



# Stimulative effects of arthropods on endomycorrhizas of sugar maple in the presence of decaying litter

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## Summary

1. We examined how *Acer saccharum* Marsh seedlings respond in terms of biomass and mycorrhizal colonization levels to the addition of (1) soil microarthropods and (2) decaying litter, under microcosm conditions.

2. The addition of fauna was associated with decreased arbuscular (–38%) and hyphal (–30%) colonization, and increased vesicular colonization (+112%), with no effect on plant biomass.

3. The addition of decaying litter was associated with decreased arbuscular colonization (–51%), increased hyphal (+24%) and vesicular (+117%) colonization, and extraradical hyphal length (+38%), and decreased shoot (–43%) and root (–23%) biomass.

4. However, there was a strong synergistic interaction between decaying litter and soil fauna and the addition of both was associated with enhanced arbuscular colonization (+59%), vesicular colonization (+85%) and increased shoot biomass (+32%), and shoot/root biomass ratio (+25%).

5. Understanding the dynamics involved in such interactions between soil organisms can have profound implications for soil management practices in agriculture, forestry and areas requiring revegetation.

*Key-words:* Acari, *Acer saccharum*, arbuscular mycorrhizas, Collembola, soil fungi

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## Introduction

Detailed investigations on nutrient cycling in soil are crucial to a better understanding of plant nutrition. Microarthropods are abundant in soil (Harding & Stuttard 1974) and are postulated to play several important roles: (1) they may increase decomposition and nutrient-cycling rates, by breaking up plant litter into smaller fragments, which are more quickly degraded by heterotrophic soil microbes (Visser 1985); (2) many species are mycophagous, so they can indirectly influence nutrient availability to plants by altering the structure and activities of microbial populations (Coleman 1985; Visser 1985); (3) they can influence nutrient cycles directly, by excreting nutrients into the soil (Hunt *et al.* 1987). Until the past decade, faunal activities were largely ignored in studies dealing with nutrient mineralization and immobilization. Recently, however, a few studies have revealed dramatic effects of soil fauna on the mineralization of N and P in soils (Ingham *et al.* 1985; Huhta, Setälä & Haimi 1988; Setälä & Huhta 1990;

Setälä *et al.* 1990), as well as on the growth and nutrient contents of plants (Setälä & Huhta 1991).

Soil microarthropods have been studied in isolation (Usher 1985) or for their potential effects on plant roots (Moore, Walter & Hunt 1988) or in terms of their effects on the general soil mycota (Visser 1985), but rarely because of their potential influence on the mycorrhizal association (Fitter & Sanders 1992). This lack of concern is surprising, because the soil-permeating hyphal networks of the mutualistic arbuscular mycorrhizal (AM) fungi associated with the roots of most plant species help them acquire inorganic nutrients in exchange for photosynthates (Harley & Smith 1983; Daniels-Hetrick 1984). Functionally, mycorrhizal plants also survive transplant shock better, are more resistant to soil-borne diseases, withstand higher soil salinity and wider extremes of soil temperature and pH (Abbott & Robson 1984; Brundrett 1991). Roots and mycorrhizas constitute 40–85% of total net primary production (Fogel 1985).

Several reports have suggested that disturbance of the AM hyphal network by soil fauna through grazing has the potential to reduce the efficacy of the mutualistic association, mainly by reducing the transport of mineral nutrients to roots (Warnock, Fitter & Usher

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1982; Finlay 1985; McGonigle & Fitter 1988; Harris & Boerner 1990). In dual pot culture, Warnock *et al.* (1982) and Finlay (1985) showed that the growth of *Allium porrum* was increased by mycorrhizal colonization and subsequently reduced by additions of the collembolans *Folsomia candida* and *Onychiurus ambulans*, respectively. A similar phenomenon was reported by Harris & Boerner (1990) who added *F. candida* to pots containing mycorrhizal *Geranium robertianum* and suggested that collembolans reduce the benefits of mycorrhizal colonization. Gut content analyses on animals from dual pot cultures revealed the presence of AM fungal hyphae and grazing of AM fungi by collembola was observed by Moore, St. John & Coleman (1985). They showed that both AM mycelium and spores were used as food sources by the animals.

