Pedobiologia **50** (2007) 505—513

Available online at www.sciencedirect.com
ScienceDirect

Pedobiologia
www.elsevier.de/pedobi

Soil faunal assemblage composition modifies root in-growth to plant litter patches

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Received 10 December 2005; accepted 17 July 2006

KEYWORDS
Litter decomposition;
Soil fauna;
Grasslands;
Soil nutrient heterogeneity;
Root proliferation;
Functional diversity

Summary

Local-scale heterogeneity in the spatial distribution of soil nutrients promotes a suite of physiological and morphological responses in plants. These responses influence the competitive ability of plants within communities and potentially plant primary productivity. There is a growing appreciation then for the need to study factors that may modulate these plant responses to soil nutrient heterogeneity. Soil fauna are potentially one such modulating factor. For example, through impacts on organic matter decomposition and distribution they may directly modify nutrient patches and therefore the stimulus plants are responding to. In addition they may modify plant root mass and architecture through processes such as herbivory, potentially altering the outcome of a plant's response to a nutrient patch. Using grassland microcosms, consisting of a multi-species plant assemblage, multiple soil horizons and a speciose soil biota, we tested whether soil faunal assemblage composition might modulate plant responses to nutrient patches represented by litterbags. We show that root proliferation into a nutrient patch, a variable which is positively related to a plant's success under conditions of interspecific competition in a nutrient-limited environment, is reduced by the presence of mesofauna, and even more so by the presence of mesofauna together with macrofauna. Reductions in this proliferation response when mesofauna were present without macrofauna appeared to be a function of reduced root density. When macrofauna were included, reduced root density, and higher rates of litter patch disappearance, together contributed to the reduction in proliferation but additional mechanisms must also

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0031-4056/$ - see front matter
doi:10.1016/j.pedobi.2006.07.001

have played a role. Our results suggest that the effects and interactions generated by soil fauna need to be explicitly considered in analyses of how plants forage for nutrients in a patchy environment.

Introduction

At the local scale, nutrients are typically patchily distributed within the soil (Jackson and Caldwell, 1993; Cain et al., 1999; Farley and Fitter, 1999). Renewed interest in the effects of this local-scale nutrient heterogeneity on plant performance (for reviews see Robinson, 1994; Huber-Sannwald and Jackson, 2001; Hodge, 2004) has shown how this may promote a variety of plant responses, including changes in biomass allocation, root morphology, nutrient uptake kinetics and root production (Hodge, 2004). These responses influence the competitive ability and survival of individual plants within communities (Hutchings et al., 2003), largely because they determine the ability of plants to acquire limiting nutrients from the environment. As such, local-scale soil nutrient heterogeneity may play a role in structuring terrestrial communities and, thus, affect the ecosystem services they provide (Bliss et al., 2002; Maestre et al., 2005; Wijesinghe et al., 2005).

There is a growing appreciation for the need to study factors that may modulate plant responses to soil nutrient heterogeneity (Hodge, 2003, 2004; Maestre et al., 2005). That soil fauna redistribute nutrients within the soil (Swift et al., 1979), regulate the liberation of nutrients in plant-available form from decomposing organic matter (Swift et al., 1979), and also influence root architecture and growth (Setälä and Huhta, 1991), suggest they are potentially a key ''modulating'' factor. However, we are only aware of two studies (Bonkowski et al., 2000; Wurst et al., 2003) that have assessed the influence of soil fauna on plant responses to soil nutrient heterogeneity.

Bonkowski et al. (2000) and Wurst et al. (2003) demonstrated that microfauna and earthworms, respectively, alter patterns of nitrogen capture from nutrient patches by plant monocultures. Typically, two mechanisms are considered key for enhanced nitrogen acquisition from patches. These are root proliferation into the patch and root physiological alterations in nutrient uptake capacity (Hodge, 2004). The former response, proliferation into the patch, is commonly observed when plants are grown under conditions of nutrient heterogeneity. Proliferation was observed by Bonkowski et al. (2000) to be positively related to nitrogen uptake from patches by plants. However, both Bonkowski et al. (2000) and Wurst et al. (2003) studied plant monocultures, whereas the magnitude of the root proliferation response is generally considered to be important under conditions of inter-, not intra-specific competition in nutrient-limited environments (Hodge, 2004). Here, we do not assess plant competition per se but rather whether soil fauna may modulate proliferation responses in multi-species plant communities. We suggest that it if they do, then the effects and interactions of soil fauna need to be considered explicitly in analyses of how plants forage for nutrients in a competitive and patchy environment.

