# The impact of altered precipitation on spatial stratification and activity-densities of springtails (Collembola) and spiders (Araneae)

JANET R. LENSING, SARA TODD and DAVID H. WISE  Department of Entomology, University of Kentucky, U.S.A.

**Abstract.** 1. A field experiment was conducted to determine how short-term changes in moisture can alter activity-densities of spiders and springtails.

2. In a Kentucky forest 10 unfenced 4-m$^2$ plots were divided into two rainfall treatments. A clear roof over five plots excluded rainfall to simulate severe drought conditions (*drought* treatment). Water was sprayed on the five uncovered plots at a rate equal to two times the long-term mean in order to establish the *high-rainfall* treatment. Activity-densities of Collembola and spiders were measured using pitfall traps designed to sample the top, middle, and bottom layers of leaf litter. The experiment ran from 20 July to 23 September 2001.

3. Overall (i.e. litter layers pooled) activity-density (mean number trapped each sampling date) of Collembola was $\approx 60\%$ lower in drought plots than in plots receiving increased precipitation. Surprisingly, overall spider activity-density was $\approx 1.6$ times greater in the drought plots.

4. Differences in rainfall affected the spatial stratification of Collembola and spiders in strikingly different ways. Activity-densities of neither group differed between drought and high-rainfall treatments in the bottom litter layer. Collembola activity-density was three times greater in the top and middle litter layers in high-rainfall plots than in drought plots. In contrast, spider activity-density did not differ between treatments in the top layer, but activity-density was decreased by 50% in the middle layer of high-rainfall plots compared with drought plots.

5. Three Collembola families (Sminthuridae, Tomoceridae, and Entomobryidae) accounted for most of the Collembola pattern. The spider response was due to altered activity-density of one family of wandering spider, the Gnaphosidae.

**Key words.** Collembola, detrital food web, drought, field experiment, forest, high rainfall, leaf litter.

## Introduction

Activities of arthropods on the forest floor can affect rates of leaf-litter decomposition and nutrient cycling (Swift *et al.*, 1979; Seastedt, 1984; Hasegawa and Takeda, 1995; Bradford *et al.*, 2002). Two ubiquitous and important groups in the leaf-litter community are Collembola and spiders. Collembola, which are among the most abundant

microbi-detritivores in the leaf litter (Swift *et al.*, 1979; Hopkin, 1997), can influence rates of litter decomposition by comminuting detritus and grazing on fungi (Seastedt, 1984; Hasegawa and Takeda, 1995). Spiders, common predators in this system, can depress Collembola densities (Wise, 2004) and indirectly impact the process of litter decomposition (Kajak *et al.*, 1991; Lawrence and Wise, 2000, 2004). Changes in the moisture content of the litter and soil can affect interactions between the faunal and microbial components of the detrital food web by altering population densities, activity, and vertical stratification of arthropods in the litter (Swift *et al.*, 1979; Hopkin, 1997).

Correspondence: Janet R. Lensing, Department of Entomology, S-225 Ag. Sci. Bldg – North, University of Kentucky, Lexington, KY 40546-0091, U.S.A. E-mail: jrlens2@uky.edu

Changes in moisture can directly affect Collembola behaviour and survival, and can indirectly affect their densities by influencing resource levels. Collembola are sensitive to changes in moisture and relative humidity (Bauer, 1979; Loring, 1981). Ferguson and Joly (2002) uncovered a strong positive correlation between Collembola densities and precipitation, and also found that experimental water supplementation increased Collembola numbers. Badejo *et al.* (1998) also found a positive relationship between soil moisture and Collembola. Additionally, irrigation treatments have been shown to increase Collembola numbers in habitats as varied as the Antarctic Peninsula region and Scandinavian coniferous forests (Convey *et al.*, 2002; Lindberg *et al.*, 2002). Most Collembola species move both laterally and vertically through the leaf litter (Greenslade and Greenslade, 1973; Filser and Fromm, 1995), apparently searching for favourable microclimates (Usher, 1970; Hijii, 1987; Sgardelis *et al.*, 1993). Bauer (1979) determined that moisture is a primary factor influencing the climbing behaviour of three species of Collembola. Hassall *et al.* (1986) found that during periods of low rainfall, most Collembola moved into the humus layer, but with increased rainfall the majority migrated into the litter, with ≈30% remaining in the humus layer. Moist habitats can indirectly benefit Collembola by enhancing the growth of fungi, a main food source. Hassall *et al.* (1986) showed that Collembola migrate upwards in response to microorganismal blooms that occur after rainstorms. Thus, larger fungal populations in wetter areas, in addition to more readily available moisture, may contribute to lowered rates of emigration by Collembola from moister areas (Knight, 1963; Knight and Read, 1969; Hassall *et al.*, 1986).

