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Litter microarthropod responses to canopy herbivory, season and decomposition in litterbags in a regenerating conifer ecosystem in Western Oregon

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Summary. The microarthropod community response to season, change in foliage litter quality during decomposition, and manipulated canopy herbivory by insects was measured in litterbags under 10-year-old Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in western Oregon. Collembola accounted for 35% of the total fauna, oribatid mites for 29%, and fungivorous actinedids for 22%.

The community structure was affected by responses to canopy defoliation, season, and changes in litter quality. Of 33 taxa, three were significantly more abundant under trees subject to lepidopteran defoliation (≤ 20% foliage removal), compared to other treatments, indicating responses to defoliator-induced changes in litter environment. Most taxa (23) showed seasonal fluctuations in abundance related to the seasonal pattern of temperature and precipitation and to the pattern of N and Ca mobilization from litterbags. Five taxa showed significant long-term trends in abundance, indicating responses to changes in litter quality, perhaps a loss of P and K.

These data indicate that microarthropod communities respond qualitatively to environmental changes, including canopy defoliation. The qualitative changes can affect decomposition processes.

Key words: Acarina – Oribatid mites – Collembola – Litter decomposition – Nutrient dynamics – *Pseudotsuga menziesii*

Litter microarthropods significantly affect nutrient cycling and ecosystem productivity through their effects on litter decomposition processes (Seastedt 1984; Moore et al. 1988). Their importance to ecosystem management goals warrants an evaluation of factors that influence microarthropod abundance and community structure. Previous studies have demonstrated microarthropod responses to variation in litter quality and litter microclimate (Santos and Whitford 1981; Seastedt and Crossley 1983; Seastedt 1984; Walter 1985; Cepeda and Whitford 1989), but not to canopy conditions.

Canopy herbivores potentially influence litter communities through effects on foliage quality, canopy coverage, and nutrient turnover, especially during outbreaks (Schowalter et al. 1986; Seastedt et al. 1988; Schowalter et al. 1991; Moore et al. 1991). Seastedt and Crossley (1983) reported that simulated throughfall, as affected by canopy herbivory, significantly increased litter microarthropod densities and litter comminution. However, litter community responses to canopy processes remain poorly understood (Seastedt et al. 1988; Moore et al. 1991).

Microarthropod communities in forests of northwestern North America have received scant attention (Walter 1985; Moldenke and Fichter 1988; Seastedt et al. 1989) despite the probable importance of litter communities to decomposition of decay-resistant conifer litter and to the productivity of these forests. Therefore, as part of a study of canopy herbivore effects on nutrient turnover (Schowalter et al. 1991), we examined the effects of herbivore treatment, season, and changes in litter quality during decomposition on microarthropod communities in litterbags.

Materials and methods

The study site was a 10-year-old regenerating Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] watershed at the H. J. Andrews Experimental Forest in western Oregon (44 °N, 122 °W). The Andrews Forest is jointly managed by the U.S. Forest Service and Oregon State University and has been the site of extensive research under the International Biological Programme (IBP) and the Long Term Ecological Research (LTER) Program.

The Andrews Forest is dominated by coniferous forest, primarily 450-year-old Douglas fir. Young forests (< 50 years) have been established through experimental harvest and regeneration.

The climate is strongly seasonal, with warm, dry summers and cool, wet winters. During this study (1984–1986), the mean growing season (April–September) temperature was 13.7 °C and the mean October–March temperature was 3.6 °; the mean April– September precipi-

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tation was 58 cm, and the mean October–March precipitation was 165 cm. These conditions were within 5% of annual averages (Gholz et al. 1985).

Watershed 10 was not burned following the harvest in 1975. At the time the present study was established in 1984, the planted Douglas firs were about 1 m high. Shrubs and herbs comprised an uneven ground cover. Litter accumulation was negligible.

Sixty Douglas fir trees (similar with respect to foliage appearance, growth form, and absence of deer browsing) were randomly allocated to six herbivore treatments: (1) no herbivore manipulation; (2) herbivore exclusion; (3) low sap-sucker abundance (<0.5 insect g^{-1} foliage); (4) high sap-sucker abundance ($>0.5\,g^{-1}$); (5) low defoliator abundance ($<0.03\,g^{-1}$); and (6) high defoliator abundance ($>0.03\,g^{-1}$). We selected a homopteran, *Adelges cooleyi* (Gillette), as the representative sap-sucker and a lepidopteran, *Lophocampa argentata* (Packard), as the representative defoliator. All plants were given the same treatment over the 3 year period and were monitored every two weeks. Target abundances of the selected herbivores were maintained by manual addition or removal. This minimized variation in herbivore abundance during the feeding period and avoided confounding effects of biocides on nutrient turnover or microarthropod abundance. All other herbivores were removed.