Our experimental systems were replicate, grassland microcosms containing a multi-species plant assemblage, natural soils and a complex soil biotic assemblage. Nutrient patches, in the context of this study, were litterbags. We posed two hypotheses on the grounds that mesofauna and macrofauna may alter root growth through processes such as herbivory and engineering (Setälä and Huhta, 1991, Bardgett and Wardle, 2003), and patch longevity and chemistry through decomposer activity (Swift et al., 1979). H_1: Given that soil mesofauna may consume roots and enhance litter decomposition rates, we hypothesise that the presence of these fauna will decrease root proliferation into nutrient patches. H_2: Given that the presence of soil macrofauna generally accelerates litter decomposition (Bradford et al., 2002b) and that macrofauna root herbivores and ecosystem engineers tend to have marked negative impacts on root densities, we predict that the presence of macrofauna in addition to mesofauna will further exacerbate negative effects of soil fauna on root proliferation.

Materials and methods

Microcosm assembly and treatment design

Fifteen terrestrial microcosms were established and maintained in the Ecotron-controlled environment facility at Silwood Park (Lawton, 1996). The microcosms were assembled from grassland at

Sourhope Experimental Farm (National Grid Reference NT855196) in Scotland, and provided a laboratory analogue of a field site undergoing intensive investigation in the UK NERC Soil Biodiversity Thematic Programme (http://soilbio.nerc.ac.uk). Soils from the site were collected, roughly homogenised by horizon, and then treated with CH_3Br to remove the seedbank, mesofauna and macrofauna. The profile was reassembled to include five horizons which were, in order from the soil surface: the FH (3.5 cm deep), H (2.0 cm), Ah 'upper' (6.9 cm), Ah 'lower' (11.4 cm), and AB (6.5 cm) horizons. This profile was established in a specially designed, lysimeter pot (1 m^2 surface area), over a 10-cm layer of gravel for drainage.

Next, seeds of the ten most dominant plants at the Sourhope grassland were collected, greenhouse germinated and introduced into the microcosms as seedlings in a randomly generated, grid pattern that was repeated for all microcosm communities. In total, 384 seedlings were introduced into each community and were in the same order of decreasing dominance as at the field site: *Agrostis capillaris* L., *Festuca rubra* L., *Nardus stricta* L., *Anthoxanthum odoratum* L., *Poa pratensis* L., *Trifolium repens* L., *Holcus mollis* L., *Potentilla erecta* L., *Galium saxatile* L., and *Luzula multiflora* (Ehrh.) Lej. All species established and persisted throughout the experiment.

Each microcosm was individually housed within a $2 \times 2 \times 2$ m Ecotron walk-in chamber. The Ecotron facility permits very tight environmental control, so that the simulated climatic conditions in each chamber are effectively identical (Lawton, 1996). Photoperiod was 18 h and included a gradual dawn and dusk of 2 h each. Temperature and relative humidity followed sine curves between 21.1 °C during the day and 9.5 °C at night, and 83% after rainfall (3.5 mm day^{-1}) and a minimum of 63%, respectively.

Soil biota was introduced selectively to create assemblages that differed in organism body size. If the adult was not soil dwelling, organisms were assigned to a size class based on their largest juvenile stage. We adhered to the general size classification for terrestrial decomposer food webs (see Swift et al., 1979), establishing three treatments that formed a gradient of increasing functional complexity: (1) microbiota only ($<100\,\mu$m diameter; primarily bacteria, fungi, Protozoa, Nematoda); (2) microbiota and mesofauna (100 μm–2 mm diameter; primarily Collembola, Acari, Enchytraeidae); and (3) microbiota, mesofauna and macrofauna (>2 mm diameter, primarily earthworms, slugs, insect larvae, staphylinid beetles). Hereafter, these treatment levels will be referred to as microbiota, mesofauna, and macrofauna communities, respectively.

