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Relationships among microarthropods, fungi, and their environment

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Abstract

Temporal and spatial relationships in a maple-forest soil among mycophagous microarthropods, total hyphal length, vesicular-arbuscular mycorrhizal (VAM) fungus spores, microfungus diversity, root biomass and some abiotic variables (temperature, water content, pH, organic matter content) were investigated. Samples were obtained from spring 1991 to winter 1992 at four soil depths. Canonical correspondence analysis was used to analyze the data. Four species of sporulating VAM fungi were identified, along with 23 species of mites and springtails, 9 of which were common. Hyphal length, VAM fungus spores, and soil animals peaked in spring and autumn. Canonical correspondence analysis suggests that animal abundance and success in the soil is dependent on a number of environmental variables. The most important variables that influence microarthropod community structure are: (i) temperature, (ii) water content, (iii) pH, (iv) total length of fungal hyphae, and (v) diversity of darkly-pigmented fungi. However, the relative importance of these variables changes with increasing soil depth. We have also shown a relationship between arthropod populations and their food supply under field conditions, a phenomenon that has been demonstrated previously under controlled laboratory conditions.

Introduction

It is difficult to observe interactions between arthropods and fungi directly in undisturbed soil. Knowledge on the ways in which these groups interact is important if we are to arrive at a better understanding of how the entire ecosystem functions. It is well known that fungi play important roles in soil fertility and primary production through their activities in organic matter decomposition and nutrient cycling, as root pathogens, and as participants in symbiotic associations with plant roots (Kendrick, 1992). A large variety of fungal taxa is typically found in most soils, although decomposers probably predominate in the litter and humus layers, while mycorrhizal symbionts are most important deeper in the soil.

Soil arthropods are very abundant in many soils and may influence fungal communities indirectly via comminution, channeling, and mixing, and directly through grazing, and dispersal of spores (Visser, 1985). Under laboratory conditions, many fungal taxa can be used as food sources by some groups of soil arthropods, especially soil mites (Acari: Arachnida) and springtails (Collembola: Insecta) (Klironomos et al., 1992; Mitchell and Parkinson, 1976; Moore et al, 1987; Moore et al., 1988; Newell, 1984a,b; Parkinson et al., 1979). Laboratory experiments presented in these papers have shown preferential feeding, with the animals grazing selectively on particular fungal groups, especially those with darkly-pigmented hyphae and spores.

In contrast to laboratory results, field work has failed to show similar trends (Anderson and Healey, 1972; Behan-Pelletier and Hill, 1983; McMillan, 1975). Researchers have correlated arthropod population dynamics with different aspects of their environment. On a large scale, the microarthropod community composition changes in response to changes in the plant community that occur along environmental gradients (Hågvar, 1982). On a smaller scale, the community is affected by spatial heterogeneity in microclimate (Poole, 1962). Temporal changes also occur in the long-term, as a result of successional processes, or of predictable seasonal shifts, and in the short-

term, because of random fluctuations in the environment (Huhta et al., 1979). However, the availability of fungi in particular microhabitats has not been shown to be important, even though the availability of food items in such microhabitats is thought to influence animal population dynamics (and consumption of fungi) (Moore et al., 1988). Gut content analyses of arthropods have shown no evidence of preferential feeding under field conditions (Anderson and Healey, 1972; Behan-Pelletier and Hill, 1983). Their inability to confirm results obtained in the laboratory with field data has led scientists to conclude that these animals are generalists in their natural habitat (Usher et al., 1982; Visser, 1985).

The greatest barriers to progress in such field work have been the shortcomings of most of the available methods (Crossley et al., 1991). As one way of dealing with difficulties in studying the ecology of soil organisms, some researchers have used indirect multivariate statistics (Andre, 1983; Bissett and Parkinson, 1979; Poursin and Ponge, 1984; Pozo, 1986; Usher et al., 1982; Widden, 1986b). However, the statistical techniques used in these studies did not follow ecological principles. They used linear response models, while it is generally believed that organisms respond to environmental gradients in a unimodal fashion (Smith, 1990).

Ter Braak (1987) and ter Braak, and Looman (1986) discussed the usefulness of nonlinear models in community analysis. Ter Braak (1986) introduced canonical correspondence analysis (CCA) as a new multivariate direct gradient analysis which is an extension to weighted averaging ordination (correspondence analysis). Using CCA, axes in the ordination are selected to be constrained linear combinations of environmental variables, so that species are related directly to a set of environmental variables. This technique has been adopted in limnological studies (Dixit et al., 1989), plant ecology (ter Braak, 1987), and mammalian ecology (Velazquez, 1993), but has yet to be applied to soil ecosystems.

In this study we simultaneously analyzed field-derived soil samples for microarthropods, soil fungi, and some abiotic variables. Then with the aid of CCA, we examined the sensitivity of microarthropods to the diverse characteristics and biological components of a maple-forest soil, especially the fungi.

Materials and methods

Site description and sampling

A 100 m^2 plot was set up in a sugar maple forest near Waterloo, Ontario, Canada. The dominant tree species throughout the site is sugar maple (*Acer saccharum* Marsh.), and the surface soil is a sandy loam with a low fertility and water holding capacity (Brundrett and Kendrick, 1988). This study was part of a larger study focusing on trophic interactions between fungi associated with the roots of *A. saccharum*, and microarthropods. Points were chosen randomly within the plot, and the closest maple tree to that point was used for that particular sample. The tree was only a reference point and samples were obtained at a random compass point, 5 m away from the tree. A preliminary survey revealed that feeder roots of *A. saccharum* were most abundant at this distance. In order to correlate fungal and environmental data with the vertical distribution of the animals, the soil profile throughout the study was divided into layers (i.e. litter (forest floor), 0–10 cm, 10–20 cm and 20–30 cm).

At each sample point (corresponding to a different layer), soil temperature was recorded and four soil subsamples were obtained with soil corers, whose relative diameters were chosen from analysis of preliminary data aimed at reducing variance between samples. The subsamples were taken adjacent to each other and as close as possible (in a circular fashion) around each temperature reading. The first subsample (6 cm diam.) was used to identify and quantify non-mycorrhizal microfungi and to measure total length of hyphae in the soil. The second subsample (2 cm diam.) was used to identify and quantify the vesicular-arbuscular mycorrhizal (VAM) fungus spores. The third subsample (8cm diam.) was used to extract, identify and quantify the soil microarthropods. The fourth subsample (6 cm diam.) was used to measure soil pH, water content, organic matter content, and root biomass. At each sampling date, 15 replicates were performed for each layer (60 samples in all), and sampling was carried out 4 times throughout the year (May 1991, July 1991, October 1991 and February 1992) to account for seasonal variation, for a grand total of 240 samples.

Microarthropods

Microarthropods were extracted using a high efficiency canister-type soil-arthropod extractor (Lussenhop, 1971). Microarthropods were sorted, counted and then

stored in 70% ethanol. Specimens requiring identification were mounted on slides using Hoyer's medium.