Our understanding of interactions between microarthropods and AM has been limited by oversimplified experimental set-ups, i.e. the addition of only one AM fungus and one arthropod species. Decomposing organic matter can greatly influence the behaviour of mycophagous arthropods but this component has never been included in arthropod/AM studies. Klironomos & Kendrick (1995a, in press) have established that the AM endophyte *Glomus macrocarpum* was less palatable to microarthropods than the common conidial fungi associated with roots, *Alternaria alternata* and *Trichoderma harzianum*, in Petri-dish experiments. Also, the animals preferred to feed on fungi found on decaying litter as opposed to the same fungi colonizing roots. When AM-fungus hyphae were grazed, there was a clear preference for the narrower hyphae, which are those further away from the root, suggesting that arthropods normally cause little disruption of AM extraradical hyphal networks, and consequently little reduction in the efficiency of AM associations. This is what one might expect, given the ubiquitous nature of the AM association. Other reports have also shown independently that the majority of microarthropods are generally most abundant in or near the litter zone in forest systems (Usher, Booth & Sparkes 1982). Such results suggest that experiments purporting to demonstrate negative effects of animals on mycorrhizas were too simple to reflect what occurs in nature, because other kinds of soil fungi have never before been included in the studies.

The purpose of this experiment is to study the effects of soil fauna on the mycorrhizal colonization of *Acer saccharum* Marsh under laboratory conditions in the presence of decaying litter.

### Materials and methods

One-year-old seedlings of *A. saccharum* were removed from a maple forest, c. 15 km west of Waterloo, Ontario, Canada (Brundrett & Kendrick 1988; Klironomos & Kendrick 1995b, in press), and

brought to the laboratory. The roots were carefully washed free of soil and plants placed in 15 cm pots containing Turface (an expanded-clay potting medium). These plants contained naturally occurring endophytic fungi in their roots, presumably including representatives of mycorrhizal, saprobic, and pathogenic groups.

Twenty pots were used for each of the four treatments of a 2 × 2 factorial experiment, where the factors were (1) addition of fauna and (2) addition of decaying litter. After 10 months of maintenance under greenhouse conditions with a low-nutrient fertilizer (half-strength Hoagland's solution), the root and shoot biomass of each seedling was recorded and mycorrhizal levels were determined. Hyphal lengths in the Turface and the number of animals in each pot were recorded. Twenty more seedlings were brought to the laboratory as 'dummy trees' for analysis of mycorrhizal colonization and plant biomass prior to manipulation.

### LITTER TREATMENT

Decaying maple litter was collected from the floor of the maple forest. The litter was stored in polythene bags and kept at 4 °C until needed. It was then carefully surface-washed with tap water to remove soil animals and 5 g portions were added to the top of the Turface potting medium.

### FAUNA TREATMENT

Twenty of each of the most common mite and collembolan species, extracted directly from the same maple-forest soil, were added to pots. The six microarthropods used in this study were collected using a canister-type soil extractor (Lussenhop 1971). Three mite species (*Lasiobelba rigida*, *Ceratozetes gracilis* and *Nothrus anaunensis*) and three springtail species (*Folsomia candida*, *Folsomia penicula* and *Tullbergia clavata*) were used in these experiments. These animals (except *F. candida*) could not be cultured successfully and so had to be extracted and sorted for each experiment. Only adult animals were used, because it has been shown that young individuals rarely move from their release site, with or without food (Johnson & Wellington 1983).

### PLANT BIOMASS

Shoots were cut off and roots were carefully separated from the Turface potting medium. Roots were cut into 1 cm fragments and 30 feeder root pieces, recognized by their characteristic beaded appearance (Kessler 1966), were removed and stored in formalin-acetic acid (FAA) for subsequent assessment of root colonization. The remaining potting media were placed in polythene bags for subsequent analyses of hyphal lengths and arthropod extractions. Shoots and the

remaining roots were oven-dried at 80 °C for 24 h prior to determining dry mass.