Soils were inoculated with microbial solutions, derived using various physical extraction techniques (Bradford et al., 2002a) from soil turves collected from the Sourhope grassland. Microfauna, mesofauna and the majority of the macrofauna were also extracted from Sourhope grassland turves and then inoculated into the microcosm communities. Nematoda and Enchytraeidae were extracted using a wet-funnel technique. Other mesofauna were dry-extracted using a Tullgren funnel designed to provide a standard faunal inoculum in terms of species diversity and abundance (design courtesy of the Soil Ecology Group at the University of Jyväskylä, Finland). For the macrofauna, standard numbers of staphylinids and chilopods, and standard biomass of tipulid larvae were collected using the same Tullgren funnel technique. Two earthworm species (*Allolobophora chlorotica* Sav. and *Lumbricus rubellus* Hoffm.) and a mollusc (*Arion ater* L.) were obtained from biological suppliers (Blades Biological, Edenbridge, UK). These macrofauna species were present at the Sourhope grassland but to obtain them in sufficient biomass to establish our experiment was deemed too destructive to the site. For densities of these fauna at the start and end of the experiment, see Bradford et al. (2002a).

Treatments were randomly assigned within five blocks defined by microcosm planting order. All microcosms were planted within a 3-day period, with blocks 1 and 2 planted the first day, blocks 3 and 4 the next, and block 5 the third day. Microbial and microfauna inoculations were made after planting and were followed, across 1 month, with mesofauna and then macrofauna inoculations. Fauna were extracted from multiple turves across multiple dates (e.g., mesofauna were dry-extracted and then inoculated on 28 different occasions across 1 month; see Bradford et al., 2002a). The intention behind multiple inoculations was to provide multiple opportunities for as many species as possible to be extracted and then successfully established in the microcosms. The block structure was used in all further set-up and in sampling, such that all procedures were conducted, in a random order, by block. Altogether, microcosm assembly (from the day turves were extracted in the field to the last faunal inoculation) took approximately 7 months. Day 1 was assigned at the end of this period, being the day after the last faunal inoculation was made. Microcosms were assembled in this gradual manner to permit adequate time for development of a "mature" grassland plant assemblage, as well as growth of

the microflora and faunal assemblages. Also, this gradual assembly diminished the nutrient pulse associated with the microcosm set-up (see Bradford et al., 2002a).

Litterbags

Litterbags (9×8 cm) were constructed from nylon mesh (Northern Mesh, Oldham, UK). The mesh had 2×2 mm square holes, providing an opening width in the diagonal of 2.8 mm. Bags were filled with 0.9–1.1 g of plant litter. Plant litter was collected green and was obtained from one of two sources: (a) *Agrostis capillaris* L. grown under a standard set of environmental conditions; and (b) from cuttings of the microcosm grassland plant assemblages. In the former case, *Agrostis capillaris* was used from a standard source to quantify impacts of the soil biota assemblage composition treatment on root proliferation separate to those that might be influenced by changes (mediated via the soil biota treatments) in the species composition and/or quality of the plant assemblage litter. We used the second set of bags, those where the litter source was the cuttings from the microcosm plant assemblages, to assess whether changes in litter species composition and/or quality contributed to treatment impacts on root proliferation. For this set of bags, cuttings from one microcosm community were returned to that same microcosm. We refer to the two litterbag types as (a) "standard" and (b) "community" bags.

Prior to use, both litter types were dried at 40 °C. The standard litter had a C:N ratio of 16.7 ± 0.68 and percentage (w/w) nitrogen content of 2.56 ± 0.105 (mean ± 1 SE, $n = 3$). Foliar chemistries for the community bags are reported in Table 1.

Across the duration of the experiment, three sets of litterbags were added in succession to the model grasslands. Sets 1, 2 and 3 litterbags were placed into the model communities on Experiment days 46, 129 and 213, respectively. For each set, six standard and six community litterbags were added to each replicate. Bags were randomly placed beneath the vegetation canopy, in contact with the surface soil horizon (FH). Three bags of each litter type (henceforth referred to as "repeat" bags) were retrieved after 14 and also after 42 days. Data from the repeats were pooled by replicate community within a time point to generate a mean value (to avoid pseudo-replication). The purpose of using repeat bags means was to minimise the contribution of microclimatic variation within a replicate community to the root proliferation and mass loss data for that replicate.

Root proliferation

For Set 1 litterbags, we did not enumerate root proliferation. It was with the 42-day bags from this set that we visually observed greater root mass in litterbags retrieved from the microfauna and mesofauna communities than in litterbags retrieved from the macrofauna community. For Sets 2 and 3 bags, we determined dry (40 °C) masses of roots and of remaining litter after separation from foreign material (soil, shoots and fauna).

