ARBOREAL ARTHROPODS: DIVERSITY AND RATES OF COLONIZATION IN A TEMPERATE MONTANE FOREST

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ABSTRACT. To investigate the micro-arthropod species inhabiting the montane forest canopy from three elevational sites (800 m, 1000 m, 1200 m) at Mt. Cain on Vancouver Island, British Columbia, Canada, we placed sterile litter bags filled with fir needles in the canopy and on the ground beside nine randomly chosen amabilis fir (*Abies amabilis*) trees. Our objectives were 1) to determine the faunal composition and diversity of micro-arthropods that colonize the needle litter microhabitat; 2) to determine the colonization rates of canopy micro-arthropod groups, specifically oribatid mites (Acari: Oribatida); and 3) to compare the rates of needle litter decomposition between the ground and canopy at different elevations, relating these results to patterns of micro-arthropod abundance. Arthropods were collected after three colonization periods (60, 120, 360 days), extracted from litter bags using a modified Lussenhop method, counted, and identified to order. Acari, Collembola, and Psocoptera were the dominant arthropods colonizing the needle litter. Two-way analysis of covariance showed ground and canopy colonization rates significantly different but with similar patterns of colonization occurring over time for all groups. Colonization rates were lower for most taxa at high elevations compared to low elevations, and most micro-arthropod taxa showed significantly different patterns of colonization across elevations. Colonization and decomposition rates were lower in the canopy than on the ground, and no differences in decomposition rates were found to occur across elevations. Our study of the colonization and decomposition of these experimental substrates will enable further assessment of the micro-arthropod diversity and decomposition processes in the montane forest. It also will contribute to our understanding of the biology of soil organisms inhabiting the lichen-rich canopy of montane amabilis fir trees.

Key words: micro-arthropod, British Columbia, canopy, needle litter

INTRODUCTION

The montane forest is a priority study area in terms of biodiversity research because of the recent geographic shift in timber extraction from low to high elevation forests. Forest extraction practices will have unknown consequences for the arthropod communities residing within this ancient forest type. Describing species assemblages, documenting their habitat preferences, and including ecological processes in the framework of arthropod biology in old-growth forests will provide information needed to conserve and maintain biological diversity (form and function) within this system (Winchester 1997). The rationale for including arthropods in biodiversity studies has been established (Wilson 1988, Winchester 1997, Ehrlich 1988, Didham et al. 1996, Verhoef & Brussard 1990).

Biodiversity research at the global level consistently has emphasized the need for studying soil organisms (Heal et al. 1994, Moore & de Ruiter 1991). Baseline data are lacking, however, on the critical roles played by soil biota and the individual roles of soil taxa in maintaining soil structure and fertility and in mediating ecosystem processes such as forest nutrient cycling. Despite some knowledge of how soil mi-

cro-arthropods maintain critical processes (Huston 1993) and of how soil organisms participate in forming soil structure (Swift et al. 1979), the organisms themselves remain a "black box." Yet they are critical to our understanding of ecosystem functioning (Freckman 1994).

Soil micro-arthropods dominate the suspended canopy soil/litter habitat (Wallwork 1976), a fact that has been documented by studies in tropical and temperate regions (Winchester 1997, Schowalter 1988, Nadkarni & Longino 1990, Paoletti et al. 1991, Wunderle 1992, Moldenke & Lattin 1990). None of these studies, however, has yet linked arthropod-abundance to biological processes and functions (e.g., influencing the rates of decomposition in the canopy soil horizon).