#### ROOT COLONIZATION

Feeder roots were stored in FAA for at least 24 h. Roots were then cleared by autoclaving for 15 min in 10% potassium hydroxide, bleached in 35% hydrogen peroxide for 30 min, acidified in FAA for 5 min and stained using Chlorazol Black E (Brundrett, Piché & Peterson 1984). Quantification of VAM colonization was performed using the magnified intersections method (McGonigle *et al.* 1990) by inspecting intersections between the microscope eyepiece cross-hair and roots at  $\times 200$  magnification. The proportions of root length containing arbuscules (AC), vesicles (VC) and hyphae (HC) were determined.

#### HYPHAL LENGTH

Total hyphal lengths were estimated by extracting hyphae from the Turface medium and measuring lengths by a gridline-intersect method (R. M. Miller & J. D. Jastrow, unpublished data). Two 5 g portions of Turface were removed from each sample, then suspended in 250 ml distilled water. To break up aggregates, 30 ml of 3.6% w/v sodium hexametaphosphate solution was added and left for 16–18 h. 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. One 6 ml aliquot per sample was removed from half-way between the beaker edge and the vortex and transferred to another beaker. To this, 250 ml distilled water was 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  $\times 1000$  g for 8 min and the supernatant was discarded. After five repetitions of the extraction protocol, no additional hyphal fragments were extracted. The efficiency of the first extraction was calculated to be 88%. To the remaining pellet, 10 ml 50% glycerol was added and the pellet was resuspended with a vortex mixer and then centrifuged at  $\times 75$  g for 30 s. The supernatant was filtered onto a 20  $\mu$ m polyester filter. The filter was carefully removed, curled and placed in a 15 ml centrifuge tube. To this 5 ml chlorazol-black stain was added and the tube was capped and vortexed for 30 s. Filters were allowed to stain in the tubes for 1.5 h. After staining, each tube was vortexed for a few seconds and decanted over a 1.2  $\mu$ m nitrocellulose filter paper. Filters were cut in half, placed on glass slides and dried at 35 °C for 15 min. For microscopy, the fil-

ters were made transparent by mounting in low-viscosity immersion oil.

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

#### STATISTICAL ANALYSES

A  $2 \times 2$  multivariate analysis of variance (MANOVA) was performed on six dependent variables: arbuscular, vesicular, and hyphal colonization, hyphal length, shoot and root biomass. Independent variables were litter (present, absent) and fauna (present, absent). Results of evaluation of assumptions of normality, homogeneity of variance-covariance matrices, linearity and multicollinearity were satisfactory. The seventh dependent variable 'shoot/root ratio' was not included in the multivariate analysis because it violated the assumption of multicollinearity. All variables were also analysed further using univariate factorial ANOVA to help determine which variables contribute to any significant differences observed in the multivariate analyses. The Tukey *post hoc* test was subsequently used to test for differences among means. All statistical analyses were performed using the SYSTAT software (Wilkinson 1990).

#### Results

In this factorial microcosm study, a combination of multivariate and univariate analyses showed that plant biomass and fungal occurrence inside and outside roots were greatly affected by additions of decaying litter and soil animals (Figs 1, 2 and 3). All plants weighed more after the experiment was over (10 months later) than prior to manipulation (Fig. 1) but the extent of weight increase was dependent on the type of treatment. In the case of mycorrhizal colonization, the different intra-radical fungal structures behaved differently in response to the fauna and litter treatments and the end result was not always an increase in colonization (Fig. 2).

With the use of the multivariate Wilks' criterion, the combined dependent variables (arbuscular, vesicular and hyphal root colonization, hyphal length, root and shoot dry weights) were significantly affected by both litter ( $F_{6,71} = 27.54$ ,  $P = 0.0001$ ) and fauna ( $F_{6,71} = 4.05$ ,  $P = 0.002$ ), and by their interaction ( $F_{6,71} = 28.97$ ,  $P = 0.0001$ ). The results reflected a moderate association between fauna and the combined dependent variables,  $\eta^2 = 0.26$ , suggesting that the presence of collembolans and mites moderately influenced plant and fungal dynamics. The association was more substantial between the dependent variables and (1) litter ( $\eta^2 = 0.70$ ), and (2) the interaction between litter