Along with Set 3 litterbags we also placed six litterbags without litter into the replicate grasslands. These bags were retrieved, and the root mass within these bags quantified, as for the bags containing litter. We also took three 5.5 cm diameter soil cores from the FH horizon of each replicate grassland, pooled the cores, and then washed and dried (at 60 °C) the roots within them to estimate root density in the surface horizon. We measured both root proliferation into the "empty" bags, and root density in the FH horizon, to gain a fuller appreciation of whether the root proliferation responses we observed were a simple function of soil root density and/or indiscriminate root foraging, or an active root foraging response to the litterbag nutrient patches. Note that we refer to the root biomass production within our litterbags as root proliferation but recognise that this is only

Table 1. Carbon to nitrogen ratios, and percentage nitrogen contents, of the community litters for the soil biota assemblage composition treatment levels for Sets 2 and 3 litterbags (see Materials and methods)

Treatment assemblage	Set 2		Set 3	
	C:N ratio	N (%)	C:N ratio	N (%)
Microbiota	23.4 ± 0.41	1.83 ± 0.033	21.6 ± 1.27	2.00 ± 0.128
Mesofauna	23.6 ± 1.34	1.82 ± 0.133	20.9 ± 1.68	2.12 ± 0.226
Macrofauna	25.6 ± 0.40	1.68 ± 0.030	24.1 ± 0.62	1.79 ± 0.044

Values are means ± 1 SE ($n = 5$).

an estimate of proliferation, which is strictly defined as initiation of new laterals (see Hodge, 2004). Hence, hereafter we refer to ''root in-growth'' when we refer to our data specifically, and ''proliferation'' when we refer to this plant strategy in a more general context.

Statistical analyses

To determine how the soil biota assemblage composition treatment affected litter mass loss, root in-growth, and FH horizon root densities, analysis of variance (ANOVA) was used. For each variable, we constructed a full interaction linear model with three factors (soil biota assemblage composition (three levels), litterbag type (two levels), litterbag set (two levels)). In each, block was included as a non-interacting factor. Litter mass loss data were expressed as ''proportion of litter mass remaining'' and were arcsine square-root transformed prior to analysis. Models were checked to ensure they met assumptions of parametric analysis; absolute root mass and the in-growth index data were natural-log transformed to meet assumptions of ANOVA. The in-growth index was used to explore whether the foraging responses were related simply to FH horizon root densities and were defined as the magnitude of the root in-growth response to a litter patch relative to the standing mass of roots in the surrounding soil. The index was calculated by dividing the litterbag root densities by the FH horizon root densities. To account for zero values (so that we could analyse these data using parametric ANOVA), to each ratio we added 1. Analyses were performed using S-PLUS 7.0 for Windows.

Results

We found little or no root in-growth to the 14 days litterbags; only data from litterbags retrieved after 42 days of exposure are therefore reported. There were significant ($P<0.05$) main effects of the soil biota assemblage composition, litterbag set and litterbag type on root in-growth as measured as the mass of roots per litterbag but no significant interactions between any of the factors (Table 2). The effect of the soil biota assemblage composition treatment was due to greater root mass in litterbags exposed to the microbiota and mesofauna communities than in those exposed to the macrofauna community (Fig. 1a); this effect alone explained more than 50% of the variation in the ANOVA model (Table 2). We present these root mass data pooled across the litterbag set and litterbag type factors (Fig. 1a). The effects of litterbag set and type were explained by less root in-growth in community than standard litterbags, and in Set 3 than Set 2 litterbags, respectively (data not shown).

To establish whether differences in litter mass remaining (Table 3) accounted, at least in part, for the differences in root in-growth mass between soil biota assemblage treatment levels, we expressed these root mass data as a proportion of the litter mass remaining. On analysing these root data expressed this way, there were no significant interactions ($P>0.05$) and no significant effect of litterbag type ($P>0.05$). Litterbag set was significant ($F_{1,44}=5.7$, $P<0.05$) but only explained about 3% of the total ANOVA model variance, whereas soil biota assemblage composition explained 43% of the model variance and was strongly significant ($F_{2,44}=28.0$, $P<0.001$). In the absence of interactions, these data are presented pooled across litterbag type and litterbag set (Fig. 1b).

