer covered by snow and evidence of soil arthropods under boxes was first observed. Surveys ended when few, if any, soil arthropods were observed under boxes. Surveys were conducted between 11.00 and 17.00 hours during

daylight. Counts of springtails and mites were an index of surface-dwelling numbers and are not considered an absolute estimate of abundance. In 1999, moisture levels were manipulated under randomly chosen box sets ($n=12$) by pouring 250 ml of water under each box in the set (total 1.25 l) after each survey. The 1997–1999 time-series data included data from the 12 plots in 1999 that were not treated experimentally with water addition (i.e. controls). Both time-series (1997–1999) and experimental (1999) data were used to determine factors affecting springtail and mite ecology.

Weather parameters for Saskatoon were measured daily at the Kernen Prairie weather station by the Agriculture Department, University of Saskatchewan (12 km N of study site). Total precipitation (mm) and average weekly temperature (°C) at 5-cm soil depth were measured as the sum and mean of daily values between weekly surveys. As there were weeks with no precipitation, 0.5 was added to precipitation before log_e transformation (Yamamura, 1999).

Time-series analysis

First, the instantaneous rate of increase (hereafter referred to as *population growth rate*) of springtails and mites was calculated each year as:

$$R_t = [\ln(N_{t+T}) - \ln(N_t)]/T$$

where N_t is the population size at time t and T is the number of days between consecutive surveys. A total of 61 surveys was conducted, and 58 population growth rates (R_t) were calculated from the results of the first (N_t) and second (N_{t+T}) surveys for each year. Four sets of analyses were conducted: the 1997–1999 time-series data and the water addition experiment (1999) were analysed separately for both springtails and mites. Although springtails and mites were analysed separately, densities of predators and prey were included in general linear models to test for predation effects. Auto-regression analysis of springtail and mite population growth rate with density and time (week, year) as explanatory variables was used to produce residuals that removed temporal effects.

To test for density dependence, current and lagged (1, 2, 3, 4, and 5 weeks) numbers of springtails and mites were used to explain population growth rate (residuals). Negative correlations between population growth rate and lagged density would suggest density dependence in the springtail and mite time-series data. Auto-regression was used to explore time lags in the effect of temperature and precipitation on springtail and mite population growth rate using correlograms.

Growth rate residuals were used as the response variable in regression analyses to determine which explanatory factors influenced growth rate, with model acceptance set at $P < 0.05$. Explanatory variables included density dependence (current and lagged density), predation (predator

density), and weather (precipitation and temperature). The complete set of explanatory variables was examined in all combinations to determine the best model according to Akaike information criteria (AIC). Thus, possible models explaining variation in mite and springtail population rate of growth (residuals) were determined based on the best compromise between parsimony and bias (Burnham & Anderson, 1998).

Mite and macro-arthropod predation as potential factors limiting springtail and mite density respectively, was examined using partial correlation analysis (Sokal & Rohlf, 1981). For example, a negative correlation between predaceous mite numbers and springtail population growth rate, R_t , was tested while controlling statistically for springtail numbers. Correlations with population growth rates are mathematically equivalent to correlations with total mortality when loss of breeding potential is treated as a *killing factor* (Clutton-Brock *et al.*, 1985). For example, a negative correlation between mite numbers and springtail population growth rate would indicate that mite predation acts as a limiting factor, assuming that predation rate is linearly proportional to the abundance of mites (Messier, 1991).

Results

Auto-regression of the 1997–1999 time-series data with lagged precipitation, temperature, and density was used to determine major explanatory variables to be included in the final model describing springtail and mite population growth rate. For precipitation, 1-week lagged precipitation explained most ($r^2=0.18$ and 0.08) variation in springtail and mite population growth rate respectively (Fig. 1a,b). For temperature, 2- and 1-week lagged temperature explained most ($r^2=0.13$ and 0.26) variation in springtail and mite population growth rate respectively (Fig. 1c,d). Most variation in population growth rate was explained by current density ($r^2=0.56$ and 0.69 for springtails and mites respectively) and 1-week lagged density ($r^2=0.93$ and 0.82) compared with 2- to 5-week lagged density ($r^2=0.01$ – 0.22) (Fig. 1e,f). Current density and 1-week lagged density were therefore used as explanatory variables in the subsequent analyses.