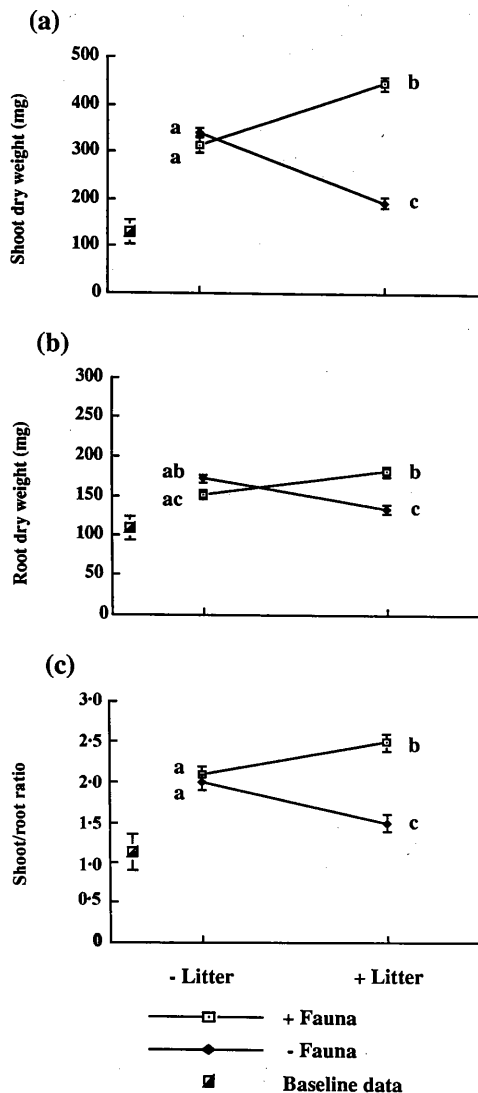


Fig. 1. Effects of litter and fauna on (a) shoot dry weight, (b) root dry weight and (c) shoot/root ratio. Points are means ( $n = 20$  per group)  $\pm 1$  SE. Different letters (a,b,c) represent differences at the significance level  $P < 0.05$ . Baseline data represent dry weights of seedlings prior to manipulation.

and fauna ( $\eta^2 = 0.71$ ). That implies that the presence of decaying litter had (1) a large influence on fungal and plant dynamics directly, and (2) a large influence on the behaviour of the arthropods, so that the combination of arthropods and decaying litter had a different effect than each one alone.

To help determine which individual plant and fungal variables were significantly affected by the fauna and litter treatments, univariate analyses were used. The addition of decaying leaf litter was significantly correlated with increased intra-radical hyphal ( $F_{1,76} = 37.55$ ,  $P = 0.0001$ ) and vesicular ( $F_{1,76} = 5.29$ ,  $P = 0.024$ ) colonization of *A. saccharum* (24% and 117%, respectively; Fig. 2). Extra-radical hyphal length ( $F_{1,76} = 31.92$ ,  $P = 0.0001$ ) increased by 38% (Fig. 3). Arbuscular colonization ( $F_{1,76} = 10.73$ ,  $P = 0.002$ )

decreased by 51% (Fig. 2). Decreases were also observed in root (23%) ( $F_{1,76} = 5.89$ ,  $P = 0.018$ ) and shoot (43%) ( $F_{1,76} = 69.59$ ,  $P = 0.0001$ ) dry weights (Fig. 1). This increase in fungal occurrence was most likely not that of mycorrhizal fungi because arbuscular colonization, root and shoot biomass were all decreased relative to control. Also, the increase was mostly that of regularly septate, melanized hyphae which are characteristic of non-mycorrhizal fungi, possibly pathogenic groups. Concurrently, the occurrence of vesicles was relatively high, a sign that the plant roots were becoming stressed.