Changes in moisture can also have direct and indirect effects on spider populations. A 5-year study uncovered a correlation between spider densities and abiotic factors, including rainfall (Dondale and Binns, 1977). Wetness of grassland sites was a key factor in explaining spider community structure in a study by Rushton *et al.* (1987). Frampton *et al.* (2000) found that the abundance of spiders and other predatory arthropods in arable farmland decreased in response to experimentally imposed drought and increased in response to irrigation. Rainfall can affect the activity and abundance of spiders indirectly by affecting prey populations of microbi-detritivores (Swift *et al.*, 1979). Chen and Wise (1999) found that adding high-quality detritus to forest-floor plots caused densities of Collembola, Diptera, and Acarina to increase, accompanied by a doubling of spider densities. In a laboratory study, Wagner and Wise (1997) demonstrated that the presence of Collembola prey in experimental habitat patches decreases the rate of emigration of juvenile wolf spiders (Lycosidae). Experiments by Harwood *et al.* (2001, 2003) showed that spiders in agricultural systems choose web sites where Collembola densities are high. These experiments and several others (Wise, 1993) clearly show that changes in prey abundance, which can be driven by changes in abiotic factors such as moisture, can influence spider behaviour and density.

The field experiment reported here was designed to uncover the short-term responses of forest-floor Collembola and spiders to opposite changes in rainfall – severe drought or a doubling of normal rates of precipitation based on the long-term average for this region. These treatment levels were chosen because models of global climate change predict similar extreme changes in precipitation (Houghton, 1997; IPCC, 1997). Although this experiment cannot address how long-term climate change will alter this system, the experiment does reveal short-term responses of arthropods to alterations in precipitation similar to those predicted to occur with climate change. In a broader context, the experiment also yields valuable information about how the basic dynamics of Collembola and spiders may change in response to abiotic conditions that vary spatially and temporally. It was predicted that activity-densities of both groups would be higher under high-rainfall conditions, and that changes in rainfall would markedly affect their vertical distribution in leaf litter. The latter response was measured by utilising a pitfall trap designed to capture arthropods in the bottom, middle, and top litter layers (Wagner *et al.*, 2003).

The primary purpose of this experiment was to determine the range of arthropods' responses to extremes of precipitation; therefore, ambient reference plots were not included in the design. Conditions can range unpredictably from much drier to much wetter than normal and often do not exhibit an intermediate value on target with long-term average rainfall. Had we known *a priori* that ambient rainfall would be an average amount, we could have compared data from ambient plots with data from the treated plots. However, since it was unlikely that ambient precipitation would be average rather than above or below average, and since this comparison was not the goal of our experiment, we used our resources to accomplish adequate replication of the two extreme rainfall treatments.

## Methods

Ten 4-m$^2$ unfenced plots, established 5–10 m apart in an oak–maple forest in Madison Co., Kentucky, U.S.A., were randomly assigned to one of two treatments: *drought* or *high rainfall*. Rainout shelters were constructed on 20 July 2001 over the five drought plots using PVC pipes and clear polyethylene plastic. The roof extended beyond the plot edge by 1 m on each side. Each shelter was equipped with a system of gutters and tubing to funnel rainwater away from the plot. From 30 July to 16 September 2001, water was sprayed weekly from a backpack sprayer on the five non-roofed, high-rainfall plots to supplement natural rainfall, yielding a rate of rainfall (natural plus added water) equal to two times the mean weekly precipitation over the last century (Kentucky Climate Center, 2001). Rates were adjusted weekly, based upon actual rainfall during the experiment and the long-term average for that time of year.