Next, auto-regression models were used to determine regulation of springtail population growth rate. First for springtails, analysis of the 1997–1999 time-series data failed to find an effect of predation by mites (i.e. no negative correlation between springtail population growth rate and mite density) (Table 1). Only a small negative effect of 1-week lagged temperature (5% of variation explained) was estimated for springtail growth rate. Hot weather resulted in a decrease in springtail numbers the following week. A strong negative correlation was detected between springtail population growth rate and 1-week lagged springtail density (79%), indicating intra-guild density dependence (Table 1). A significant, positive effect on springtail population growth rate was estimated for current springtail density (8% of variation explained). The strong negative association of

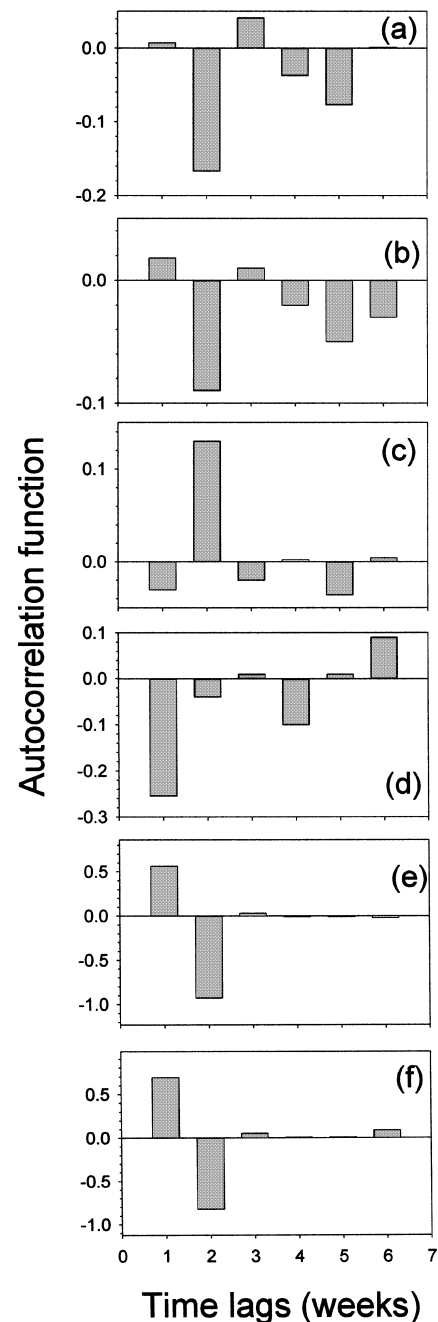


Fig. 1. Autocorrelation function for soil arthropod time series 1997–1999. (a) Springtail population growth rate as a function of weekly time-lagged precipitation [\log_e transformed precipitation (mm)+0.5]. (b) Mite population growth rate as a function of weekly time-lagged precipitation [\log_e transformed precipitation (mm)+0.5]. (c) Springtail population growth rate as a function of weekly time-lagged temperature (\log_e transformed temperature, °C). (d) Mite population growth rate as a function of weekly time-lagged precipitation (\log_e transformed temperature, °C). (e) Springtail population growth rate as a function of weekly time-lagged density (\log_e transformed springtail density). (f) Mite population growth rate as a function of weekly time-lagged precipitation (\log_e transformed mite density).

Table 1. Auto-regressive coefficient estimates based on general linear model delineating factors affecting springtail population growth rate 1997–1999 time-series data ($F_{2,57} = 138.5$, $P = 0.001$)†. Detrending of time series was achieved by calculating residuals from regression over time (year and weekly survey) and using the first difference for population growth rate ($DX_t = X_t - X_{t-1}$, where $X_t = \log_e N_{t+1} - \log_e N_t$). Variables considered most influential according to the most parsimonious model (Akaike information criteria) are delineated *.

Source	Coefficient	Partial r^2	F	P
Intercept	+0.542 ± 0.076	–	–	0.001
*Current springtail density	+0.0393 ± 0.0054	0.070 (0.08)§	52.2	0.001
*Lagged springtail density	–0.141 ± 0.0066	0.608 (0.85)	452.9	0.001
Mite density	+0.0022 ± 0.0058	0.0002	0.15	0.70
Precipitation (mm)‡	+0.0049 ± 0.011	0.0003	0.21	0.65
*Temperature	–0.0413 ± 0.025	0.004 (0.05)	2.78	0.10

† $R^2 = 0.93$ (adjusted $R^2 = 0.92$).