The addition of fauna, however, was associated with a decrease in intra-radical hyphal (30%) ( $F_{1,76} = 12.86$ ,  $P = 0.0006$ ) and arbuscular (38%) ( $F_{1,76} = 6.64$ ,  $P = 0.01$ ) colonization (Fig. 2). No significant effect

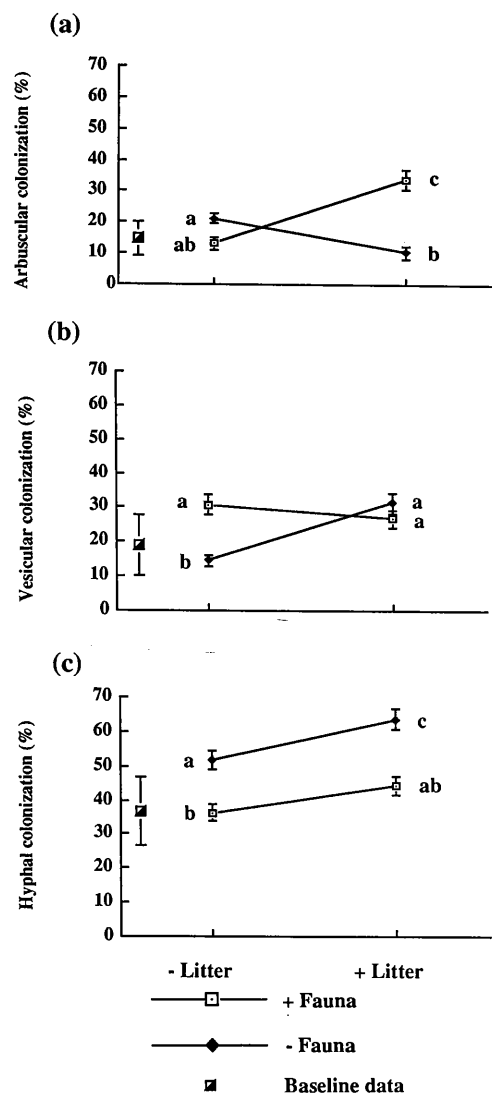


Fig. 2. Effects of litter and fauna on (a) arbuscular, (b) vesicular and (c) hyphal colonization of *Acer saccharum* seedlings. Points are means ( $n = 20$  per group)  $\pm 1$  SE. Different letters (a,b,c) represent differences at the significance level  $P < 0.05$ . Baseline data represent percentage colonization of field-collected seedlings prior to manipulation.

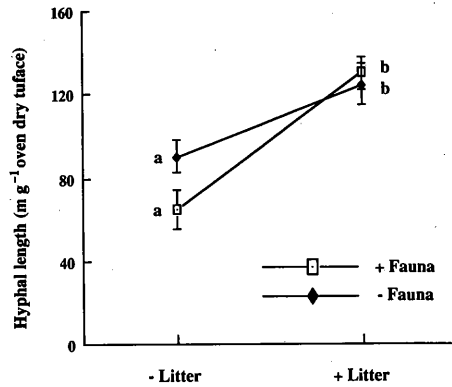


Fig. 3. Effects of litter and fauna on the extra-radical hyphal length in the microcosms. Points are means ( $n = 20$  per group)  $\pm 1$  SE. Different letters (a,b) represent differences at the significance level  $P < 0.05$ .

on the extra-radical hyphal length ( $F_{1,76} = 1.26$ ,  $P = 0.27$ ) was evident (Fig. 3). Vesicular ( $F_{1,76} = 4.54$ ,  $P = 0.04$ ) colonization was increased by 112% (Fig. 2). No effect was observed on root ( $F_{1,76} = 0.48$ ,  $p = 0.49$ ), or shoot ( $F_{1,76} = 0.26$ ,  $P = 0.61$ ) dry weights (Fig. 1). Decreased arbuscular levels suggest that the arthropods negatively affected mycorrhizal functioning. The mechanisms of this phenomenon are unclear but possibly a result of severing the extra-radical hyphal network. Even though the plants did not show differences in terms of plant biomass with the presence of animals, initial signs of stress were becoming apparent as the occurrence of vesicles was relatively high.

Interaction effects between litter and fauna were significant for arbuscular ( $F_{1,76} = 46.26$ ,  $P = 0.0001$ ) and vesicular ( $F_{1,76} = 17.33$ ,  $P = 0.0001$ ) colonization and for root ( $F_{1,76} = 33.92$ ,  $P = 0.0001$ ) and shoot ( $F_{1,76} = 103.04$ ,  $P = 0.0001$ ) dry weights. The simultaneous addition of fauna and decaying litter was related to the highest increase in arbuscular (59%) and vesicular (85%) colonization (Fig. 2), as well as shoot dry weight (32%) and shoot/root ratio (25%) (Fig. 1). The lowest levels of arbuscular and vesicular colonization were associated with the simultaneous absence of litter and fauna (Fig. 2). No interaction effects were observed for intra-radical hyphal colonization ( $F_{1,76} = 0.58$ ,  $P = 0.45$ ) (Fig. 2) or extra-radical hyphal length ( $F_{1,76} = 3.02$ ,  $P = 0.09$ ) (Fig. 3).