Activity-densities of Collembola and spiders were measured with stratified pitfall traps that preferentially sampled either the bottom, middle, or top layer of leaf litter (Wagner *et al.*, 2003). Traps consisted of a 20-cm piece of 9-cm diameter PVC pipe containing a cup filled with a 50% ethylene glycol–50% water mixture. A 2-cm slit was cut into the PVC either 5 cm from the end of the pipe for the traps sampling the top and bottom litter layers, or 9 cm from the end of the pipe for traps sampling the middle litter layer. Two thin pieces of wood extended 3 cm on either side of the slit in order to capture only those animals moving laterally within the specific litter layer (see diagram of trap in Wagner *et al.*, 2003). Three traps, each one sampling a different litter layer, were placed ≈0.5 m apart in the centre of each plot. Traps were opened for 48 h on the 10–12 August, 17–19 August, 25–27 August, and 16–18 September 2001. Collembola and spiders were identified to family.

Effects of the rainfall treatments on overall Collembola and spider activity-densities (litter layers pooled) were first evaluated by repeated-measures ANOVA [adjusted univariate ANOVA (Greenhouse–Geisser, or G–G) and MANOVA (Wilks' $\lambda$)] over sampling date. Since treatment–date interactions were not close to statistical significance ($Ps > 0.40$), sampling dates were pooled in order to test for effects of litter layer. This latter analysis is a traditional split-plot design with litter layer as the within-subjects factor. For overall Collembola and spider numbers, as well as for activity-densities of individual families, the interaction between rainfall treatment and litter layer was tested by both an adjusted univariate ANOVA [Greenhouse–Geisser (G–G)] and MANOVA (Wilks' $\lambda$). These approaches take into account the correlation among the within-subjects factor, litter layer, since the top, middle, and bottom litter layers were all sampled within the same replicate plots. The results from both tests are presented since MANOVA has low power due to the number of replicates and treatment levels in our experimental design (von Ende, 2001). Within a single litter layer, simple one-way ANOVA was used to determine the impact of rainfall treatment on activity-densities. Data were log-transformed to reduce variance heterogeneity in the tests for treatment–date interaction (data pooled over litter layer) and in some analyses of Collembola and spider family level responses (data pooled over sampling dates). Overall Collembola data (pooled over sampling dates) were log-transformed to meet the sphericity assumption. All other tests met the sphericity assumption without data transformation (all $Ps$ between 0.06 and 0.98). Analyses were performed using Statistica (StatSoft Inc., 2001, Version 6.0). Plot means ± SE are reported.