Temperate canopy systems, characterized by low faunal diversity, represent relatively simple soil sub-systems for study compared to the more complex tropical canopy or forest floor sub-systems, thus lending themselves to manageable analysis (Wallwork 1983). In temperate coniferous forests, needle fall is a major pathway of nutrient and energy flux, but most forest nutrient cycling research has focused on the organic litter that accumulates on the forest floor and not the simplified canopy soil layer. The fauna that colonize these canopy resources and participate in the decomposition and regulation of nutrient

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transfer rarely are studied. For example, Acarina (mites), specifically the Oribatida ("beetle mites"), are the dominate fauna, in terms of individuals and species, in the following habitats: northern temperate forests (Moldenke & Lattin 1990, Wallwork 1983), Sitka spruce canopy moss mats (Behan-Pelletier & Winchester 1998, Winchester 1997), boreal spruce forest canopies in Sweden and Finland (Pettersson et al. 1995, Laine et al. 1990), rain forest canopies in Australia (Walters 1993), and montane rain forest canopies in Costa Rica (Nadkarni & Longino 1990). The sheer numbers of these minute arthropods suggest that they play key but virtually unexplored roles in the forest canopy soil system (Walters & O'Dowd 1995). On the ground, mites affect soil energetics and soil fertility (Crossley 1977, Lebrun 1979). They act as secondary decomposers by conditioning the organic debris for action by the primary microbial decomposers (Seyd & Seaward 1984). Some act as primary decomposers themselves (Luxton 1979). Oribatids contribute to humus formation by direct consumption and break-up of fallen plant material and fungal-decayed litter, as well as by eating and distributing fungi and their spores (Norton 1985).

Little published data exist for comparing dominant micro-arthropods that colonize organic litter on the ground and in the canopy (Trave 1963, Spain & Harrison 1968, Nadkarni & Longino 1990, Winchester 1997, Behan-Pelletier & Winchester 1998). The community structure of forest canopy and ground micro-arthropods in the temperate montane forest of the Pacific Northwest is unknown and has never been studied systematically. In this paper we outline the faunal composition and diversity of micro-arthropods that colonize the needle litter microhabitat of amabilis fir (*Abies amabilis* Douglas ex J. Forbes) in a montane forest. We compare, during a one-year period, the rates of micro-arthropod groups colonizing needle litter, specifically the Acari (Oribatida), from experimental substrates (litter bags) with the rates of needle litter decomposition between the ground and canopy at different elevations on Mt. Cain on Vancouver Island.

MATERIALS AND METHODS

We sampled canopy and ground arthropods in a high elevation forest at Mt. Cain (50°13′N, 126°18′W) on northern Vancouver Island, British Columbia, Canada (FIGURE 1). The study area is in a relatively unfragmented ancient forest (>700 years) interspersed with variously aged stands of intensively managed forest and sub-alpine ponds. The area lies within the Coast-
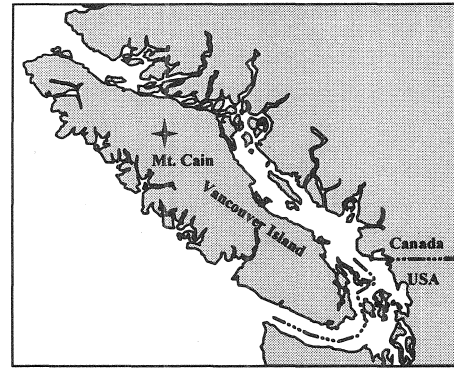

FIGURE 1. The Mt. Cain study site (star) on Vancouver Island, British Columbia, Canada.

al Western Hemlock (CWH) and Mountain Hemlock (MH) biogeoclimatic zones (Pojar & Mackinnon 1994). The CWH and MH zones occur along the B.C. coast and occupy elevations from sea level to 900 m and from 800 m to 1800 m respectively. The climate is characterized by short, cool, dry summers and long, wet winters with heavy snow cover. Mean annual precipitation ranges from 1700 to 5000 mm, of which 20–70% is snow (Pojar & Mackinnon 1994). Trees dominating the study area are mountain hemlock [*Tsuga mertensiana* (Bongard) Carrière], amabilis fir (*Abies amabilis*), western red cedar (*Thuja plicata* Donn ex D. Don), and yellow cedar [*Chamaecyparis nootkatensis* (D. Don) Sudworth]. We chose amabilis fir as our sample trees because in dense, fully stocked stands, advanced regeneration of this fir is often more abundant than for other species. Although mountain hemlock is the climax species in the area, amabilis fir trees were chosen for the study because amabilis fir will eventually become the dominant tree in a managed landscape (Meidinger & Pojar 1991).