The three collembolans, *F. candida*, *F. penicula* and *T. clavata*, and the mite *N. anaunensis* were more abundant in microcosms containing litter (Figs. 4 and 5). The fecundity of the other two mite species, *L. rigida* and *C. gracilis*, was not significantly influenced by the litter treatment (Fig. 4). The collembolan *F. candida* was the only animal of the six to be found in pots that received no faunal supplements (Fig. 5). Pots that received a litter treatment (no fauna) contained the most 'contaminant' collembolans (Fig. 5), whereas 'contaminant' mites were found in greatest

abundance in microcosms containing no faunal additions, irrespective of litter treatment (Fig. 4). The source of arthropod contamination was the greenhouse, because the animals observed were never found in the maple forest soil (Klironomos & Kendrick 1995b). Also, other pots in the greenhouse, which were not part of this experiment, were also contaminated with the same arthropod species (unpublished observations).

## Discussion

Our data show clearly that the concurrent addition of decaying litter and microarthropods can stimulate mycorrhizal colonization and the growth of *A. saccharum*. The interaction between litter and fauna was synergistic and was associated with highest arbuscular levels and shoot dry weights. Shoots increased, whereas roots did not, resulting in an increase in the shoot/root ratio. However, if either treatment (litter or fauna) was excluded, opposite effects were recorded, with reduced arbuscular and plant biomass levels.

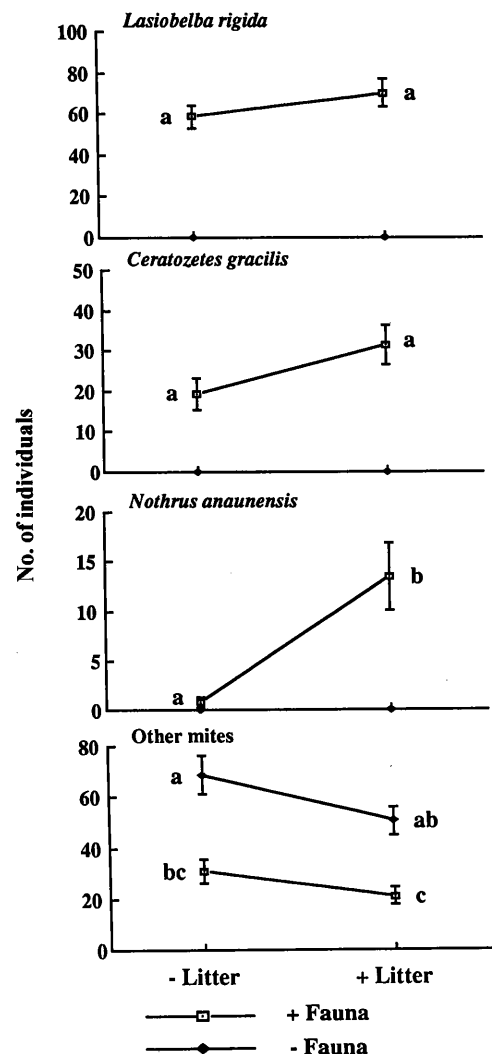


Fig. 4. Number of mites extracted from the microcosms after harvest.