VAM fungus spores

Spore abundance was calculated directly by extracting vesicular-arbuscular mycorrhizal (VAM) spores from soil using a wet-sieving technique developed for soils containing high levels of organic matter (Peter Moutoglis and Paul Widden, Concordia University). Each sample was agitated in a blender with 250 mL of water at high speed for 1 min. The resulting suspension was passed through two sieves (1000 and 500 m) using a high pressure water hose, collected in a large plastic tub, and then passed through another two sieves (250 and 45 m). Material retained by the 45 μm sieve was resuspended in 1 L of water, allowed to stand, and decanted through another 45 μm sieve (this process was repeated 3 times). The resulting material was collected in a beaker containing 40–60 mL of water.

The spore suspension was equally divided between two 50–mL centrifuge tubes, floated on top of a 60% sucrose solution, and then centrifuged at 680 g for 20 min. Material in the water and at the water sucrose interface was collected with a pasteur pipette and passed through a millipore filter. The spores were collected on 1.2 μm gridded (3mm $\times$ 3mm) nitrocellulose filter paper, and washed with distilled water under a filtration vacuum to spread spores evenly over the entire grid.

Populations of spores were estimated by counting all the spores present on ten randomly chosen squares from the entire grid. A subsample of spores from the grid was mounted in a polyvinyl-alcohol mounting medium and examined under differential interference-contrast illumination, and identified using the compilation of VAM fungi by Berch (1988).

Non-mycorrhizal microfungi

The serial washing technique (Harley and Waid, 1955) was used before plating 2010mm root fragments of *A. saccharum* on 2% malt extract agar, with 50 mg L^{-1} Rose Bengal added (Bragulat et al., 1991). Fungi were identified to the genus level using Domsch et al. (1980). The numbers of genera of darkly-pigmented and non-pigmented fungi were recorded.

Total length of hyphae

Total hyphal lengths were estimated by extracting hyphae from soil and measuring lengths by a modified gridline-intersect method (Michael Miller and Julie Jastrow, Argonne National Lab). Two 5-g portions of soil were removed from each sample, then suspended in 250 mL distilled water. To break up soil aggregates, 30 mL of 3.6% w/v sodium hexametaphosphate solution was added and left for 16–18 hrs. Samples were then stirred to break up any remaining aggregates. The soil suspension was agitated at high speed in a blender for 2 min. The suspension was then stirred with an electronic stir-bar at such a speed that the vortex was about half way between the top of the suspension and the bottom of the beaker. A six-mL aliquot was removed from half way between the beaker edge and the vortex and transferred to another beaker. To this, 250 mL distilled water were added along with 30 mL 3.6% w/v sodium hexametaphosphate solution. The diluted suspension was slowly stirred again to resuspend hyphae, then 10-mL aliquots were taken and transferred to 50 mL centrifuge tubes.

Samples were centrifuged at 1000 *g* for 8 min and the supernatant was discarded. After five repetitions of the extraction protocol, the efficiency of the first repetition was calculated to be 56%. To the remaining pellet, 10 mL 50% glycerol were added and the pellet was resuspended with a vortex mixer and then centrifuged at 75 g for 30 sec. The supernatant was filtered onto a 20 m polyester filter. The filter was carefully removed, curled and placed in a 15 mL centrifuge tube. Five-mL chlorazol-black stain were added, and the tube was capped and vortexed for 30 sec. Filters were allowed to stain in the tubes for 1.5 hrs. After staining, each tube was vortexed for a few seconds and decanted over a 1.2 μm nitrocellulose filter paper. Filters were cut in half, placed on glass slides and dried at 35°C for 15 min. For microscopy, the filters were made lucent by mounting in low-viscosity immersion oil.

Slides were viewed at 100 $\times$ magnification through a 10 $\times$ 10 grid reticle placed in the eyepiece. Using the gridline intersect method, intersections were counted for 6 horizontal and 6 vertical alternating lines. This was done for 70 fields of view and hyphal length $gram^{-1}$ dry soil was calculated as in Newman (1966).

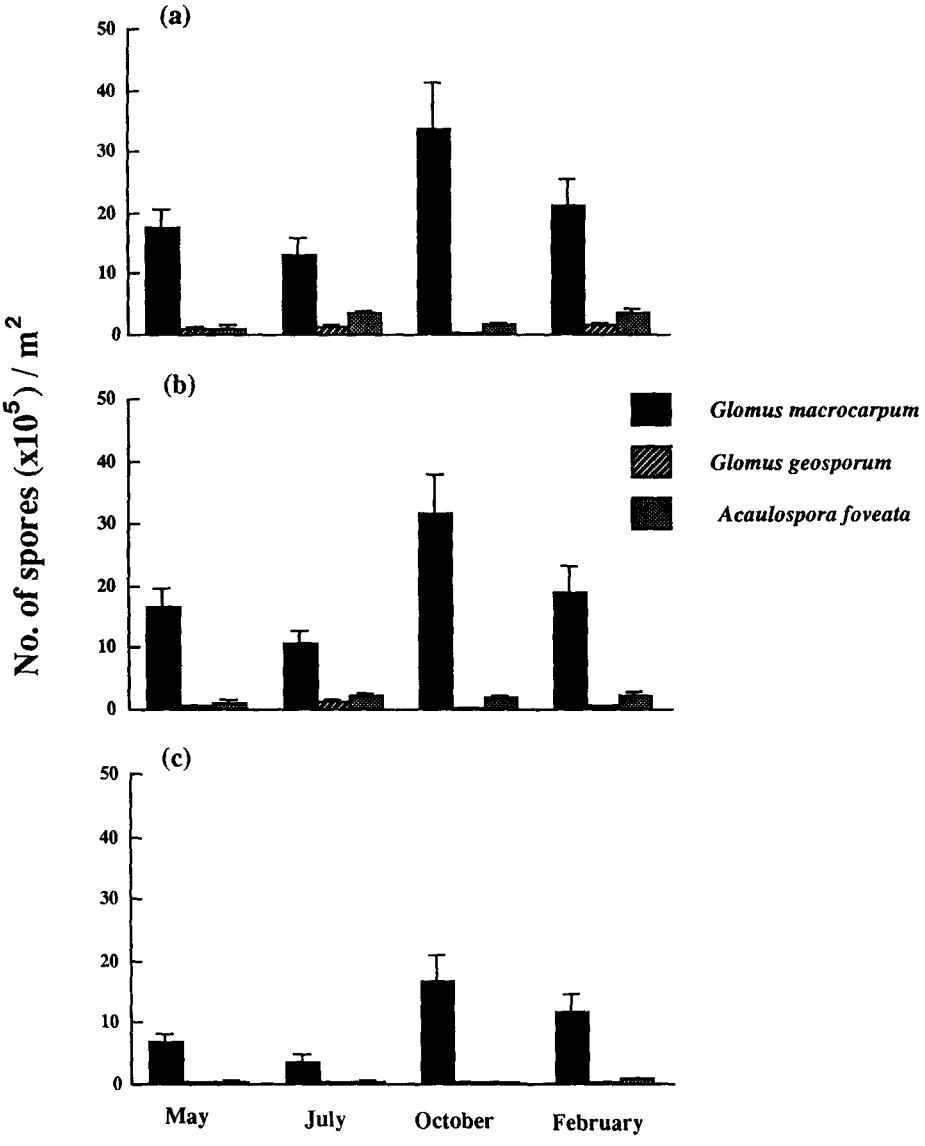

Fig. 1. Mean abundance of spores 10^5 of three species of vesicular-arbuscular mycorrhizal fungi in the (**a**) 0-10 cm, (**b**) 10-20 cm, and (**c**) 20-30 cm soil layers, from May 1991 to February 1992. Spores were absent from the litter layer. Error bars represent standard error of the mean.