‡ $\log_e(\text{precipitation} + 0.5)$.

§Partial r^2 for best model *.

1-week lagged density and weaker positive association of current density resulted in a cyclic pattern of striking increases and abrupt population decreases (Fig. 2).

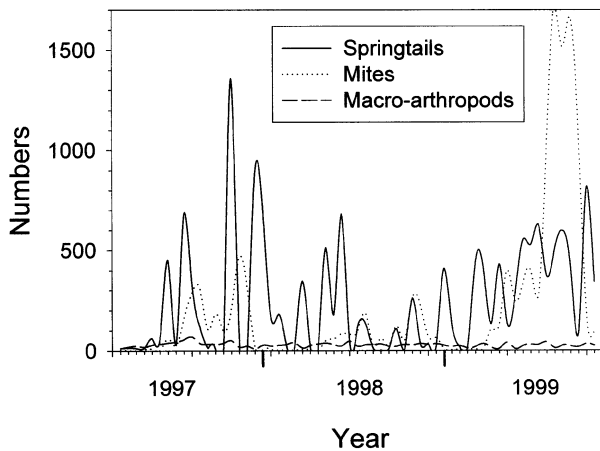


Fig. 2. Natural logarithm of the weekly numbers of springtails, mites, and macro-arthropods (spiders, beetle adults and larvae, and centipedes) for an aspen forest in Saskatchewan, Canada, 1997–1999.

Table 2. Auto-regressive coefficient estimates based on general linear model delineating factors affecting springtail population growth rate with experimental water treatment in 1999 ($F_{6,37} = 42.01$, $P = 0.001$)†. Detrending of time series was achieved by calculating residuals from regression over time (weekly survey) and using the first difference for population growth rate ($DX_t = X_t - X_{t-1}$). Variables considered most influential according to the most parsimonious model (Akaike information criteria) are delineated *.

Source	Coefficient	Partial r^2	F	P
Intercept	+0.254 ± 0.053	–	–	0.001
*Current springtail density	+0.0418 ± 0.0090	0.076 (0.23)§	21.6	0.001
*Lagged springtail density	–0.108 ± 0.0098	0.430 (0.58)	121.7	0.001
Mite density	–0.0024 ± 0.0089	0.0003	0.07	0.79
Water	–0.012 ± 0.015	0.002	0.61	0.44
Precipitation (mm)‡	+0.000 ± 0.005	0.0000	0.00	0.99
*Temperature	–0.0072 ± 0.0034	0.016 (0.05)	4.48	0.04

† $R^2 = 0.89$ (adjusted $R^2 = 0.87$).

‡ $\log_e(\text{precipitation} + 0.5)$.

§Partial r^2 for best model *.

For the 1999 water-addition experiment, no regulating effect of mites on springtail was established (Table 2). Again, springtail population growth rate was correlated negatively with a 1-week lagged density (58% of variation explained), and correlated positively with current springtail density (23%; Table 2). A weak, negative relationship between springtail growth rate and temperature (5%) was detected. Also, water addition to the soil under boxes was not a significant factor in describing springtail population growth; however springtail numbers were correlated strongly with precipitation (Fig. 3), and water addition resulted in a significant increase in springtail numbers (Fig. 4).

Analysing the 1997–1999 time-series data to determine factors influencing mite population growth rate did not find a significant effect due to macro-arthropod predators or to springtail density (Table 3). A negative effect of precipitation and a positive effect of temperature on mite population growth rate were detected, however a negative correlation was found between mite population growth rate and 1-week lagged mite density (20% of variation explained), indicating intra-guild density dependence (Table 3). Also, a significant, positive effect on mite population growth rate occurred for current mite density (54%).