Defoliation occurred during the period March–June each year, and averaged 0% foliage removal in the undefoliated treatments, 5% in the low defoliator treatment, and 15% in the high defoliator treatment; defoliation significantly ($P<0.05$) increased water and soluble N, K, and Ca inputs to litter (Schowalter et al. 1991). Only K inputs to litter were significantly affected by the sap-sucking herbivores.

Litterbags were placed under each tree to measure the herbivore effects on litter decomposition. Insufficient litter was provided by the study trees, so senescent Douglas fir needles were shaken from mature trees. Litterbags constructed from 1 mm polyester mesh (10×10 cm) were filled with 3.00 g of bulk needle litter. This mesh size was adequate to retain the needles, to permit gas exchange, and to allow entry by microarthropods (Fogel and Cromack 1977; Seastedt 1984; Walter 1985). Ten litterbags were placed under each study tree in March 1984. Two litterbags were collected from each tree after 3, 9, 15, 21, and 27 months, i.e., in June (dry season) and January (wet season) each year. Harvested litterbags were sealed in small plastic bags and returned to Corvallis, where litterbags from half the trees in each treatment were extracted in Tullgren funnels over ethanol (Seastedt 1984; Walter 1985).

Numbers of arthropods were counted, divided by the litter mass (after drying at 50 °C), and pooled by tree and collection date. Some infrequent taxa were pooled in order to obtain sufficient numbers for statistical analysis. All taxa were analyzed using a repeated measures analysis of variance, with herbivore treatment and collection date as the main effects (Milliken and Johnson 1984). A method developed by Greenhouse and Geisser (1959) was used to estimate the Box (1954) correction, which accounts for autocorrelation arising from repeated sampling from the study trees. Since the assumptions of homogeneity of variance and normality could not be met with the original data, a rank transformation was used (Conover and Iman 1981). All analyses were performed using SAS statistical software (SAS Institute 1982).

The litter from each litterbag was dried at 50 °C, weighed, and ground to pass a 40-mesh screen. The samples were analyzed for N and P using standard micro-Kjeldahl and autoanalyzer techniques, and for K and Ca using standard atomic absorption spectrophotometry (following perchloric acid digestion). Nutrient contents in the litterbags were calculated by multiplying the litter mass by the nutrient concentration.

Results

The mean abundance (number of individuals per g litter) of the various microarthropod taxa is shown in Table 1. Fungivores accounted for 85% of the total fauna recovered from the litterbags. Collembola (35%), oribatid mites (29%), and fungivorous actinedid mites (22%) dominated the litterbag community.

Table 1. Mean abundances of microarthropods extracted from Douglas fir needle litterbags under young Douglas fir at the H. J. Andrews Experimental Forest in western Oregon between June 1984 and June 1986 (3–27 months of decomposition)

Taxon	Mean abundance (no. g^{-1} litter)	Percentage of total fauna
Fungivores		
Achipteria	0.20 (0.17)	1
Eremaeus	0.26 (0.12)	1
Leuroxenillus	0.20 (0.14)	1
Metrioppia	0.20 (0.11)	1
Propelops	1.64 (0.53)	8
Zygoribatula	1.22 (0.79)	6
Other oribatids (20 spp.)	2.16 (0.62)	11
Eupodid sp.	0.26 (0.10)	1
Nanorchestes sp. 1	0.83 (0.33)	4
Nanorchestes sp. 2	0.93 (0.31)	5
Actinedid sp.	2.44 (0.86)	12
Entomobrya triangularis	2.35 (0.86)	11
Entomobryid sp.	0.71 (0.33)	3
Hypogastura	1.05 (0.44)	5
Neelid sp.	0.27 (0.17)	1
Podurid sp. 1	0.19 (0.14)	1
Podurid sp. 2	0.23 (0.24)	1
Tetracanthella	0.42 (0.26)	2
Tomocerus flavicormis	1.79 (0.42)	9
Other Collembola (4 spp.)	0.23 (0.11)	1
Diplopods (3 spp.)	0.07 (0.04)	0
Herbivores		
Adelges cooleyi	0.16 (0.09)	1
Other insects (5 spp.)	0.10 (0.10)	0
Predators		
Vegaiid sp.	0.48 (0.24)	2
Zerconid sp.1	0.42 (0.22)	2
Zerconid sp. 2	0.51 (0.31)	2
Other gamasids (5 spp.)	0.03 (0.03)	0
Tarsonemid sp.	0.32 (0.57)	2
Other actinedids (16 spp.)	0.43 (0.14)	2
Other arachnids (3 spp.)	0.12 (0.05)	1
Miscellaneous (12 spp.)	0.21 (0.07)	1
Pauropod sp.	0.16 (0.14)	1
Total	20.63 (4.0)	99

Means (±SEM), $n = 30$

Three taxa (two oribatid mites, *Achipteria* and *Eremaeus*, and a species of pauropod) were significantly ($P<0.05$) affected by canopy herbivore treatment (Table 2). All three taxa were more abundant under trees subjected to defoliation compared to other treatments.