Environmental variables

Soil temperature

A digital thermometer (± 0.1°C) was used to record soil temperature at each sampling site. The thermometer was stabbed into the soil to the appropriate depth and allowed to equilibrate (approx. 30 sec) before the temperature was recorded.

Soil water content

Twenty g of soil was weighed, then oven heated at 80°C for 24 hrs. Soil was then reweighed and water content calculated as percent dry mass of soil.

pH

Twenty mL of distilled water was added to 20 g of soil in a beaker. After 20 min of intermittent stirring to allow the paste to reach equilibrium, pH was measured electrometrically.

Organic matter

Percent organic matter in the soil samples was calculated by igniting oven dry soil with a flame for 30 min as described by Pramer and Schmidt (1964).

Root biomass

Fifty grams of soil was washed with a jet of water over a 500 ±m sieve, separating roots from soil. The roots were oven-dried at 80°C for 24 hours and root content was calculated as percent dry mass of soil.

Statistical analysis

One way analysis of variance (ANOVA) was used to compare values of environmental variables among soil layers. ANOVA was also used to compare environmental parameters among seasons. The Tukey post-hoc test was used to compare differences between means. Pearson correlation coefficients were used to assess relationships between variables. All means are provided with standard errors. The significance level for all statistical tests was $p \leq 0.05$. All analyses described above were performed using the software package 'SYSTAT' (Wilkinson, 1990).

Canonical correspondence analysis was performed with the Fortran package 'CANOCO' version 3.12 (ter Braak, 1992). This program is designed to perform a variety of multivariate analyses utilizing an iterative ordination algorithm. In our study it was performed to explore the distribution of microarthropods in relation to the measured environmental parameters. In the final analysis, some soil environmental variables were omitted (see results) because they exhibited high variation inflation factors (VIF) and were found not to significant explain any additional variance of the arthropod species data ($p \leq 0.05$). This was tested using forward selection of variables along with a Monte-Carlo test with 99 unrestricted permutations (ter Braak, 1992). Ter Braak (1986) explained that a high VIF value occurs when a variable is almost perfectly correlated with other variables and thus has no unique contribution to the regression equation. These variables are unstable and therefore have no interpretive value. Nine arthropod species and eleven environmental variables were originally included in each analysis. Unrestricted Monte-Carlo permutation tests were also used to test the significance of the first two CCA ordination axes.

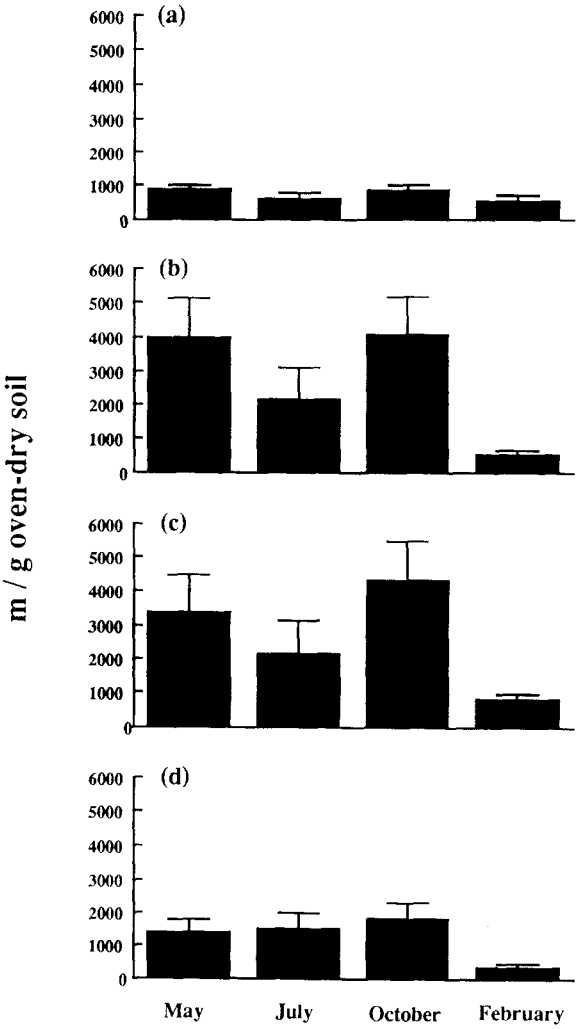

Fig. 2. Mean length of fungal hyphae in the (**a**) litter, (**b**) 0–10 cm, (**c**) 10–20 cm, and (**d**) 20–30 cm soil layers, from May 1991 to February 1992. Error bars represent standard error of the mean.

Results

Table 1 summarizes characteristics of the various environmental variables, at the 4 different soil depths, and across seasons. In spring and summer, mean litter temperatures were 15 and 19°C, respectively, and decreased with soil depth, whereas in autumn and winter, mean litter temperatures were 10 and -1°C, respectively, but increased with soil depth. Comparison of temperature and moisture values, across seasons, revealed a negative relationship between these two variables (r=-0.82, p=0.000). In summer moisture levels were low and temperatures high, whereas in winter the opposite was the case. Mean pH in the

Table 1. Summary of environmental variables at different seasons and depths of soil from May 1991–February 1992. Variables are temperature, pH, % water content, % organic matter (roots included), % root biomass, and the number of genera of darkly-pigmented and non-pigmented fungi. Values represent the mean along with the standard error in brackets (n=15)

		Temp (°C)	pH	% Water content	% O.M.	% Root biomass	Dark fungi (no. of genera)	Light fungi
May								
	Litter	15.1 (0.6)	6.1 (0.6)	97.7 (22.2)	82.2 (8.2)	0.0 (0.0)	1.9 (1.4)	4.4 (2.5)
	0-10c m	13.9 (0.7)	5.6 (0.4)	108.7 (19.9)	11.8 (0.9)	3.2 (1.6)	0.7 (1.0)	4.3 (2.3)
	10-20cm	12.0 (0.7)	5.9 (0.3)	113.6 (22.7)	11.2 (0.9)	3.3 (2.0)	0.7 (1.0)	3.5 (2.7)
	20-30cm	11.8 (0.4)	5.7 (0.6)	137.2 (27.1)	5.9 (0.8)	1.3 (0.9)	0.4 (0.8)	3.4 (2.3)
July								
	Litter	19.0 (0.9)	5.7 (0.5)	33.1 (14.8)	85.3 (7.6)	0.0 (0.0)	1.8 (1.3)	4.5 (2.1)
	0-10cm	17.1 (0.6)	5.6 (0.6)	58.1 (15.1)	12.2 (0.9)	3.7 (1.5)	0.5 (0.7)	4.7 (2.5)
	10-20cm	16.2 (0.6)	5.5 (0.5)	71.1 (17.8)	11.3 (0.8)	3.5 (1.5)	0.3 (0.5)	3.3 (1.9)
	20-30cm	15.9 (0.5)	5.8 (0.7)	72.6 (20.2)	6.3 (0.8)	1.5 (1.0)	0.3 (0.6)	4.4 (2.2)
October								
	Litter	10.0 (0.7)	6.1(0.7)	84.3 (30.7)	80.9 (8.5)	0.0 (0.0)	1.9 (1.5)	4.0 (2.0)
	0-10cm	9.9 (0.5)	5.6 (0.5)	101.9 (18.2)	12.7 (0.9)	3.2 (1.5)	0.7 (0.9)	3.0 (1.8)
	10-20cm	10.6 (0.6)	5.5 (0.5)	95.0 (19.9)	11.1(1.4)	3.2 (1.6)	0.3 (0.5)	3.7 (2.1)
	20-30cm	10.7 (0.7)	5.4 (0.6)	94.9 (25.1)	7.2 (1.4)	1.7 (0.9)	0.5 (0.7)	4.1 (1.7)
February								
	Litter	-1.0 (0.9)	6.2 (0.5)	217.3 (45.0)	81.7 (9.6)	0.0 (0.0)	0.7 (0.9)	4.1(2.2)
	0-10cm	0.1 (0.8)	5.7 (0.4)	179.3 (20.9)	12.6 (1.3)	3.7 (1.5)	0.3 (0.5)	4.0 (1.9)
	10-20cm	0.9 (0.6)	5.9 (0.5)	162.2 (24.9)	11.2 (1.3)	2.9 (1.6)	0.7 (0.8)	4.0 (1.6)
	20-30cm	0.7 (0.6)	5.9 (0.6)	150.2 (25.6)	6.6 (1.3)	2.3 (1.1)	0.4 (0.6)	3.9 (1.8)