Sampling Design

The sampling design was based on a comparison of three different trees sampled at each of three elevations: 800 m, 1000 m and 1200 m. We sampled the trees using simple rope-climbing techniques to access the canopy. Twelve litter bags (10 × 20 cm in size with a 0.5 mm mesh) filled with 10 grams of amabilis fir needles were sterilized by freezing and thawing the plant material during two 24-hour periods to eliminate arthropods. Litter bags were attached randomly to each of three branches, at similar heights, from the trunk to the end of each limb in each tree. To ensure that colonization resulted because of the litter itself and not because of

microclimatic conditions created by the litter bag, control litter bags filled with Styrofoam chips were used. To determine the location of actively colonizing arthropods, we used control litter bags to separate amabilis fir needle litter bags into three groups at varying distances along each branch. Three litter bags and a control also were staked to the forest floor beneath each tree to test for differences between canopy and ground fauna (Winchester 1993).

Following 60, 120, and 360 day colonization times (beginning 22 May 1997), one randomly chosen litter bag from each of the three distances along each branch was removed. One randomly chosen control bag also was removed from each branch. In all, 81 canopy litter bags were collected during each colonization time, placed in plastic bags, and stored inside a cooler (5°–10°C) for no more than 3 days. Micro-arthropods were extracted from the needle litter during a 48-hour period using a modified Lussenhop extractor (Lussenhop 1971). As the needle litter dried out, arthropods sensitive to desiccation moved downwards through the sample and fell into a collecting container of picric acid. The abundance of individuals in each arthropod order was recorded, and specimens were stored in 75% ethanol. Immature arthropods were included in the analyses.

This sampling design reflected the a priori expectation that the abundance of arboreal arthropod assemblages would differ following each colonization time and among different elevations, individual trees, and fixed distances along each branch. Previous forest floor studies have shown changes in species diversity, specifically oribatid mites, colonizing different litter types across different elevations over time (Walters 1985).

Statistical Analysis

The abundance of individuals colonizing the needle litter was expected to increase rapidly and reach a plateau; thus data were modeled with logarithmic curves. Because a logarithmic relationship best represented the data points, all data were fitted to a logarithmic relationship to give comparable results.

Data were tabulated in terms of number of individuals per litter bag. A two-way analysis of covariance (ANCOVA) was used to test the main effect of colonization time and ground versus canopy colonization rates, as well as the interaction effect of ground versus canopy rates of colonization across elevations for all arthropods and Acari. Data were expressed as the log mean number of individuals ± 1 standard deviation. Log (days), elevation, and ground versus canopy

Table 1. Diversity and composition of the arthropod fauna collected from amabilis fir tree (*Abies amabilis*) needle litter bags following a one-year colonization period, starting 22 May 1997, at Mt. Cain on Vancouver Island, B.C., Canada. Data for both ground and canopy needle litter bags were pooled and expressed as the absolute number of individuals/litter bag collected from a total of 243. Unknowns consist of early larval stages.

Order	No. of individuals	% total
Acari	1292	56.9
Collembola	554	24.4
Psocoptera	101	4.4
Diptera	95	4.1
Araneae	25	1.1
Coleoptera	20	0.9
Thysanoptera	6	0.3
Hymenoptera	6	0.3
Unknown	172	7.6
Total	2271	100

were the main effects (all variables being fixed); and a significance level of 0.05 was used. Interaction terms are reported where significant (Krebs 1989). The original data were log-transformed ($\ln X+1$) to remove heteroscedasticity (Zar 1974), and analysis of covariance was carried out using SPLUS 4.5 for Windows (MathSoft Inc. 1996).