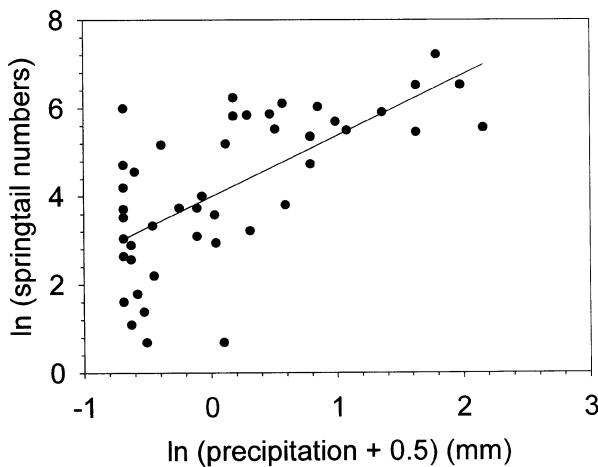


Fig. 3. The effect of precipitation on springtail numbers in 1999.

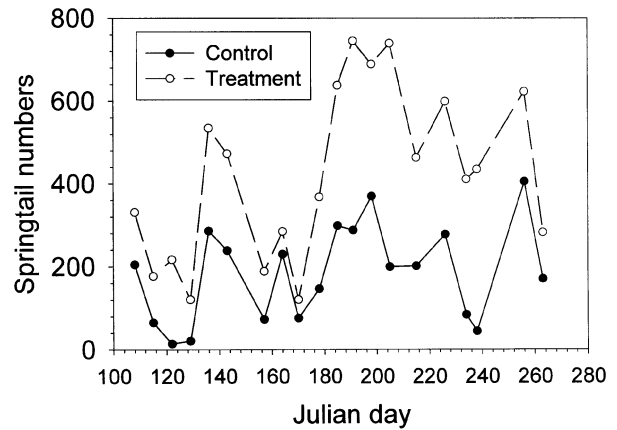


Fig. 4. Springtail numbers under treatment (250 ml water added after each survey) and control boxes (1999).

Table 3. Auto-regressive coefficient estimates based on general linear models delineating factors affecting mite population growth rate 1997–1999 time-series data ($F_{5,57} = 36.07$, $P = 0.001$)[†]. Detrending of time series was achieved by calculating residuals from regression over time (year and weekly survey) and using the first difference for population growth rate ($DX_t = X_t - X_{t-1}$). Variables considered most influential according to the most parsimonious model (Akaike information criteria) are delineated *.

Source	Coefficient	Partial r^2	F	P
Intercept	-0.0706 ± 0.076	–	–	0.36
*Current mite density	$+0.0948 \pm 0.010$	0.371 (0.54) [§]	86.12	0.001
*Lagged mite density	-0.112 ± 0.0091	0.658 (0.20)	152.9	0.001
Springtail density	-0.0018 ± 0.0064	0.0004	0.08	0.78
Macro-arthropods	$+0.00023 \pm 0.015$	0.0000	0.00	0.99
*Precipitation (mm) [‡]	-0.0268 ± 0.010	0.027 (0.06)	6.36	0.014
*Temperature	$+0.134 \pm 0.072$	0.015 (0.04)	3.44	0.069

[†] $R^2 = 0.78$ (adjusted $R^2 = 0.76$).

[§]Partial r^2 for best model *.

[‡] $\log_e(\text{precipitation} + 0.5)$.

Table 4. Auto-regressive coefficient estimates based on general linear model delineating factors affecting mite population growth rate with experimental water treatment in 1999 ($F_{6,37} = 9.41$, $P = 0.001$)[†]. Detrending of time series was achieved by calculating residuals from regression over time (weekly survey) and using the first difference for population growth rate ($DX_t = X_t - X_{t-1}$). Variables considered most influential according to the most parsimonious model (Akaike information criteria) are delineated *.

Source	Coefficient	Partial r^2	F	P
Intercept	$+0.219 \pm 0.24$	–	–	0.37
*Current mite density	$+0.0824 \pm 0.016$	0.311 (0.44) [§]	27.18	0.001
*Lagged mite density	-0.0721 ± 0.014	0.309 (0.11)	27.01	0.001
Springtail density	$+0.0262 \pm 0.017$	0.027	2.40	0.13
Water	-0.0266 ± 0.025	0.014	1.18	0.29
Precipitation (mm) [‡]	-0.00556 ± 0.0092	0.004	0.37	0.55
*Temperature	$+0.146 \pm 0.099$	0.025 (0.05)	2.18	0.15

[†] $R^2 = 0.65$ (adjusted $R^2 = 0.58$).

[‡] $\log_e(\text{precipitation} + 0.5)$.

[§]Partial r^2 for best model *.