Table 2. Summary of the analyses of the root in-growth mass data

Source of variation	df	ss	% ss	ms	*F*	*P*
Biota assemblage	**2**	**65.58**	**54.12**	**32.79**	**37.81**	**<0.0001**
Litterbag set	**1**	**9.50**	**7.84**	**9.50**	**10.95**	**0.0019**
Litterbag type	**1**	**4.31**	**3.56**	**4.31**	**4.98**	**0.0309**
Block	4	1.32	1.09	0.33	0.38	0.8204
Assemblage × set	2	1.12	0.92	0.56	0.65	0.5288
Assemblage × type	2	0.95	0.78	0.48	0.55	0.5807
Set × type	1	0.03	0.02	0.03	0.03	0.8589
Assemblage × set × type	2	0.73	0.61	0.37	0.43	0.6556
Residual	44	38.16	31.49	0.87		
Total	59	121.71		2.06		

Values were natural-log transformed prior to analysis. Significant effects ($P<0.05$) are shown in bold.

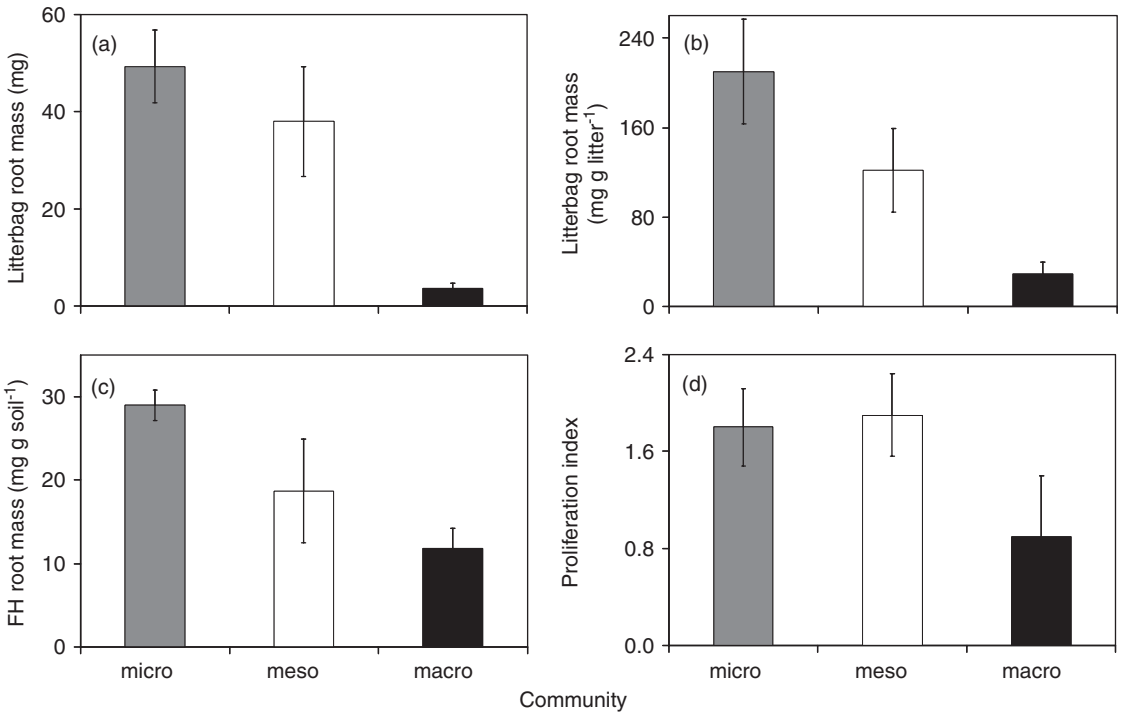

Figure 1. Soil biota assemblage composition effects on root in-growth to litterbags (a), root in-growth relative to litter mass remaining (b), FH soil horizon root densities (c), and an index of relative root proliferation (d; see main text). The soil biota assemblage composition levels were microbiota (micro), mesofauna (meso) and macrofauna (macro); see main text for a full description of these community treatments. Values for litterbag root masses (a, b) were calculated from data pooled across litterbag type and set. Values for the proliferation index were calculated from Set 3 litterbag data pooled across litterbag type. Values are means $\pm$1 SE ($n = 5$).

The greatest root densities were observed in the microbiota community and the lowest densities in the macrofauna community (Fig. 1b).