RESULTS

In all, 2251 arthropods were collected; they belonged to two classes: Arachnida (58%) and Insecta (42%). The numerically dominant taxa colonizing both the ground and canopy needle litter were the Acari (mites), Collembola (springtails), Psocoptera (bark lice), and Diptera (flies) (TABLE 1).

Relative abundance for all micro-arthropods colonizing litter bags at each of the three elevational sites increased as time progressed in both the canopy and on the ground (FIGURE 2). Total arthropod abundance was higher by a factor of 2.2 on the ground than in the canopy for all sites. Relative proportions of the same taxa colonizing canopy needle litter also were similar on the ground.

Acari, composed primarily of oribatids, was the most abundant order, comprising 57.0% of all arthropods collected (TABLE 1). Acari followed similar patterns when compared to all arthropods collected (FIGURE 2). More individuals were collected on the ground than in the canopy. The most abundant insect order was Collembola, comprising 24.4% of the total arthropod fauna (TABLE 1). More individuals were collected on
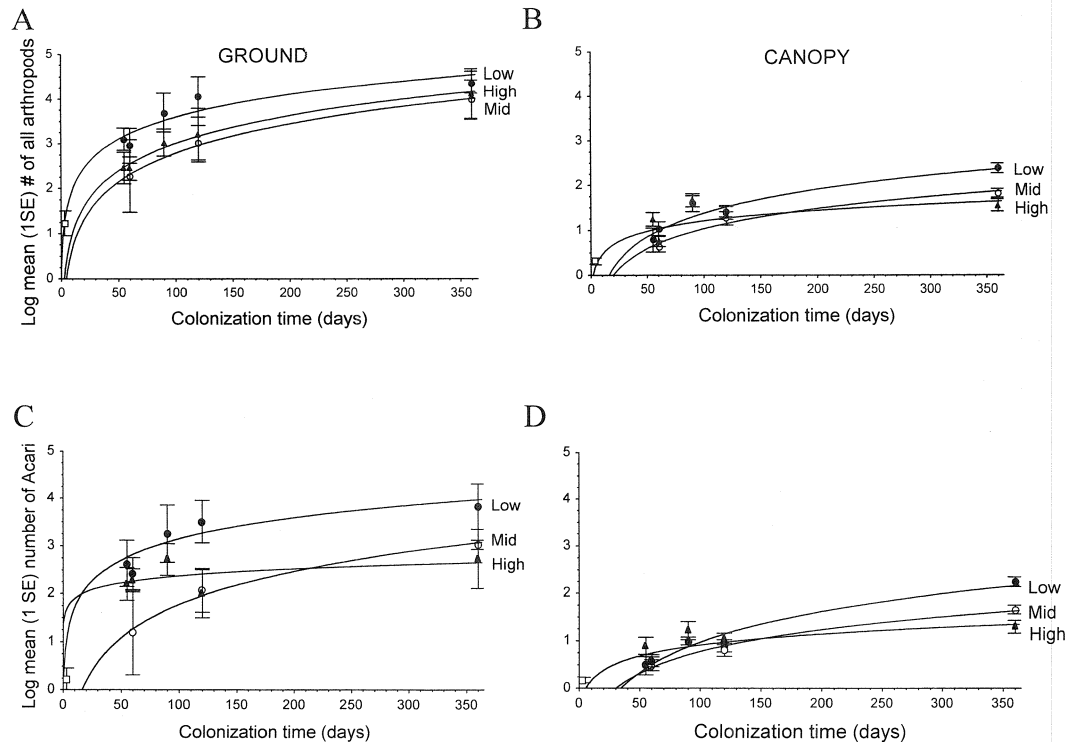
FIGURE 2. Relationship between colonization times (60, 90, 120, and 360 days) and the log (mean number of individual micro-arthropods) ± 1 standard error colonizing *Abies amabilis* fir trees at Mt. Cain for **A.** Ground micro-arthopods; **B.** Canopy micro-arthropods; **C.** Ground Acari; and **D.** Canopy Acari. Low, mid, and high elevation colonization rates are represented by closed circles, open circles, and triangles, respectively. Solid lines are fitted logarithmic relationships.