woodlot was 5.8. A significant difference was detected among layers ($F_{3,236}$=5.08, p=0.002), as the litter was less acidic than the bottom 3 layers ($p \leq 0.05$). No significant variations were detected among seasons ($F_{3,236}$=2.90, p=0.07). Organic matter content in the litter layer consistently averaged above 80%, throughout the year. However, with increasing soil depth considerable reduction was apparent (r=-0.81, p=0.000). Root biomass levels were not similar in the various layers ($F_{3,236}$=104.17, p=0.000), the highest levels found at a depth of 0–20 cm ($p \leq 0.05$). No roots were found in the litter layer, and only few thicker and highly lignified roots could be found below a depth of 20 cm. Feeder roots were consistently found at depths of 0–10 cm. More genera of darkly-pigmented microfungi ($F_{3,236}$=20.30, p=0.000) were isolated from the litter layer than from other layers ($p \leq 0.05$). The number of genera of non-pigmented microfungi did not differ with depth and was greater than that of darkly-pigmented fungi, irrespective of depth ($F_{3,236}$=0.87, p=0.46) or season ($F_{3,236}$=0.67, p=0.57).

Vesicular-arbuscular mycorrhizal fungus spores were not present in the litter layer, but were abundant in the top 20 cm of soil (Fig. 1). The dominant taxon was *Glomus* spp. with a peak abundance in autumn with spore densities decreasing continuously throughout the following seasons. *Glomus geosporum* (Nicolson and Gerdemann) Walker and *Acaulospora foveata* Trappe and Janos were the other sporulating species detected, though both were present in lower numbers than *Glomus* spp. *Glomus hoi* Berch and Trappe was detected only occasionally (data not included) with the wet sieving method, though its numbers may have been underestimated because most spores of this species would pass through the 45 μm sieve used to collect spores in this study. Many of the *Glomus* spp. spores were later identified as those of *G. macrocarpum* Tulasne and Tulasne, so we refer to this group of spores by

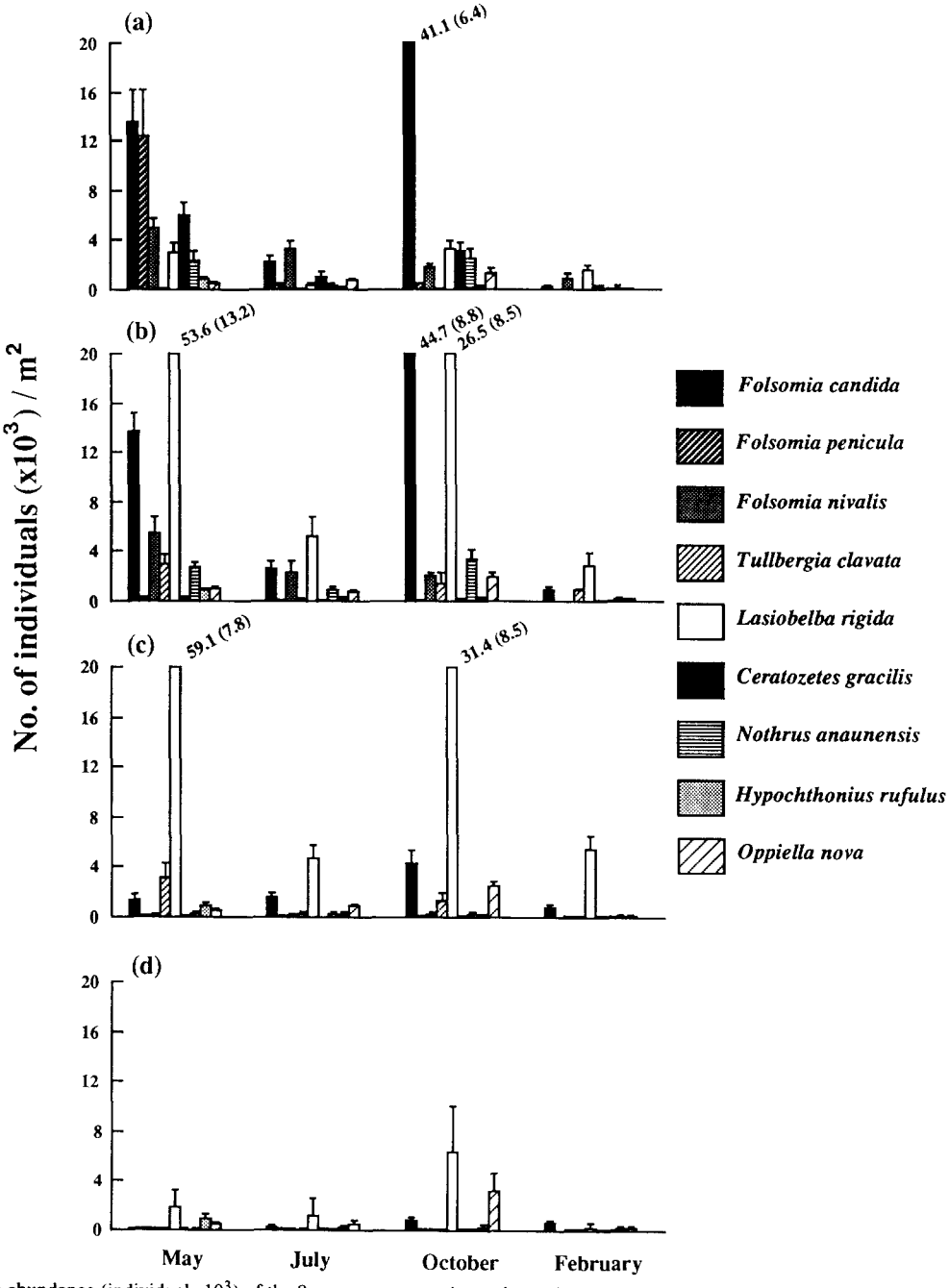

Fig. 3. Mean abundance (individuals 10^3) of the 9 most common microarthropod species in the (**a**) litter, (**b**) 0–10 cm, (**c**) 10–20 cm, and (**d**) 20–30 cm soil layers, from May 1991 to February 1992. Error bars represent standard error of the mean.

that name. It should be kept in mind, however, that because of the current requirements of the identification process (Morton, 1988), not all spores could be positively identified as *G. macrocarpum*.