Most taxa (28) showed a significant relationship with the collection date. The treatment × date interaction was significant only for the pauropod species, which was present only in the January collections. The predominant trend (23 taxa) was a seasonal fluctuation in abundance between January (wet season) and June (dry season) each year (Fig. 1). Overall, abundances were more than three times higher in January than in June. This pattern was in contrast to the trends in N and Ca contents of the litterbags (Fig. 2), but because of high variability, the arthropod abundances were not significantly correlated with nutrient contents in the litterbags. *Nanorchestes* sp. 1

Table 2. Effects of canopy herbivory treatments on three microarthropod taxa showing significant responses in litterbags under young Douglas fir at the H.J. Andrews Experimental Forest in western Oregon

Treatment	Microarthropods (no. g^{-1} litter)		
	Achipteria sp.	*Eremaeus* sp.	Pauropod sp.
Unmanipulated	0.16 (0.07) ab	0.26 (0.09) ab	0.43 (0.29) a
Exclusion	0.14 (0.12) bc	0.14 (0.07) b	0.07 (0.04) abc
Low sap-sucker	0 (0) c	0.13 (0.06) b	0.02 (0.01) c
High sap-sucker	0.02 (0.02) bc	0.18 (0.10) b	0.19 (0.17) c
Low defoliator	0.23 (0.17) abc	0.07 (0.05) b	0.03 (0.02) bc
High defoliator	0.65 (0.34) a	0.77 (0.20) a	0.21 (0.09) ab

Means (± SEM), $n = 30$; means in columns followed by the same letter do not differ significantly ($P < 0.05$; Fisher's protected least significant difference test, using rank-transformed data)

showed the opposite pattern, being more abundant in June than in January each year. Herbivorous and miscellaneous insects occurring in the litterbags during January were probably overwintering.

The second significant temporal pattern (five taxa) was a tendency towards a long-term change in abundance over the 27-month period. Four taxa (*Metrioppia*, a eupodid species, *Hypogastura*, and podurid sp. 1) showed rapid colonization and peak abundance in the first collection, followed by a general decline in numbers. This decline followed the pattern of loss of organic matter, K and P from litterbags (Fig. 2), but the abundances of these arthropods were not significantly correlated with nutrient contents in the litterbags. The fifth taxon, predaceous actinedids, increased significantly in abundance after 1.5 years.

Discussion

This study demonstrated that litter microarthropod communities in western Oregon are similar to communities in other forest, grassland, and desert ecosystems (Seastedt and Crossley 1983; Santos and Whitford 1981; Seastedt 1984). We also demonstrated that community structure reflects responses to a variety of environmental conditions, including canopy herbivory. The response to seasonal conditions contributed most to community structure in this study, as in previous studies (Seastedt and Crossley 1983; Seastedt 1984; Walter 1985; Moldenke and Fichter 1988; Cepeda and Whitford 1989), but responses to canopy herbivory and litter condition also influenced the community structure qualitatively. In turn, qualitative changes in community structure may alter litter decomposition processes.

Three subdominant microarthropod taxa, *Achipteria*, *Eremaeus*, and a pauropod species, were significantly more abundant under trees subjected to experimental defoliation. Although these taxa together represented ≤4% of microarthropod numbers overall, in winter, and in undefoliated treatments, the proportion of these species increased to 20% of microarthropods under trees subjected to 10–20% defoliation, occurring in June 1986 when