TABLE 2. Results of the two-way analysis of covariance comparing the colonization rates for Acari and all arthropods collected from the canopy and the forest floor of nine *Abies amabilis* trees at Mt. Cain on Vancouver Island, Canada. The main effects tested and outlined are log (days), elevations, and ground versus canopy. Interaction terms are reported. All values reported are significant except ⊕.

	Effect	$F_{1,2}$	P value
log (Acari + 1)	Log (days)	156.087	0.001
	Ground/canopy	184.716	0.001
	Elevation	13.456	0.001
	Interaction	5.705	0.004
log (Total + 1)	Log (days)	132.949	0.001
	Ground/canopy	273.346	0.001
	Elevation	7.739	0.001
	Interaction	0.977	0.378⊕

Note: $F_{1,2}$ = F-ratio with degrees of freedom shown; P value = level of significance.

the ground than in the canopy. Psocoptera, comprising 4.5% of the total arthropod fauna, failed to colonize ground needle litter bags but did colonize canopy litter bags. Other arthropods, comprising 14% of the arthropod fauna, colonized both the canopy and ground needle litter bags. These orders included Diptera, Hymenoptera, Coleoptera, Araneae, and Thysanoptera. Unknown arthropods were composed of very early larval stages.

Colonization rates for all micro-arthropods colonizing the needle litter bags showed a significant increase following each colonization time ($P < 0.001$) (TABLE 2). The total number of individuals colonizing litter bags between ground and canopy differed ($P < 0.001$). A significant effect of elevation was observed on the total number of arthropods colonizing needle litter bags ($P < 0.001$). With no interaction effect evident, the same colonization patterns on the ground and in the canopy for all micro-arthropods may be occurring at different elevations.

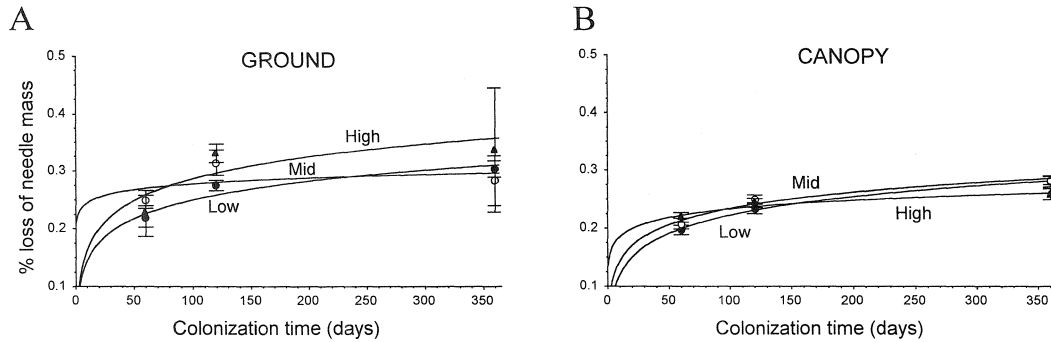Following each colonization time, the abundance of Acari showed a significant increase (P

FIGURE 3. Changes in *Abies amabilis* needle litter decomposition rates as a function of time following 60, 120, and 360 day decomposition times on Mt. Cain for **A.** Ground litter bags and **B.** Canopy litter bags. Low, mid, and high elevation decomposition rates are represented by closed circles, open circles, and triangles, respectively. Solid lines are fitted logarithmic relationships.

< 0.001) (TABLE 2). The total number of Acari colonizing litter bags between the ground and the canopy was significant ($P < 0.001$), as was the effect of elevation on the abundance ($P < 0.001$). The interaction effect ($P < 0.004$) indicates that different colonization patterns on the ground and in the canopy may be occurring at different elevations for the Acari group.