Total length of hyphae in the soil was also highest in the top 20 cm with mean lengths peaking in spring and autumn (Fig. 2). No attempt was made to distinguish between mycorrhizal and non-mycorrhizal fungi, because such discrimination is difficult and unreliable.

Thirteen mycophagous mite species, *Lasiobelba rigida* (Ewing), *Ceratozetes gracilis* (Michael), *Nothrus anaunensis* (Can and Franz.), *Hypochthonius rufulus* (C.L. Koch), *Oppiella nova* (Oudemans), *Archiphthiracarus* sp., *Ceratozetes* sp., *Galumna* sp., *Phauloppia* sp., *Rhysotritia ardua* (C.L. Koch), *Scheloribates lanceoliger* (Berlese), *Suctobelbella* sp., and *Xylobates* sp., and ten collembolan species, *Folsomia candida* Willem, *Folsomia penicula* Bagnall, *Folsomia nivalis* (Packard), *Tullbergia clavata* Mills, *Isotoma ekmani* Fjellberg, *Onychiurus similis* Folsom, *Onychiurus subtenuis* Folsom, *Tullbergia granulata* Mills, *Tullbergia krausbaueri*, and *Tullbergia* sp. were identified but only the first 5 mite species and 4 collembolan species were common (Fig. 3). The nine arthropod species showed different responses to season and soil depth. Generally, soil arthropods were most abundant in spring and autumn. *F. candida* was the dominant species in autumn (approx, 90 000 individuals m^{-2} to a depth of 30 cm) and *L. rigida* was the dominant species in spring (approx. 117 000 individuals m^{-2} to a depth of 30 cm). These two species, however, were not concentrated at the same soil depth, although there was some overlap (Fig. 3). *F. candida* was abundant in the litter layer and in the top 10 cm of soil. *L. rigida*, on the other hand, was rarely found in the litter, but was numerous in the top 20 cm of soil. All but one of the microarthropod species moved deeper into the soil in winter. The movements of *F. penicula* remain unknown because it was not recorded in the winter.

Canonical correspondence analysis results are displayed by an ordination diagram where environmental variables are depicted by arrows, and species are marked by points. Ordination axes are presented in sequence of variance explained by linear combinations of environmental variables. Figure 4 is an ordination of the complete dataset. With forward selection of variables in CCA, 6 of the 11 environmental variables were significant ($p \leq 0.05$, 99 unrestricted permutations) in explaining the arthropod species data, and accounted for 95% of the variance of all 11 variables. These included percent organic matter, hyphal length, number of darkly-pigmented fungal genera, pH, water content, and temperature. In total, the 6 variables explained 41% of the variance of the species data. With CCA constrained to the 6 environmental variables, the eigenvalues of CCA axes 1 (0.26) and 2 (0.16) explained 35.5% of the cumulative variance of the arthropod species data (Table 2; Fig. 4). The species-environment correlations were high (axis 1 = 0.87 and axis 2 = 0.77) and Monte Carlo permutation

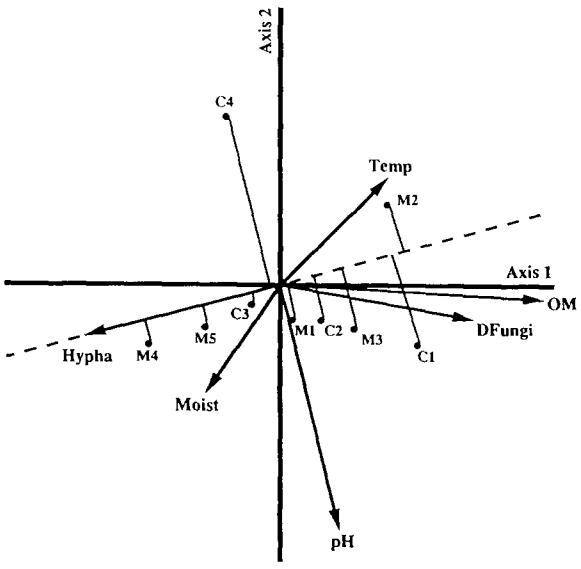

Fig. 4. CCA ordination biplot of the total dataset showing environmental variables (arrows) and microarthropod species distribution (dots). Positioning of microarthropod species along the hyphal length arrow indicates the approximate ranking of the weighted averages of taxa with respect to hyphal length. C1=*Folsomia candida*, C2=*Folsomia penicula* C3=*Folsomia nivalis*, C4=*Tullbergia clavata*, M1=*Lasiobelba rigida*, M2=*Ceratozetes gracilis*, M3=*Nothrus anaunensis*, M4=*Hypochthonius rufulus*, M5=*Oppiella nova*, Hypha=Total length of hyphae, Moist=Percent water content, pH=soil pH, DFungi=Number of genera of darkly-pigmented fungi, OM=Percent organic matter, Temp=Temperature.

tests (99 unrestricted permutations) showed that both axes were significant ($p \leq 0.05$).

The diagrams produced in CCA are useful not only for expressing patterns of variation in species composition, but also the main relations between species and environmental variables. Environmental arrows point toward the maximum change of a parameter, and arrow length indicates its importance in data interpretation. The position of the environmental arrow depends on the eigenvalues of the axes and the intraset correlations of that environmental arrow (ter Braak, 1986). The length of an arrow is equal to the rate of change in weighted average predicted from the biplot, and therefore explains the extent of variation in species distribution along the parameter. Long arrows correlate more strongly with ordination axes than short arrows, and have greater reliability in predictive applications.

From Figure 4, the relative contributions of the environmental variables to the CCA axes can be interpreted by examining the t-test scores of the canonical coefficients between the environmental variables and the ordination axes (ter Braak, 1992). Three variables,

Table 2. Results of ordinations by canonical correspondence analysis (Figs. 4–8): eigenvalues, correlation coefficients and % variance for the first two axes significant ($p \leq 0.05$) in unrestricted Monte Carlo permutation tests (99 permutations); ns, not significant ($p \leq 0\ 05$)

	Soil Layers									
	Litter Layer		0–10 cm		10–20 cm		20–30 cm		Total Dataset	
Axis	1	2	1	2	1	2	1	2	1	2
Eigenvalues	0.19*	0.08ns	0.16*	0.07ns	0.21*	0.10ns	0.28*	0.14*	0.26*	0.16*
Species-environment correlations	0.85	0.82	0.90	0.88	0.95	0.85	0.84	0.70	0.87	0.77
Cumulative % variance of species data	23.2	34.8	22.5	35.3	21.1	33.8	14.7	22.5	24.1	33.5
Cumulative % variance of species-environment relation	43.8	65.8	43.9	68.9	44.4	71.2	41.4	63.1	57.6	80.0

percent organic matter ($t_{0.05(2)233} = 3.3$) number of genera of darkly-pigmented fungi ($t_{0.05(2)233} = 2.5$) and hyphal length ($t_{0.05(2)233} = -2.1$) contributed significantly to axis 1 and one variable, pH ($t_{0.05(2)233} = -2.7$), contributed to axis 2 ($p \leq 0.05$). The first axis of the explanatory CCA could, therefore, be interpreted as a gradient of soil depth. Species common to higher soil layers (highly organic regions) were found towards the right side of the ordination. The second axis appeared as a gradient of pH. Species located in the upper portion of the of the ordination were most common in acidic patches of soil. From Figure 4, it is evident that *F. candida* and *C. gracilis* inhabit the higher soil layers, whereas *H. rufulus* is most common deeper in the soil. Such trends are also consistent with the animal distributions presented in Figure 3. The ordination also suggests that *T. clavata* is most common in regions of low soil pH. Pearson correlation analysis between this animal species and pH shows that this is indeed the case (r=-0.59, $p \leq 0.000$).