This combination of a strong, positive relationship with current density and a weaker, negative relationship with 1-week lagged density resulted in less erratic changes in mite abundance relative to springtails (Fig. 2).

A similar general linear model predicted mite population growth rate using the 1999 water-addition experiment (Table 4). No evidence for density-dependent predation effects on mite population growth rate was found for

macro-arthropod numbers or springtail density (Table 4). Mite population growth rate was greater in areas with greater springtail density (5% of variation explained), and was correlated negatively with 1-week lagged mite numbers (11%) and positively with current mite density (44%). Water treatment and precipitation had no significant effect on mite population growth rate.

Discussion

Contrary to the top-down hypothesis (Hairston *et al.*, 1960), evidence was found for bottom-up control of springtail and mite abundance that may relate to low productivity on the prairies (Knapp *et al.*, 2001). Time-series analysis suggests that seasonal population eruptions are the consequence of the interplay between the endogenous factors (density-dependent food limitation) and exogenous factors (variation in temperature, e.g. Pech *et al.*, 1992). Density dependence in springtail and mite population dynamics was demonstrated by a negative correlation between population growth rate and 1-week lagged density. Possible density-dependent mechanisms include intraspecific interactions or the effects of generalist predators (Hanski *et al.*, 1991). In order for mite predation of springtails, or macro-arthropod predation of mites, to be density dependent, and therefore regulatory, there must be density dependence in both the functional and numerical responses (Messier, 1996), except where the predator exhibits a sigmoidal functional response. As mite numbers did not correlate with springtail population growth rate and did not exert a negative influence on springtail population growth rate, it is argued that predation by mites did not regulate springtail numbers. Similarly, macro-arthropod predation of mites did not correlate with mite population growth rate. Finally, analyses of time-series data and experimental addition of water indicated that springtail and mite numbers were partly a function of temperature. Springtail reproduction is probably temperature and ground moisture dependent (Hopkin, 1997). Similarly, temperature influences the life cycle of mites (Wright & Chambers, 1994). Results from the addition of water generally support the view that variation in rainfall and temperature regulate springtail and mite densities through intra-guild competition for resources (rainfall) and seasonal conditions (temperature) suitable for reproduction. The results of this study suggest that changes in springtail and mite numbers may be explained primarily on the basis of climate and competition for food, and secondarily by predation. Although not investigated, other factors such as parasites or disease may influence springtails and mites through density-dependent regulation.

This experiment was designed to determine the dynamic role of precipitation in affecting changes in numbers of litter-dwelling springtails and mites. Thus, which particular enemies play an important role in causing springtail and mite oscillations is unknown. Springtails and mites are the most numerous micro-arthropods but contribute only 3.9

and 1.9% of faunal biomass respectively (S.H. Ferguson, unpublished). In comparison, ants dominate, contributing 30.5% of total biomass (S.H. Ferguson, unpublished). Schaefer (1995) estimated that $\approx 1\%$ of faunal biomass consisted of springtails. Hence, the production of springtail biomass is low compared with predation by a diverse and abundant predator community. Because some springtail populations are prone to predation and live in a super-abundance of detritus and fungal mass, some researchers have argued that springtails endure high predation pressure and tend to be predator regulated (Schaefer, 1995; Bilgrami, 1997). For example, field experiments with artificial manipulations of spider and centipede density demonstrate the importance of these predatory populations for limiting springtail density (Schaefer, 1995), although more systematic and realistic experiments are required to provide convincing documentation. Also, simulations of the predator-prey interactions of a predaceous mite and a springtail in a microcosm experiment indicated sensitivity to changes in predator search rate, capture efficiency, habitat selection, stored reserves, and springtail survival and reproduction (Axelsen *et al.*, 1997). Springtails, however, are a diverse group of soil arthropods hosting a diverse predator community associated with the soil ecosystem.

Other researchers have noted weak or no effects of predators on prey in soil systems (Laakso & Setälä, 1999). Although predators can have an indirect effect on the rate at which microbes are consumed, the micro-flora can compensate for biomass consumption by altering rate of turnover (Mikola & Setälä, 1998). This should, in turn, help to buffer microbial-mediated processes against the effect of top predators. Numerous researchers have reported a positive correlation between moisture content and density of soil-dwelling springtails (Erasmus & Ryke, 1970; Badejo & Van Straalen, 1993; Badejo *et al.*, 1998). Precipitation is related to primary productivity (Rosenzweig, 1968) and has a strong effect on population dynamics of vertebrate populations (Swanson, 1998). A thin, chitinous exoskeleton limits springtail distribution within ecosystems to sites with adequate moisture (Christiansen, 1992).