Decomposition rates were very slow in the montane forest compared to results found in Oregon (Schowalter & Sabin 1991). Obvious differences in decomposition rates were observed between the needle litter bags on the forest floor and in the canopy (FIGURE 3). The ground needle litter bags generally showed a higher decomposition rate than those in the canopy. No apparent differences in decomposition rates were observed across the different elevations.

DISCUSSION

Our results clearly indicate that Acari, Collembola, Psocoptera, and Diptera are the major arthropod orders colonizing needle litter in the montane forest. These results are in agreement with studies in both the temperate and tropical regions (Walters 1985, Nalini & Longino 1990, Wunderle 1992, Winchester 1997). The composition and abundance of arthropods in our study are most similar to those described in a study by Pettersson et al. (1995) on the effects of forestry on canopy-living invertebrates in natural and managed boreal spruce forest in Sweden and in a study by Laine et al. (1990) on similar boreal comparisons from northern Finland. Acari, Araneae, Collembola, and Psocoptera dominated these canopies.

Spider colonization, low in our study, probably was related to the litter bag mesh size. Spiders, however, are found to be the dominant macro-arthropods residing in montane canopy, when various other collecting techniques are employed (Winchester & Fagan 1999). Other factors, such as the reduced epiphyte loading in amabilis fir trees (except moulds, fungi, mosses, and lichens), also may account for the low abundance of certain arthropod taxa and the overall lower abundance of arthropods in the montane compared to other coastal forests. For example, the abundance of mites in the Sitka spruce forest on Vancouver Island (Behan-Pelletier & Winchester 1998) far exceeds that in the montane canopy, because the canopy of Sitka spruce consists of deep (>5 cm) moss mats capable of supporting a larger fauna. Results of our study and others (Pettersson et al. 1994, Laine et al. 1990) also suggest that northern latitude forests may have similar micro-arthropod communities at the ordinal level residing in different forest canopy types. Since only one tree species was studied, the diversity of micro-arthropods colonizing needle litter bags in mixed stands may be higher than our study concludes.

Similar proportions of the same arthropod groups colonized needle microhabitat in the canopy and on the forest floor. The abundance of organisms colonizing ground litter bags was higher than organisms colonizing litter bags in the canopy. Nadkarni and Longino (1990) found similar results in a tropical montane ecosystem. Results of both these studies imply that temperate and tropical montane ecosystems share a fundamentally similar arthropod community.

Assumptions made about the montane forest ecosystem without the inclusion of both divisions likely will lead to incorrect and erroneous management decisions. For example, in our study, two of the three trees sampled at the low elevation were colonized by Psocoptera; but no colonization occurred in any of the forest floor

litter bags. Arboreal specificity was reported by Behan-Pelletier and Winchester (1998) and Winchester (1997). The high numbers of Psocoptera collected at the low elevation were unexpected and suggest that interactions may be occurring at the low elevation which are not found at the high elevation. The high abundance of Psocoptera, however, may be caused by strictly seasonal differences conducive to population explosions or certain habitat requirements. By examining the Acari colonization results, we confirmed that differences in colonization patterns on the ground and in the canopy at different elevations were occurring and that our assumption with regard to Psocoptera may be correct.

Colonization Patterns and Rates in the Montane

The temperate montane forest canopy is dominated by lichens. In addition, similar accumulations of conifer needle litter in the crown region of the trees, on branches, and in the forks of branches are apparent. In a system lacking deep moss mats (Winchester 1997), the composition and diversity of organisms that colonize lichen/needle microhabitats were expected to vary according to the different structural components making up this canopy type; yet Acari and Collembola still dominated. Similarities in the dominant taxonomic orders were expected, as this organic material resembles in composition the major organic layer on the forest floor. The presence of lichens in the canopy, however, may alter the microclimate near the litter bags, thus providing more colonization sites favorable for micro-arthropods (Stubbs 1989). In this way, lichens may alter the rate of colonization by certain groups utilizing this resource and may influence the overall species composition and abundance of arthropods in the canopy (Schowalter 1988).