In addition to interpreting the environmental arrows in the CCA diagram by their length, additional information about species-variable relationships can be obtained by their orientation. Each environmental variable can be considered an axis in the ordination diagram by extending the arrow in both directions as shown for the "hyphal length" variable (Fig. 4). From each species location, a perpendicular line may be drawn to each extended environmental arrow. The line dropped from each species to the arrow approximates the relative position of the center of each species distribution. For example, *H. rufulus* was positively related with hyphal length (r=0.49, p=0.03), whereas *C. gracilis* was negatively correlated (r=0.56, p=0.01). Species found on or near the center of the axis are considered to be generalists (ter Braak, 1986).

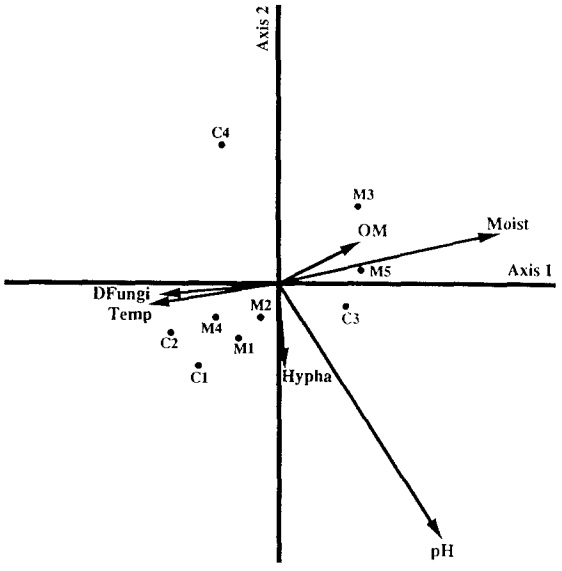

Fig. 5. CCA ordination biplot of the litter layer showing environmental variables (arrows) and microarthropod species distribution (dots). C1=*Folsomia candida*. C2=*Folsomia penicula*, C3=*Folsomia nivalis*, C4=*Tullbergia clavata*. M1=*Lasiobelba rigida*, M2=*Ceratozetes gracilis*, M3=*Nothrus anaunensis*, M4=*Hypochthonius rufulus*, MS=*Oppiella nova*, Hypha=Total length of hyphae, Moist=Percent water content, pH=soil pH, DFungi=Number of genera of darkly-pigmented fungi, OM=Percent organic matter, Temp=Temperature.

Since CCA of the entire dataset suggested that soil depth was a significant determinant in animal distribution, we decided to separate the data by depth, and repeat the CCA for each of the 4 different soil lay-

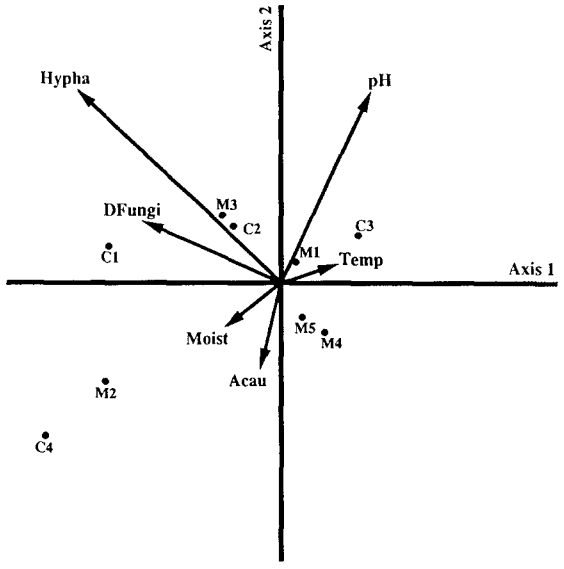

Fig. 6. CCA ordination biplot of the 0-10 cm soil layer showing environmental variables (arrows) and microarthropod species distribution (dots). Cl=*Folsomia candida*, C2=*Folsomia penicula*, C3=*Folsomia nivalis*, C4=*Tullbergia clavata*. Ml=*Lasiobelba rigida*, M2=*Ceratozetes gracilis*, M3=*Nothrus anaunensis*, M4=*Hypochthonius rufulus*, M5=*Oppiella nova*, Hypha=Total length of hyphae, Moist=Percent water content, pH=soil pH, DFungi=Number of genera of darkly-pigmented fungi, Temp=Temperature, Acau=Number of spores of *Acaulospora foveata*.

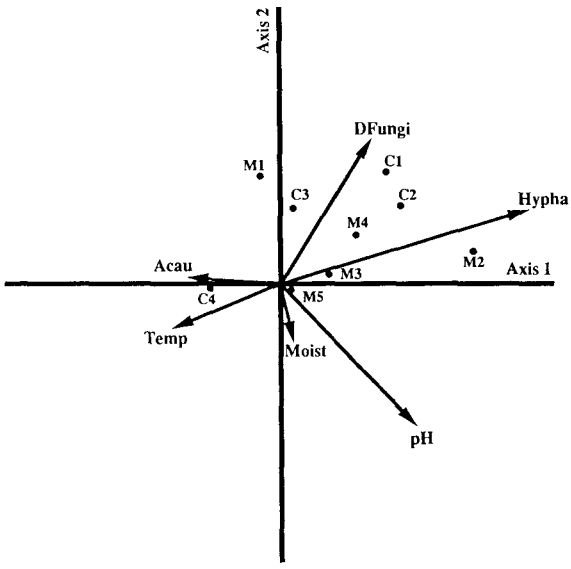

Fig. 7. CCA ordination biplot of the 10-20 cm soil layer showing environmental variables (arrows) and microarthropod species distribution (dots). Cl=*Folsomia candida*, C2=*Folsomia penicula*, C3=*Folsomia nivalis*, C4=*Tullbergia clavata*. Ml=*Lasiobelba rigida*, M2=*Ceratozetes Gracilis*, M3=*Nothrus anaunensis*, M4=*Hypochthonius rufulus*, M5=*Oppiella nova*, Hypha=Total length of hyphae, Moist=Percent water content, pH=soil pH, DFungi=Number of genera of darkly-pigmented fungi, Temp=Temperature, Acau=Number of spores of *Acaulospora foveata*.

ers. Again, for each separate analysis, only a subset of the environmental variables were significant ($p \leq 0.05$, 99 unrestricted permutations). In the litter, 0–10 cm, and 10–20 cm layers, 6 variables were significant in explaining the arthropod species data, and 4 were significant in the lowest layer (20–30 cm). These variables accounted for 94, 90, 91 and 96% of the variance of all 11 variables. These variables are shown in Figures 5 to 8, and their relative importance can be compared by the length of their respective arrows. They explained 47, 39, 44, and 34% of the variance in the species data. In each of the separate analyses, the eigenvalues for the first 2 axes of each ordination were lower than in the CCA of the total dataset (Table 2), and explained a lower percentage of the cumulative variance of the arthropod data. In all 4 analyses, axis 1 was significant ($p \leq 0.05$) but axis 2 was significant only in the canonical ordination of the 20–30 cm layer (Table 2).