Next, we wished to establish whether the soil biota assemblage composition effects on litterbag root densities (Fig. 1b) were likely to be a function of active root foraging or an artefact of standing soil root densities and/or indiscriminate root foraging. Mean standing root densities in the FH horizon were greatest in the microbiota community and least in the macrofauna community (Fig. 1c); this effect was marginally significant ($F_{2,8} = 4.4$, $P = 0.05$). There were, however, no significant differences ($P > 0.05$) between assemblage treatment levels for the root masses recovered from empty litterbags, which were invariably small. That is, the mean $\pm$1 SE values (mg root) were: 2.8 ± 0.73, 2.4 ± 0.88 and 2.3 ± 1.10 for the microbiota, mesofauna and macrofauna microcosm empty litterbags, respectively. These values are approximately equivalent to the root masses recovered from the filled litterbags in the macrofauna communities, and at least 10-fold smaller than those masses recovered from litterbags in the microbiota and mesofauna communities. Although these data from the ''empty'' litterbags suggest that roots actively foraged into the litter patches, those data for the FH horizon root densities suggest that the magnitude of this root foraging response (Figs. 1a and b) might be simply related to the FH horizon root densities. That is, where proliferation was highest, so was FH horizon root density (Figs. 1b and c).

To explore whether the foraging responses were related simply to FH horizon root densities, we devised a ''proliferation index'', defined as the magnitude of the root in-growth response to a litter patch relative to the standing mass of roots in the surrounding soil; the idea being that higher soil root densities would facilitate greater root in-growth responses. The index was calculated by dividing the litterbag root densities by the FH horizon root densities (see Materials and Methods for full details of how this index was calculated). The significant effect of soil biota assemblage composition ($F_{2,20} = 5.6$, $P < 0.05$) was clearly the result of the lower index values for the macrofauna community replicates (Fig. 1d). There was no significant effect ($P > 0.05$) of litterbag type.

Table 3. Effects of the soil biota assemblage composition, litterbag set and litterbag type on litter mass remaining

Litterbag set	Treatment assemblage	Litterbag type	Mass remaining (%)
2	Microbiota	Standard	37.8 ± 4.54
2	Mesofauna	Standard	37.9 ± 2.13
2	Macrofauna	Standard	28.3 ± 2.93
2	Microbiota	Community	26.8 ± 3.56
2	Mesofauna	Community	36.0 ± 4.15
2	Macrofauna	Community	21.5 ± 3.15
3	Microbiota	Standard	35.8 ± 3.96
3	Mesofauna	Standard	42.3 ± 5.99
3	Macrofauna	Standard	23.3 ± 3.86
3	Microbiota	Community	27.8 ± 3.13
3	Mesofauna	Community	36.8 ± 7.89
3	Macrofauna	Community	7.4 ± 1.78

Values are means (percentage of original mass) ± 1 SE ($n = 5$). There was a significant interaction between treatment assemblage and litterbag set ($F_{2,44} = 4.9$, $P < 0.05$); the other interactions were non-significant ($P > 0.05$). The interaction most likely resulted from the fact that litter mass loss in the macrofauna community was even more pronounced when compared to the other two communities for the Set 3 than Set 2 bags. To explore this interaction, we analysed each set individually using ANOVA. For both Sets 2 and 3 bags, there were no interactions between biota assemblage and litterbag type ($P > 0.05$) but both main effects were strongly significant (Set 2: $F_{2,20} = 7.5$, $P < 0.01$ for assemblage; $F_{1,20} = 9.8$, $P < 0.01$ for litterbag type; Set 3: $F_{2,20} = 19.9$, $P < 0.001$ for assemblage; $F_{1,20} = 10.3$, $P < 0.01$ for litterbag type).

Discussion

There was support for our first hypothesis, that the presence of mesofauna will decrease root proliferation into nutrient patches. That is, on a mean basis there was less absolute root mass (Fig. 1a), and less root mass relative to the litter mass remaining (Fig. 1b), in the litterbags placed in the mesofauna communities than those placed in the microfauna communities. We hypothesised that this result would be observed because mesofauna would (a) reduce patch size by enhancing litter decomposition or redistribution and (b) lower root densities through processes such as herbivory. Our data do not support mechanism (a): there was more litter mass remaining in mesofauna than microfauna communities (Table 3). There was, however, support for mechanism (b): there was lower FH horizon root density in the mesofauna than microfauna communities (Fig. 1c). Indeed, when we expressed in-growth as an index of litterbag to soil root densities, there was no apparent difference in the in-growth response between mesofauna and microfauna communities (Fig. 1d) suggesting that the lower FH horizon root mass was a contributing factor to the lower root in-growth per se when mesofauna were present.