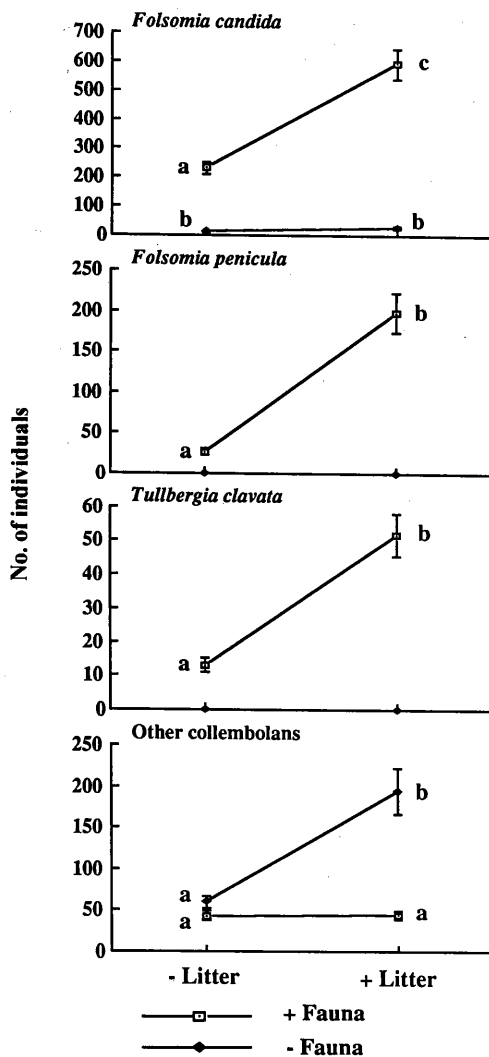


Fig. 5. Number of collembolans extracted from the microcosms after harvest.

These results were of particular interest because all previous reports showed only negative effects of soil arthropods on arbuscular mycorrhizas and plant growth (Warnock *et al.* 1982; Finlay 1985; Harris & Boerner 1990). We now think this may have been because they did not include any non-mycorrhizal fungi in their experimental systems. In those studies, arthropods degraded the mycorrhizal status of plants, causing a decrease in P uptake. Our results were consistent with these findings when we added fauna, but no decaying litter, to the microcosms; *A. saccharum* responded with decreased levels of hyphal, arbuscular and vesicular root colonization, although no significant difference was observed in plant biomass.

It is difficult to know exactly which mechanisms were involved in affecting the mycorrhizas and plant growth, because direct observation was not possible. Nevertheless, a survey of the literature suggests that these results form part of a general pattern.

In the absence of litter, the mycophagous arthropods had no choice but to feed on fungi present in the

rhizosphere. Saplings could have been infected with pathogenic as well as mycorrhizal fungi before transplanting and although the animals prefer to graze on pathogenic fungi (Klironomos & Kendrick 1995a), an arthropod 'overload' in the mycorrhizosphere, could result in a greater possibility of arthropod/AM fungus contacts. AM fungal hyphae can be abundant around roots of *A. saccharum* (Klironomos *et al.* 1993) and grazing of the extra-radical network can obviously lead to reductions in nutrient uptake (Fitter & Sanders 1992) and therefore reductions in the potential yield of plants.

The addition of litter to the microcosms may have diverted the majority of animals to this substrate and away from the rhizosphere, where AM fungi are found. Leaf litter on the forest floor is actively decomposed by many species of fungi at once (Kendrick & Burges 1962; Pugh 1974), making it a good food source for mycophagous animals. Mites and collembolans have previously shown a preference for a litter habitat rather than for the deeper layers of soil (Klironomos & Kendrick 1995a), although some species are forced to the lower layers by fluctuations in temperature and moisture (Klironomos & Kendrick 1995b) and by interspecific interactions among the fauna (Klironomos & Kendrick 1995a). Species still found near the rhizosphere preferred to feed on conidial fungi (Klironomos & Kendrick 1995a) so, by selectively grazing non-mycorrhizal fungi, they may indirectly be helping AM fungi to colonize the maple roots successfully, and helping limit colonization by detrimental fungi. Also, grazing on the extraradical AM network by the soil fauna is reduced, so AM fungi can function more effectively. Without a healthy extra-radical hyphal network, no nutrient benefit is gained, even with high intra-radical colonization levels (Friese & Allen 1991).