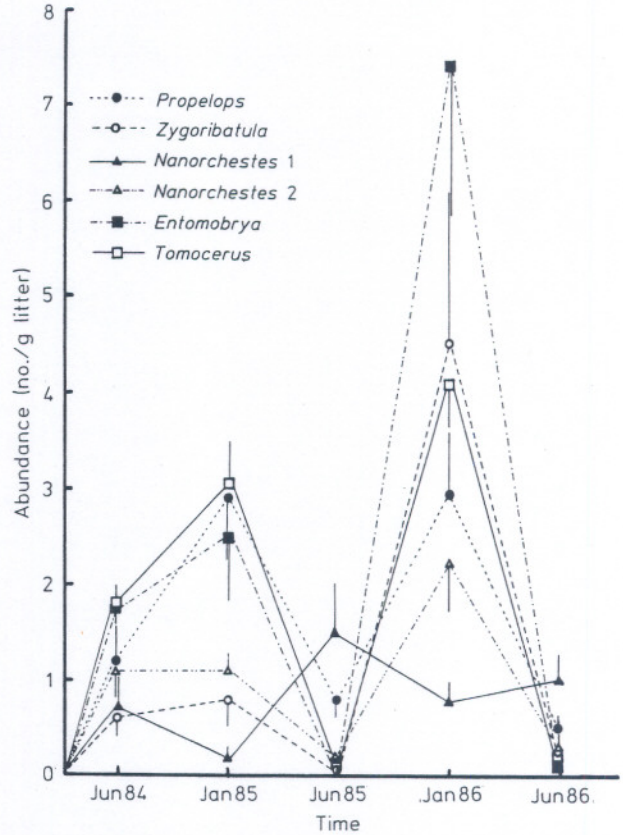

Fig. 1. Seasonal abundance of dominant microarthropod taxa showing significant responses to season in litterbags under young Douglas fir at the H. J. Andrews Experimental Forest in western Oregon. *Vertical bars* represent SEM; $N = 30$

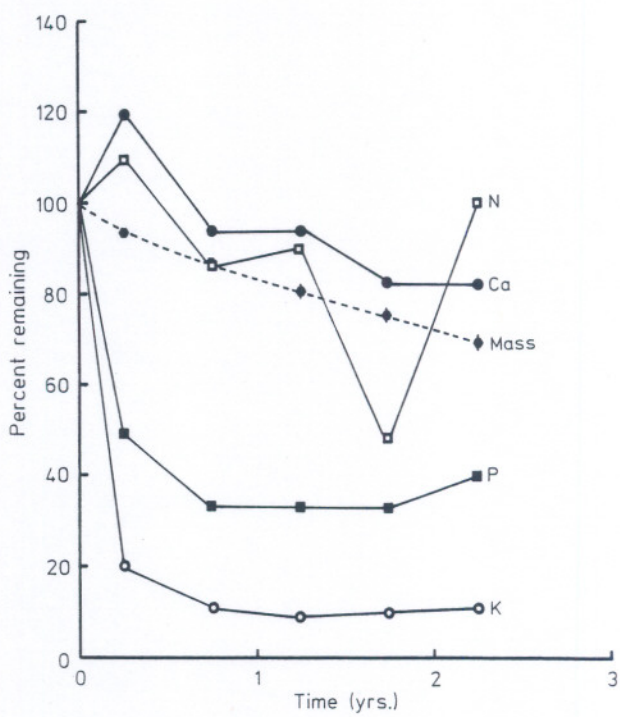

Fig. 2. Mass loss and elemental (N, P, K, Ca) dynamics of Douglas fir needle litter in litterbags under young Douglas fir at the H. J. Andrews Experimental Forest in western Oregon. *Bars* representing SEM are narrower than the symbols (<1%) for most points; $N = 60$

populations of other taxa were minimal. This qualitative change in microarthropod community structure could influence decomposition processes.

The mechanism by which herbivory influenced litter microarthropods was not apparent. However, the defoliator significantly increased light and water penetration of the canopy and significantly increased N, K, and Ca flow to the litter during the period of defoliation (Schowalter et al. 1991). The microarthropods presumably responded to changes in litter microclimate and/or resource suitability and availability resulting from defoliation. Seastedt and Crossley (1983) reported that simulated throughfall, similar to the increase in throughfall caused by defoliators in the present study, significantly increased microarthropod densities and litter comminution rates in a hardwood forest. Although the herbivore treatment did not significantly affect decomposition in our study (Schowalter et al. 1991), changes induced in the litter community structure might affect the decomposition of refractory Douglas fir litter after a longer period.

The seasonal pattern of microarthropod abundance probably reflects the seasonal pattern of precipitation in this region, i.e., cool, wet winters and warm, dry summers (Gholz et al. 1985; Moldenke and Fichter 1988). The relationship between microarthropod abundance and the N and Ca contents of the litterbags does not show cause and effect, but is consistent with previous studies showing that litter microarthropods had a significant effect on nutrient mineralization from litter (Santos and Whitford 1981; Seastedt 1984). Our results indicate that N and Ca were mobilized from litterbags during periods of high precipitation and high microarthropod abundance, and immobilized during periods of low precipitation and low microarthropod abundance.

Some taxa showed a long-term trend in abundance. The rapid colonization of litterbags, followed by a general decline in abundance over the period of litter decomposition, suggested a response to declining litter quality (Santos and Whitford 1981; Seastedt 1984), perhaps to loss of labile mass, K, and P. Predaceous actinedids probably increased in abundance over time as more prey became available.

In conclusion, our data indicate that the microarthropod community structure reflects responses to a variety of environmental conditions, including canopy processes. Response to seasonal climatic factors contributed most to community structure in this study. Although relatively few taxa responded to canopy herbivory, qualitative changes in microarthropod communities could affect decomposition processes during periods of defoliation. The taxa that respond to defoliation may become less abundant or disappear if defoliation is prevented or suppressed. These results demonstrate the importance of canopy processes, seasonal conditions and litter quality to litter microarthropod communities.

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