Most long-term census data on insect and vertebrate species have been analysed on a yearly time scale so that abundance in any given year is related to that in the previous year (Turchin, 1990; Royama, 1992; Turchin & Taylor, 1992; Perry *et al.*, 1993), yet dynamics of populations within years (e.g. seasonality) form the basis of many insect population dynamics (Sequeira & Dixon, 1997). Clearly, important population regulatory processes, such as reproductive life cycles, may be operating on shorter time scales than annual abundance. The multiple peak populations of soil-dwelling springtails during the annual cycle arise from the many generations of springtails during that cycle (Badejo & Van Straalen, 1993; Schaefer, 1995; Badejo *et al.*, 1998). The decline in populations after each peak may indicate the end of a generation as the pattern of fluctuation in the populations differs with different genera (Badejo *et al.*, 1998). This implies that each genus has a particular life history and that the population dynamics of each genus

can be influenced by variation in micro-environmental attributes. For example, one genus (*Rhodanella* sp.) inhabiting the litter layer produced large swarms after rainfall in the litter layer of an undisturbed forest soil (Lasebikan *et al.*, 1985).

Apparently, predation of springtails by mites has no dynamic feedback; contrary to speculation that predation by mites regulates springtails (Hågvar, 1995). Possibly, the low productivity of prairie ecosystems did not support a predator capable of regulating springtails and mites (Oksanen & Oksanen, 2000; Ferguson, 2001). For this system, the average predator-induced mortality may be very high and the intrinsic rate of population increase low, yet still predators had no dynamic impact. Hence, fluctuations in predator-imposed mortality may affect springtail density in a stochastic manner but they cannot drive a regular oscillation. It is worth examining further the lack of correlation between prey and predators. Note that the slopes of the relationship between springtail and mite numbers and population growth rate were shallow (slope = -0.11 and -0.09 for springtails and mites respectively), suggesting that a large variation in numbers is possible. For example, a four-fold increase in springtails occurred in 1999 with addition of water. By definition, a regulatory force increases in effect at high densities and decreases at low densities. Regulation by mite predation cannot occur if mite population size does not respond to springtail density. In fact, during late summer, mites outnumbered springtails. Feeding by mites on their own faecal matter (coprophagy) in the absence of prey suggests that adult mites can delay starvation in the absence of prey (2–5 weeks; Bilgrami, 1994, 1997; Wright & Chambers, 1994), whereas adult mites can live for 4–5 months with food (Wright & Chambers, 1994). Mites generally do not show cannibalistic behaviour (Bilgrami, 1997) although under extreme conditions without food for long periods, adults will cannibalise larvae and nymphs (Wright & Chambers, 1994). More research is needed to clarify the feeding behaviour of mites over time (i.e. functional response) to address the possible implications for regulation of their prey.

In conclusion, springtail and mite population density was determined primarily by endogenous factors (delayed density-dependent regulation), which provided a reasonable description of density changes without invoking top-down predation. The predominant factor explaining springtail and mite population growth was 1-week lagged density, whereas including temperature in the model together with delayed density-dependent factors explained additional variance in springtail and mite density. Regulation may occur by means of density-dependent processes acting within years whereas changes in year-to-year abundance may be due to differences in annual temperature and precipitation that may vary spatially with primary productivity (Knapp & Smith, 2001). Future studies should use experimental approaches to understand the effects of delayed density dependence and rainfall on the demographic processes of survival, reproduction, immigration, and recruitment of springtails and mites.

Acknowledgements

Q. Ferguson helped to design the study and conduct the field surveys. D. O. Joly was supported by a University of Saskatchewan Graduate Scholarship and subsequently a Natural Sciences and Engineering Council Postgraduate Scholarship. S. H. Ferguson received financial support from post-doctoral funding from the University of Saskatchewan and the Government of the Northwest Territories. We benefited from the constructive comments and criticisms of B. Patterson and two anonymous reviewers.

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Accepted 13 January 2002