In the absence of arthropods, litter had a negative effect on plant biomass and arbuscular levels. The fungal saprobes growing on litter could be detrimental to plant growth in a number of ways. (1) Nutrient immobilization. Microbial decay of litter results in immobilization of nutrients in microbial tissues (Ingham *et al.* 1985). The C:N ratio of leaf litter is high (Jensen 1974), therefore the tendency is for available N to be immobilized during decomposition (Williams & Gray 1974). (2) Phytotoxin production. Phytotoxic substances are produced by saprobic fungi (Drew & Lynch 1980). For example, patulin, an antibiotic and mycotoxin produced by *Penicillium urticae* (McCalla & Norstadt 1974), was thought to be responsible for the toxicity experienced in mulch farming. (3) Infection of roots (Garrett 1956). In the present study, the decrease in arbuscular colonization was associated with higher hyphal colonization, which may be largely by non-AM fungi invading the interior of roots. The proportion of the total intra- or extra-radical hyphae that is produced by AM fungi is not known. In this study, we did not attempt to discrimi-

nate between AM and non-AM fungi. Many pathogens found in the rhizosphere have a saprobic existence prior to becoming parasites (Lynch 1985). Such fungi have been shown to compete with mycorrhizal fungi for root resources (Bagyaraj 1984). Under this stress, mycorrhizas tend to form more vesicles and less arbuscules (Daniels-Hetrick 1984), a phenomenon also detected in our study. Although certain non-mycorrhizal fungi can produce vesicles (Hornby 1990), the ones observed here showed characteristic elongate and spherical morphologies (Cooke, Widden & O'Halloran 1992), and were often seen connected to arbuscules, so we are confident that they belonged to AM fungi.

Nitrogen which is immobilized is not lost but is temporarily retained in the microbial biomass. Fragmentation and comminution of organic matter by soil animals enhance the rate of organic matter decomposition (Visser 1985), and grazing of litter-inhabiting fungi by the fauna may help liberate N and make it available to the plant. Similarly, the effects of phytotoxicity and root infection by litter fungi may be suppressed by the feeding actions of microarthropods which can significantly alter the distribution and succession of fungi on decomposing leaf litter (Klironomos, Widden & Deslandes 1992). Comminution of the litter by the fauna can reduce fungal species numbers, because some fungi are more sensitive than others to damage or destruction of their thallus (Visser 1985).

That the decaying litter is of adaptive significance to the animals is indicated by their high fecundity (Figs. 4 and 5) and the high number of contaminant collembolans, in the presence of litter (Fig. 5), which is consistent with their food preferences (Klironomos & Kendrick 1995a). There were two exceptions; *L. rigida* and *C. gracilis* did just as well in the absence of litter (Fig. 4), even though they prefer to feed on litter-grown fungi (Klironomos & Kendrick 1995a). These anomalies in the data could result from the evolution by the animals of strategies to avoid competitors (Vegter 1983). In nature, these animals are common in the mineral soil layers, even though they prefer the litter habitat. Additional evidence of competition is the high mite contamination in the absence of faunal augmentation (Fig. 4). Such interactions between the fungus, the substrate and the animals, and the possible evolution by fungi of defense systems aimed at grazers or by arthropods to avoid competition, are always likely to complicate the interpretation of laboratory data on the relationships between feeding preferences and fitness.

In this paper we have shown that microarthropods may stimulate mycorrhizal colonization of plants in the presence of litter. This is possibly a result of selective grazing by the animals on the non-mycorrhizal fungi (Klironomos & Kendrick 1995a). In the absence of litter, the animals may spend more time feeding on mycorrhizal fungi. These results are significant

because they point out interactions in soil that can greatly affect plant performance. Because their extraradical hyphal network must persist over a period of months in order to be of value to their plant symbionts, AM fungi may have adapted over their 350-million-year history to be less palatable to soil arthropods than are other non-AM fungi. Grazing of non-mycorrhizal fungi in the rhizosphere may help to protect the plant against pathogens and parasites, and may help the establishment and functioning of AM. The soil fauna should, therefore, be considered in the formulation of management plans for plant ecosystems.

In conclusion, this type of experimental work also needs to be performed with ectomycorrhizal systems, because the symbiosis is structurally and functionally different from AM systems (Allen 1991) and even fewer papers have dealt with this interaction (Fitter & Sanders 1992). The number of research papers published on mycorrhizas every year is substantially high, yet judging from the lack of experimental ecological research in the field (Klironomos & Kendrick 1993), and the present results, it is safe to conclude that we have a poor understanding of the important interactions between mycorrhizal fungi and other biotic and abiotic components of the soil.

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