Since some ordination axes were not significant at different depths, we did not attempt to interpret them, but instead focused on the individual variables that accounted for a significant percent of the arthropod species data ($p \leq 0.05$). In the litter layer, these variables were water content (18% of the explained variance), temperature (11%), number of genera of darkly-pigmented fungi (6%), pH (6%), hyphal length (3%), and organic matter (3%) (Fig. 5). This suggests that opposing trends of temperature and moisture (seasonal variability) were important in this layer. Organic matter content was also important, but to a lesser extent than in the analysis of the entire dataset. In the 0–10 cm soil layer, the significant variables and their relative importance to arthropod distributions were different (Fig. 6). They included hyphal length (15%), pH (8%), water content (5%), temperature (4%), number of genera of darkly-pigmented fungi (4%), and number of spores of *A. foveata* (3%). The same variables were significant in the 0–10 cm layer (Fig. 7), but their relative importance values differed: hyphal length (19%), number of genera of darkly-pigmented fungi (10%), pH (6%), temperature (3%), water content (3%), number of spores of *A. foveata* (3%). These results imply that in the 0–20 cm layer, fungi (hyphal biomass in soil and diversity of fungi associated with roots) may be more important than moisture and temperature for microarthropod distribution. In the lowest soil layer

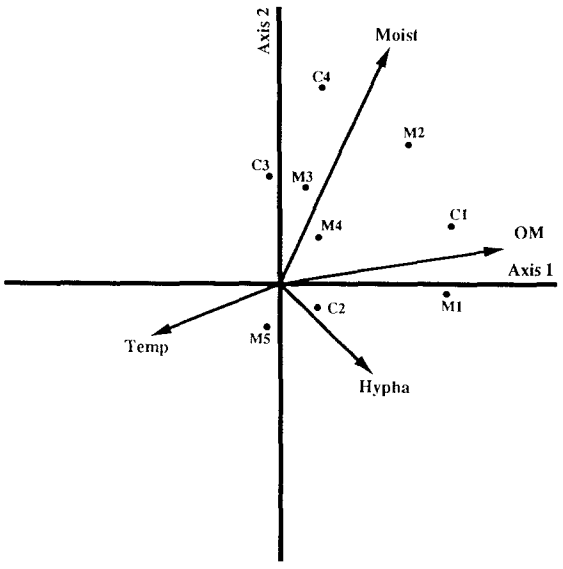

Fig. 8. CCA ordination biplot of the 20-30 cm soil layer showing environmental variables (arrows) and microarthropod species distribution (dots). C1=*Folsomia candida*, C2=*Folsomia penicula*, C3=*Folsomia nivalis*, C4=*Tullbergia clavata*. M1=*Lasiobelba rigida*, M2=*Ceratozetes gracilis*, M3=*Nothrus anaunensis*, M4=*Hypochthonius rufulus*, M5=*Oppiella nova*, Hypha=Total length of hyphae, Moist=Percent water content, Temp=Temperature, OM=Percent organic matter.

sampled (20–30 cm depth) (Fig. 8), a different set of environmental variables significantly accounted for the variance in the arthropod data. They were organic matter (16%), water content (11%), temperature (4%), and hyphal length (3%). Variables that never explained any significant ($p>0.05$) amount of variation in the arthropod data (Figs. 4–8) included root biomass, number of genera of non-pigmented microfungi, and VAM fungus spores (except for *A. foveata*).

Discussion

Data from this study clearly show that environmental parameters in the various horizons differ greatly and that the distribution of living organisms in the soil varies, both horizontally and vertically. The soil system is heterogeneous, and adjacent microhabitats may possess differing physical, chemical and biological properties, a concept that has been known for decades (Fitter et al., 1985). Abundance and distribution of the soil fauna depends on a multivariate array of environmental parameters. The most important variables influencing the distribution of microarthropods in the maple-forest soil suggested by canonical correspondence analysis were: (a) water content, temperature and pH in the litter zone; (b) total hyphal length, diversity of darkly-pigmented microfungi, and pH in the top 20 cm of soil; and (c) water content, temperature, organic-matter content, and total hyphal length, at depths below 20 cm.

It should not be assumed that these are the only variables that influence arthropod populations in soil. In fact, the variables included in the present analyses (selected because of our interest in trophic interactions) account for approximately 35% of the variance of the arthropod data (Table 2). The remaining variance could be explained by unmeasured environmental variables (i.e. inorganic nutrient availability, soil water potential, etc...) which are recognized as significant (Wallwork, 1976).

The influence of soil pH, temperature, and water content on the distribution of the soil fauna (Anderson, 1978; Joosse et al., 1973; Joosse, 1981; Leinaas, 1978; Pool 1962; Stanton, 1979; Usher et al., 1982; Verhoef and Witteveen, 1980; Verhoef and Van Selm, 1983) and soil mycota (Bissett ad Parkinson, 1979; Carreiro and Koske, 1992; Christensen, 1969; Gochenaur, 1978; Morrall, 1974; Shameemullah and Parkinson, 1971; Widden and Abitbol, 1980; Widen, 1986a, b) is well known. Temperature and water content change dramatically with season, but also within seasons (vertically and horizontally). These two variables are extremely important to the community structure of soil organisms. Our study provides evidence that some arthropods do well in warm, dry conditions, whereas others prefer colder and moister conditions. The upper litter zone is the region where temperature and moisture change most dramatically, especially between seasons, so these two variables are most important in this layer of the forest floor. Deeper in the 0–20 cm soil layers, temperature and moisture are less important. Moisture becomes important once again at layers below 20 cm where organic matter is greatly reduced (Table 1). Increased levels of organic matter help retain water in the soil (Donahue et al., 1983), so the lowered organic matter content in the 20–30 cm layer may limit the availability of water.

Very little information is available on optimum temperature regimes for the various species of microarthropods studied here. Also, interpretation of relationships among soil arthropods and moisture and temperature are complicated by the fact that the major environmental trend, which is for the soil to be driest during warm periods of the year, runs counter to the

trend for many animals to be adapted to warm-moist conditions. Such adaptations are evident from attempts to culture animals in the laboratory (Usher and Stoneman, 1977). This may be one reason why many animal species are located in the middle of the temperature-moisture axis in the total dataset. The tendency we have detected for soil arthropods not to respond in a linear fashion to the cold-wet, warm-dry gradient that often occurs in nature is also implicit in many studies of seasonality, where an overall reduction in the numbers of many species of animals has occurred during warm, dry periods (Hågvar, 1983; Hale, 1966; Poole, 1962; Takeda, 1987; Usher, 1970). This may explain the strong tendency for samples to separate into "extreme" (winter and summer) species and "temperate" species in the canonical ordinations.