## Results

### General pattern of response

Collembola exhibited higher activity-density in the high-rainfall plots [ Fig. 1a; $F_{1,8}$(main effect) = 27.62, $P < 0.001$], whereas spider activity-density was higher in the drought
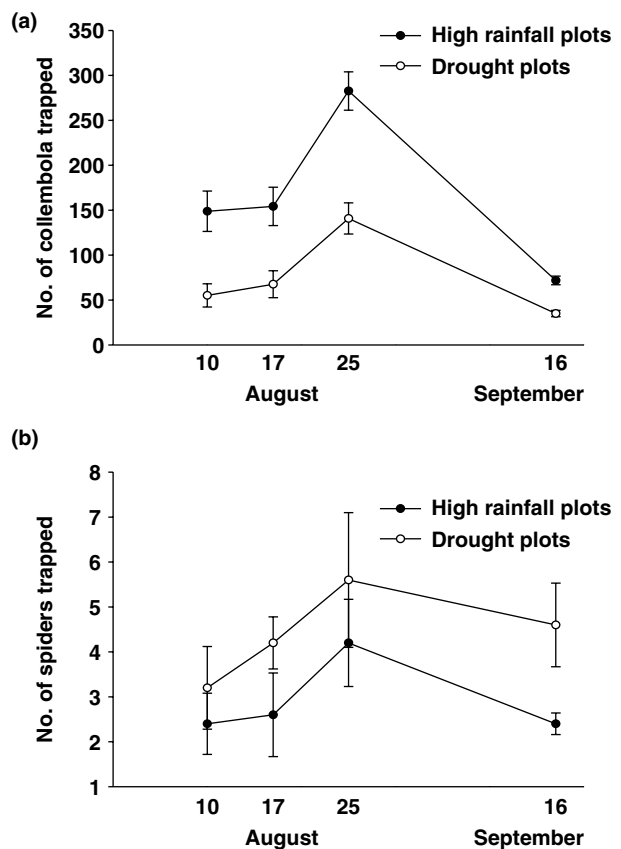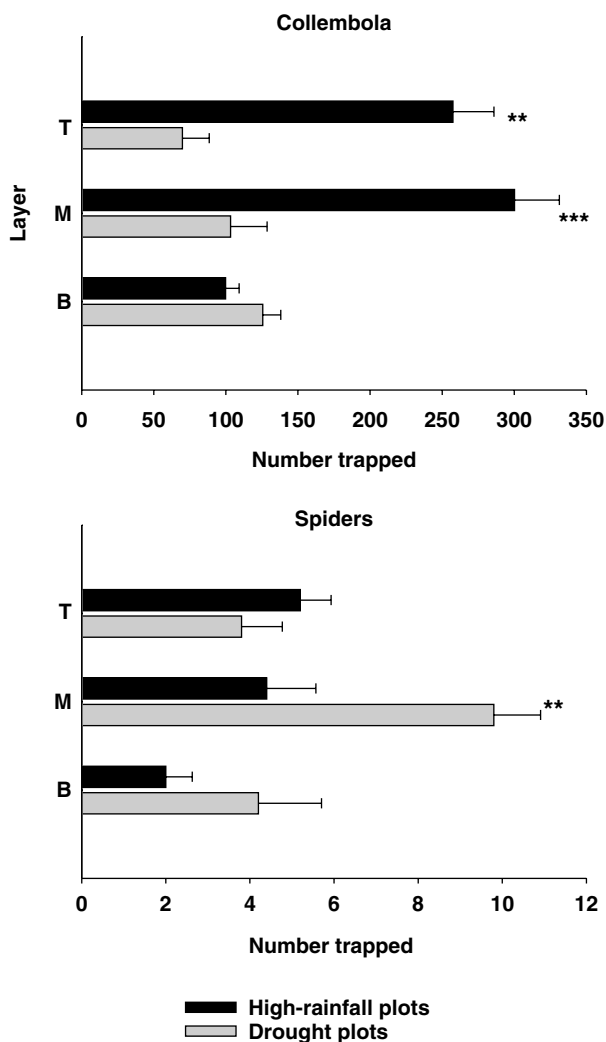


**Fig. 1.** Total number of (a) Collembola and (b) spiders trapped per sampling date. Means ± SE are shown.

plots [Fig. 1b; $F_{1,8}$(main effect) = 5.79, $P = 0.043$]. The treatment–date interaction was not significant for Collembola [$P(G–G) = 0.43$; $P$(Wilks' $\lambda$) = 0.76] or spiders [$P(G–G) = 0.83$; $P$(Wilks' $\lambda$) = 0.69]. Therefore, data were pooled over dates in order to test for an interaction between rainfall treatment and litter layer.