The initial high rates of colonization exemplified by both the forest floor fauna and the canopy fauna may relate to the use of green needle litter or the placing of litter bags near lichen material containing organisms capable of quickly infiltrating the experimental substrate. Green needles may be a food resource for certain groups of organisms. Recognizing that forest floor fauna are more abundant than canopy fauna, the higher densities and rates of colonization by forest floor fauna suggest that food and habitat resources may be more of a limiting factor on the ground than in the canopy. Lower densities and initial colonization rates by arboreal fauna suggest that their limiting factors may be more abiotic in nature. This idea has been suggested by Danks and Foottit (1989). The struc-

ture of arctic communities may depend more on the tolerances of individual species to abiotic factors than on interactions among species. Similar to arctic fauna, the arboreal fauna must contend with greater environmental extremes and severe microclimatic conditions compared to the forest floor fauna. For example, tree crowns are subject to greater amounts of insolation, wind, desiccation, and precipitation cycles than is the forest floor (Lawton 1982). Extreme variability in the moisture content of the litter substrate, which determines to a large degree the number of micro-arthropods present (Metz 1971), also may affect the rates of micro-arthropod colonization.

Decomposition Rates and Micro-Arthropod Abundance

The low temperature and high moisture content of montane soil promotes slow litter decomposition (Meidinger & Pojar 1991). Results from our study confirm these findings. The relatively constant climatic conditions on the forest floor compared to the canopy may explain why decomposition rates are slightly greater on the forest floor. In tropical regions, the decomposition process is related to termite activity; whereas in colder parts of the world, termites are absent, and different groups of organisms are involved with decomposition (Freckman 1994). Studies on why certain species colonize more frequently (Simberloff 1978) and on whether a rigid order of colonization is correlated with the frequency of the respective species in these types of litter habitats would yield knowledge of interest.

In our study, similar decomposition and micro-arthropod colonization patterns were observed for both the forest floor and the canopy. Decomposition occurred in a similar fashion. Rates of colonization in the montane, however, are influenced more by elevational differences than are rates of decomposition. Longer study periods are required to confirm these findings.

SUMMARY

Montane fauna show strong affinities to other temperate forest canopy/ground fauna, including high population densities of dominant species, abundant non-insect predators, and the absence of ants as well as termites. Information collected for forest management purposes without the inclusion of both arboreal and forest floor micro-arthropods, especially the dominant groups (i.e., Acari and Collembola) involved in the major biological processes such as decomposition and nutrient cycling will present a highly skewed vi-

sion of ecosystem dynamics in the montane forest.

Many studies have suffered from drawing weak functional inferences from empirical data on arthropod species richness and abundance without directly measuring the functional process (Didham 1997). This kind of inference is no substitute for simple experimental manipulation. Manipulation of needle litter bags in the suspended soil system of the temperate montane forest canopy allows direct measurement of needle litter decomposition rates. Our results show that the temperate forest canopy, because of its simplicity, serves as a good model for examining ecosystem functioning. Target taxa such as mites also provide a model system in which to study the effects of such things as forest fragmentation and its effect on loss of biodiversity and associated changes in rates of ecosystem functioning (Didham 1998). To a large extent, the decomposer organisms control nutrient supply and, since this supply is limiting, strongly influence primary productivity (Seastedt and Crossley 1988). Perturbation of the decomposer community has far-reaching impacts on the nutrient supply and retention and hence on the stability of the montane ecosystem. By relating changes in species-abundance patterns directly to changes in rates of needle litter decomposition, we can obtain a functional relationship of decomposition processes and forest nutrient cycling dynamics to the impact of perturbations on micro-arthropod biodiversity in the montane forest. Few studies on the responses of decomposers to habitat fragmentation and isolation have revealed marked changes in decomposer abundance and species diversity; but such studies rarely have measured the quantitative impact of loss of biodiversity on decomposition processes. Future canopy research should focus on such measurements.

ACKNOWLEDGMENTS

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