The organic matter content of soils has previously been positively correlated with fungal biomass (Bååth and Söderström, 1982; Dowding and Widden, 1974) or with the occurrence of certain species of fungi (Brown, 1958; Kendrick, 1962; Morrall, 1974). Several studies on the dynamics of soil microarthropod community structure, reporting relationships between fauna, soil depth and organic matter content, have also been published (Anderson, 1978; Hågvar, 1983; Hale, 1966; Takeda, 1978; Takeda, 1987; Usher, 1970). Organic matter content appears not to be a very important factor in the top 20 cm of soil, perhaps because this region is very rich in organic matter anyway, with little variation between or within seasons. However below 20 cm, where percent organic matter is greatly reduced (Table 1), it becomes more influential since it may be a limiting factor. Organic matter is limiting among layers but not within layers. Therefore this vertical distribution should be considered in studies trying to correlate soil biomass or activity with organic matter. Also, analysis of available carbon instead of total organic matter may reveal clearer relationships.

Direct grazing on active roots by arthropods such as symphylans, millipedes, and collembolans has been previously reported (Brown, 1985). However, most studies have shown indirect effects on roots caused by arthropods grazing on VAM fungi in the rhizosphere (McGonigle and Fitter, 1988; Moore et al., 1985; Rabatin and Rhodes, 1982; Rabatin and Stinner, 1985; Warnock et al., 1982). Many groups of fungi, saprobic, pathogenic, and mycorrhizal, colonize active roots. Results of the present study suggest that the arthropod community may not be directly attracted to root biomass, but may respond positively to roots that are colonized by a high diversity of darkly-pigmented microfungi. Darkly-pigmented conidial fungi are typically less abundant than non-pigmented fungi in forest soils (Hudson, 1968). The former are most common on living plants, and it is thought that the dark pigments of these fungi protect them from ultraviolet radiation in the canopy (Pugh and Boddy, 1988). On the forest floor they are most common in the litter layer, and are less evident in the 0–30 cm soil layers (Table 1), although some genera appear to be genuine soil-inhabitants (Domsch et al., 1980).

Since VA mycorrhizal fungi which colonize roots of *A. saccharum* could not be isolated using synthetic media, the abundance of VAM-fungus spores was measured, but no significant correlation between such spores and animal distribution was detected. The ordinations showed that sporulation by *G. macrocarpum*, and *G. geosporum* was not important in influencing animal distributions. Sporulation by *A. foveata* did appear in the ordinations of the 0–10 cm and 10–20 cm soil depths as being of some significance. However, it is difficult to tell whether sporulation by this species is significant or whether the really important factor affecting microarthropod distribution is pH, which is strongly negatively correlated ($r=-0.73$, $p=0.000$) with sporulation by *A. foveata*. *Acaulospora* species typically do better under acid conditions, and this species has been negatively correlated with pH in at least one other maple forest (Klironomos et al., 1993). In the litter zone, where no roots could be found, the animals still responded positively to a high diversity of darkly-pigmented microfungi colonizing decaying leaf litter, as previously reported for a conifer forest by Kendrick and Burges (1962).

An interesting interaction detected by canonical correspondence analysis was the positive correlation between the total length of soil hyphae and the distribution of microarthropods. The reciprocal nature of correlations makes the interpretation of this relationship especially difficult since both fungi and arthropods can influence the other's population dynamics (Coleman, 1985). Mycophagy can stimulate fungal growth directly, by the removal of senescent tissues and inhibitory compounds (Hanlon, 1981; Hedlund et al., 1991). Also, certain fungi can stimulate microarthropod fecundity rates (Klironomos et al., 1992). Usher (1976) suggested that the patchy distribution of either food or soil water was the most probable cause of microarthropod aggregation in natural ecosystemss, and many microarthropod species are considered to be mycophagous in the field (Moore et al., 1988). Nevertheless, only one other study found a positive

correlation between fungal and fungal feeder densities (McBrayer et al., 1974), and this was with protozoans. Whittaker (1974) reported a negative relationship between mite density and fungal mycelial length in a number of tundra sites. However, no correlation was found between the number of Collembola and the mycelial length in the same sites. These results and the ones obtained in the present study suggest that observations on one group of soil arthropods should not be turned into generalizations about the entire arthropod fauna.

Total hyphal lengths measured in this maple-forest soil were extremely high, compared to one other maple site (Klironomos et al., 1993). Most of the hyphae in the top 20 cm of soil were almost certainly part of the extraradical network of VAM fungi, characterized by coarse, irregular, non-septate hyphae. However, since we could not reliably differentiate between hyphae of the mycorrhizal Glomales and those of other soil fungi, especially zygomycetes (Domsch et al., 1980) some of which have similar characteristics, we cannot be specific concerning the effect of VAM-fungus hyphae on microarthropod distribution.

Numerous laboratory studies have reported on the food preferences of microarthropods (Klironomos et al., 1992; Mitchell and Parkinson, 1976; Moore et al., 1987, 1988; Newell, 1984a,b; Parkinson et al., 1979; Visser and Whittaker, 1977;). The apparent importance of darkly-pigmented fungi revealed by CCA may be very significant, because previous studies have shown that microarthropods have a clear feeding preference for darkly-pigmented fungi on decaying litter (Klironomos et al.,1992; Mitchell and Parkinson, 1976; Moore et al., 1987, Parkinson et al., 1979; Visser and Whittaker, 1977). With the aid of multivariate statistics, animal distribution has been related to fungal distribution in the field. This observation, contrary to the widespread belief, indicates that in their natural habitat, soil arthropods are not generalists.

This study has clearly demonstrated that canonical correspondence analysis (CCA) is a useful ecological ordination technique, because CCA generates ordination biplots from which one can easily visualize and quantify the environmental factors determining species distribution. Of the factors we measured, temperature, water content, pH, and fungi (total hyphal length and diversity of darkly-pigmented microfungi) were the most important features of the environment influencing the microarthropod community. The influence of different environmental parameters at different depths was made evident. This study provides evidence that at different soil depths, animals behave differently with respect to their environment. Animals migrate vertically in the soil, driven or attracted by changes in temperature, moisture and fungal biomass. Their abundance and success in the various habitats depends on a number of environmental variables. Our analysis of field conditions suggests that fungal community dynamics may be significant to microarthropod community structure, a phenomenon that has been demonstrated previously in controlled laboratory experiments, and has shown a relationship between arthropod populations and their food supply in the field. The analysis also suggests that microarthropods may have minimal direct effect on roots and VAM fungus spores but may strongly influence the extra-radical hyphal network of VAM. However, CCA gives only descriptive, "correlation-type" data. Like other ordination analyses, CCA is at best a "hypothesis generator", and so results obtained in this study need to be tested experimentally. More work is needed, because grazing of the extraradical hyphae of VAM fungi by arthropods has the potential to reduce the efficacy of mycorrhizal associations, mainly by limiting the transport of mineral nutrients to roots (Fitter and Sanders, 1992; Lussenhop, 1992). Our experiments on this aspect of the relationship will form the basis of a subsequent communication.

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