The effects of rainfall on activity-density differed by litter layer, with Collembola and spiders exhibiting markedly different patterns. Collembola responded differently to the rainfall treatments depending on the litter layer sampled [tests for interaction: $P(G–G) = 0.004$; $P$(Wilks' $\lambda$) = 0.02]. Activity-density of Collembola in the high-rainfall plots was triple that in the drought plots in the top (Fig. 2; $F_{1,8} = 9.87$, $P = 0.01$) and middle (Fig. 2; $F_{1,8} = 20.48$, $P = 0.002$) layers, with no significant effect in the bottom layer (Fig. 2; $F_{1,8} = 3.02$, $P = 0.12$). Likewise, the response of spiders to rainfall treatment depended on the litter layer sampled [$P(G–G) = 0.04$; $P$(Wilks' $\lambda$) = 0.06]. Spiders responded to altered rainfall only in the middle litter layer, with increased rainfall lowering activity-density by ≈50% compared with drought plots (Fig. 2; $F_{1,8} = 11.22$, $P = 0.01$). Differences between rainfall treatments were not significant for spiders in either the top (Fig. 2; $F_{1,8} = 0.57$, $P = 0.47$) or bottom (Fig. 2; $F_{1,8} = 2.42$, $P = 0.16$) litter layers.

**Fig. 2.** Activity-densities of Collembola and spiders in the three litter layers. T, top litter layer; M, middle layer; B, bottom layer (means $\pm$ SE are shown; $**P < 0.01$; $***P < 0.001$).

*Family level responses*

*Collembola.* Individuals from four Collembola families (Entomobryidae, Hypogastruridae, Sminthuridae, and Tomoceridae) were commonly found in the pitfall trap samples (Table 1). The response of entomobryids to rainfall treatment varied with litter layer [$P$(G–G) = 0.005; $P$(Wilks' $\lambda$) = 0.003]. In the top litter layer, entomobryid activity-density was three times higher in high-rainfall than in drought plots (Table 1; $F_{1,8} = 16.00$, $P = 0.004$). Tomocerids also exhibited a rainfall treatment × litter layer interaction [$P$(G–G) = 0.02; $P$(Wilks' $\lambda$) = 0.05]. Activity-density of tomocerids in the top litter layer of the high-rainfall treatment was five times greater than in that layer in the drought treatment (Table 1; $F_{1,8} = 33.60$, $P = 0.0004$), and four times greater in the middle litter layer (Table 1; $F_{1,8} = 6.52$, $P = 0.034$). Hypogastrurids showed similar trends with

greater activity-density in the high-rainfall plots, but these results were not statistically significant. The largest response was shown by the sminthurids, whose response to rainfall treatment again varied markedly with litter layer [$P$(G–G) < 0.0001; $P$(Wilks' $\lambda$) < 0.0001]. Sminthurid activity-density was over an order of magnitude greater in both the top and middle litter layers in high-rainfall plots compared with drought plots (Table 1; $F_{1,8} = 55.4$, $P < 0.0001$ and $F_{1,8} = 225$, $P < 0.0001$ respectively). In the bottom layer the responses of each Collembola family to rainfall manipulation followed the general pattern described for total Collembola, with no response from any family except for Sminthuridae (Table 1; $F_{1,8} = 32.19$, $P < 0.0001$).

*Spiders.* Spiders that were consistently trapped represented four families: Gnaphosidae, Lycosidae, Thomisidae, and Theridiidae (Table 1). Lycosids (wolf spiders), which were the most frequently trapped family in all litter layers, did not respond to differences in rainfall. Thomisids and theridiids also showed no clear response to the rainfall treatment. In contrast, gnaphosid spiders, rare in the top and bottom litter layers in both treatments, exhibited marginally greater activity-density in the middle layers of drought than high-rainfall plots [Table 1; $F_{1,8} = 6.76$, $P = 0.032$; the rainfall treatment × litter layer interaction was not statistically significant: $P$(G–G) = 0.21; $P$(Wilks' $\lambda$) = 0.1].