Our second hypothesis, that the presence of macrofauna in addition to mesofauna will further exacerbate negative effects of soil fauna on root proliferation, was strongly supported. There was evidence that both of our hypothesised mechanisms, these being that macrofauna presence in the microcosms would be associated with the lowest root densities and greatest rate of patch decomposition, contributed to the low root in-growth responses observed in the microcosms containing macrofauna. Certainly, mass loss from litterbags was much greater in the macrofauna communities than either of the two simpler communities (Table 3) and FH horizon root densities were markedly lower (Fig. 1c). The low proliferation index (Fig. 1d) suggests that the impacts of macrofauna presence within the soil assemblages was more than an additive function of lower litter mass remaining and lower soil root densities, otherwise the proliferation index should have been equivalent to the other two treatment communities.

In addition to lower litter mass remaining and soil root densities, other mechanisms may have contributed to the low root in-growth we observed when soil macrofauna were present in the microcosms. For example, earlier work on the communities showed that mycorrhizal abundance was lower in the macrofauna communities (Bradford et al., 2002a) and the presence/absence of mycorrhiza has been shown to modulate plant responses to nutrient patches (Hodge, 2003). Further, different grassland plant species differ in the magnitude of their potential proliferation responses (Hodge, 2004) and Bradford et al. (2002a) showed that there was a shift in the plant species assemblage composition in the presence of macrofauna, which may then have been related to different potential in-growth responses of the plant assemblages in the different treatment communities. The macrofauna inoculation also included root herbivores such as *Tipula paludosa* (Diptera: Tipulidae), which may have fed directly on new root growth. Also, the quality of the litter patch influences the magnitude of proliferation (Maestre et al., 2005) and the lower litter mass remaining in the macrofauna communities may have been of lower quality. This possibility is supported by earlier work by Bradford et al. (2002b) which showed that the C:N ratio of litter remaining after 35 days of treatment exposure was greatest in the macrofauna communities. This may be especially relevant because proliferation responses of herbaceous species typically take about 35 days to develop (Hodge, 2004),

providing ample time for changes in litter chemistry through the action of soil biota.

Any one, or a combination of all, of the potential direct and indirect mechanisms (mentioned in the paragraph above) by which soil fauna may affect plant assemblage root proliferation into nutrient patches, may have contributed to the low root proliferation index observed in the macrofauna community. While the current study cannot disentangle the contributions of these different mechanisms, it highlights the fact that soil biotic assemblage structure may be a key modulating factor of plant responses to patchily distributed nutrients. Bonkowski et al. (2000) demonstrated this potential for soil microfauna, and Wurst et al. (2003) did so for earthworms. However, neither of these studies used multi-species plant assemblages. The latter condition is highly relevant because spatial heterogeneity in soil nutrient distribution, and plant proliferation responses to this, is considered to play a key role in plant success under conditions of interspecific competition.

Mycorrhiza (Hodge, 2003), protozoa and nematodes (Bonkowski et al., 2000), and earthworms (Wurst et al., 2003) have all previously been shown to modulate plant responses to nutrient heterogeneity. The current study demonstrates the potential for soil mesofauna, and soil mesofauna and macrofauna together, to modulate root proliferation responses to patchily distributed nutrients. In contrast to the previous studies, the current study was performed in a highly complex, biotic community, containing a multi-species plant assemblage, distinct soil horizons, a simulated diurnal climate and a speciose soil fauna (Bradford et al., 2002a). Although the current research was performed in a microcosm set-up, meaning we must extrapolate to the field with caution, the complexity of the model system does suggest that soil fauna may be a key modulating variable of plant responses to soil nutrient heterogeneity in the natural world. They may achieve this through one or both of two general mechanisms: (a) modification of plant root systems, and/or (b) the decomposition/redistribution rate of the patch. In our study, there was evidence that both root systems and patch decomposition/redistribution were affected by the faunal treatments but other mechanisms (e.g., shifts in mycorrhizal abundance to the treatments) may also have played a role in regulating the proliferation responses. Clearly, the role of soil fauna needs to be explicitly recognised in studies of plant-nutrient interactions. Theories explaining plant foraging behaviour in patchy environments need to acknowledge how soil biota can influence this activity.

Acknowledgements

We thank T. Hefin Jones for constructive comments on an earlier draft of this manuscript. The UK Natural Environment Research Council (NERC) provided funding under the UK Soil Biodiversity Thematic Programme (GST 2119) and as core support to the CPB.

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