## Discussion

This experiment demonstrates how altered rainfall affects the activity-densities and spatial stratification of two major groups of leaf-litter arthropods. In addition, the results show that responses of arthropods to altered rainfall may not always be in the expected direction. Collembola activity-density was, as predicted, higher in the high-rainfall plots than in the drought plots, due to three times more animals trapped in the top and middle litter layers in those plots. Individuals from four Collembola families contributed to this pattern, with responses ranging from doubled activity-density in high-rainfall plots compared with drought plots to over a 10-fold difference between treatments in numbers of sminthurid Collembola trapped. Overall spider activity-density was unexpectedly lower in high-rainfall plots, due primarily to lower numbers of one family, the Gnaphosidae, captured in the middle litter layer. Activity-density of gnaphosids, typically among the most common cursorial spiders in this forest-floor system (Wagner *et al.*, 2003; J. R. Lensing, pers. obs.), was three times higher in the middle layer of the drought plots than the high-rainfall plots.

There is more than one possible explanation for the unexpected response by gnaphosids. First, in the drought plots these spiders could have left the top litter layer and moved to the middle layer in search of moisture or prey. Wagner *et al.* (2003) found that under non-drought conditions, gnaphosids were very rare in the bottom litter layer

**Table 1.** Mean ± SE of predominant Collembola and spider families found in the top, middle, and bottom layers of the leaf litter, and the total for combined litter layers.

| Family | Rainfall treatment | Litter layer | | | |
|---|---|---|---|---|---|
| | | Top | Middle | Bottom | Total |
| **Collembola**[a] | | | | | |
| Entomobryidae | High | 191.6 ± 27.7 | 167.6 ± 26.1 | 75.0 ± 9.5 | 434.2 ± 57.0 |
| | Drought | 62.2 ± 16.8 | 91.4 ± 24.5 | 107.2 ± 17.7 | 260.8 ± 35.5 |
| Sminthuridae | High | 40.6 ± 9.8 | 99.2 ± 17.8 | 7.2 ± 0.8 | 147.0 ± 26.8 |
| | Drought | 1.4 ± 0.5 | 1.0 ± 0.3 | 2.0 ± 0.5 | 4.4 ± 0.4 |
| Hypogastruridae | High | 14.0 ± 3.4 | 15.6 ± 4.5 | 11.2 ± 4.1 | 40.8 ± 7.8 |
| | Drought | 5.0 ± 2.4 | 6.4 ± 1.2 | 11.6 ± 5.8 | 23.0 ± 7.0 |
| Tomoceridae | High | 9.6 ± 1.3 | 17.4 ± 5.0 | 3.0 ± 1.0 | 30.0 ± 5.8 |
| | Drought | 1.2 ± 0.6 | 4.0 ± 1.8 | 4.4 ± 3.2 | 9.6 ± 4.8 |
| **Spiders**[b] | | | | | |
| Cursorial | | | | | |
| Lycosidae | High | 3.8 ± 0.7 | 3.4 ± 0.7 | 1.4 ± 0.7 | 8.6 ± 0.9 |
| | Drought | 2.2 ± 0.8 | 4.4 ± 0.8 | 2.4 ± 0.8 | 9.0 ± 1.6 |
| Gnaphosidae | High | 0.6 ± 0.4 | 0.2 ± 0.2 | 0.2 ± 0.2 | 1.0 ± 0.5 |
| | Drought | 1.2 ± 0.8 | 3.0 ± 1.2 | 0.6 ± 0.4 | 4.8 ± 1.7 |
| Thomisidae | High | 0.6 ± 0.4 | 0.4 ± 0.4 | 0 | 1.0 ± 0.8 |
| | Drought | 0.2 ± 0.2 | 1.6 ± 0.5 | 0.6 ± 0.6 | 2.4 ± 0.8 |
| Web-builders | | | | | |
| Theridiidae | High | 0.2 ± 0.2 | 0.4 ± 0.2 | 0.4 ± 0.4 | 1.0 ± 0.5 |
| | Drought | 0.2 ± 0.2 | 0.6 ± 0.2 | 0 | 0.8 ± 0.4 |

[a]Collembola of the families Isotomidae and Onychiuridae were found only rarely in the pitfall trap samples (15 individuals and six individuals trapped during the experiment, respectively) and so are excluded from the table although they were included in analyses of total Collembola.
[b]Spiders of the families Ctenidae, Clubionidae, Pisauridae, and Segestriidae were found only rarely in the pitfall trap samples (one individual of each family trapped during the experiment) and so are excluded from the table although they were included in analyses of total spiders.

and most common in the top layer, with intermediate numbers in the middle litter layer. In the current experiment, drought conditions caused a shift in spatial stratification such that there were more gnaphosids trapped in the middle layer than in either the top or bottom layers. Secondly, predators of gnaphosids may have been less numerous in the drought treatment, thereby leading to an increase in activity or in actual densities. Centipedes, for example, can prey on spiders (Bristowe, 1941; Lewis, 1981) and are very sensitive to moisture conditions (Curry, 1974), typically selecting microsites with high humidity (Albert, 1983). However, centipedes may also have been more active in the drought plots due to searching for more favourable microsites. An increase in activity of a potential predator could have led to increased activity by gnaphosids. Data are not available from this study to test these possible explanations, because sampling methods other than pitfall trapping, such as sifting or extracting litter, give better estimates of centipede numbers (J. R. Lensing, pers. obs.).

Effects of altered rainfall on both spiders and Collembola undoubtedly are more complex than pitfall trapping alone reveals. Different sampling techniques can yield very different estimates of Collembola and spider densities (Hopkin, 1997; Harwood *et al.*, 2001, 2003; Wagner *et al.*, 2003). Pitfall traps are effective in sampling species that are active on the surface and in interstitial spaces of the litter, whereas the use of temperature/humidity gradients in the laboratory to extract arthropods from litter samples may produce better estimates of densities of arthropods such as those Collembola that are less active, or that are primarily associated with the soil–litter interface (Joosse and Kapteijn, 1968; Snider and Calandrino, 1987; Hopkin, 1997). For example, Collembola of the family Onychiuridae may have responded to the rainfall manipulation, but this response may not have been detected since only pitfall trapping was utilised. Wagner *et al.* (2003) used pitfall trapping and a specialised litter-extraction technique to sample spider families at this same study site. They found that 60% of all spiders caught in pitfall traps were non-web building cursorial spiders (primarily families Clubionidae, Ctenidae, Gnaphosidae, Lycosidae, Salticidae, and Thomisidae), whereas cursorial spiders accounted for only 21% of the spiders in the litter-extraction samples. Pitfall trapping severely underestimated densities of the Dictynidae, which are very abundant, small-bodied web spinners. Therefore, it is likely that web-building spiders, such as dictynids and linyphiids, may have shown a response to altered rainfall that was not detected in this experiment because pitfall trapping was the only sampling method used.

This experiment utilised open, unfenced plots. Therefore, responses by Collembola and spiders to the rainfall treatments were likely due to changes in rates of immigration or emigration as well as to changes in survival, fecundity, or localised activity levels (Swift *et al.*, 1979; Hassall *et al.*,

1986; Sgardelis *et al.*, 1993; Hopkin, 1997). Further experimentation utilising a range of sampling methods (e.g. direct density estimates in addition to pitfall trapping) in both open and closed plots would be needed to tease apart these different responses.

This study shows how extreme changes in litter moisture can impact activity-densities of two major groups of arthropods in the forest-floor food web. Similar extreme changes in rainfall are predicted to occur with global warming (Houghton, 1997; IPCC, 1997), but such differences in moisture can also occur over shorter timescales, and between different forest sites. Changes in the behaviour and abundance of Collembola and spiders, as well as changes in the interactions between these groups, could have consequences for the functioning of this subsystem of the forest ecosystem, since the activities of both groups can impact rates of leaf-litter decomposition (e.g. Swift *et al.*, 1979; Seastedt, 1984; Kajak *et al.*, 1991; Hasegawa and Takeda, 1995; Bradford *et al.*, 2002; Lawrence and Wise, 2000, 2004). This experiment has not identified the mechanisms underlying the responses shown to altered rainfall. Nevertheless, this study has demonstrated clear, short-term effects on activity-densities of a major microbi-detritivore and predator in the leaf-litter community, effects that were both predicted and unexpected.

## Acknowledgements

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