Microfaunal interactions in the rhizosphere, how nematodes and protozoa link above- and below-ground processes

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I. The plant as a bridge between above- and below-ground populations and processes

The living plant is the basis of existence for several groups of organisms both above- and below-ground. These organisms include, for example, mycorrhizal fungi, free-living rhizosphere organisms, foliar and root herbivorous insects, root pathogenic fungi and nematodes. These organisms affect plant growth, and are affected by plant growth, but we currently have an incomplete understanding of the cumulative and interactive effects of all these organisms since our knowledge is mainly based on isolated investigations of single organism groups. To further our understanding we need to know how these consumer organisms develop and interact with one another during plant growth (i.e. the

above-/ below-ground multitrophic interactions *sensu* Masters et al., 1993; van der Putten et al. 2001). Should the plant be regarded solely as a supplier of carbon to the various consumers, or as an organism that interacts with its consumers forming a bridge between above- and below-ground populations and processes? We take the view that supporting microbial interactions in the rhizosphere must be of fundamental importance for plants to justify this significant input of carbon, which could otherwise be used to construct light-capturing or defensive structural tissues aboveground. In this chapter we bring together our knowledge of microfauna (nematodes and protozoa) in the rhizosphere with the latest experimental findings on plant-microbe interactions to conclude that the connection between plants and soil animals is far more than simply that of resource and consumer. Our premise is that the role of these organisms is more than simply a trophic one (i.e. who eats who and how much) but their interactions and signaling with other rhizosphere and foliar inhabiting organisms, and the plant itself, are more pervasive. Since small trade-offs in plant fitness due to functional shifts at the microbial level in the rhizosphere can influence the outcome of competition in plant communities (Bonkowski and Roy 2005), microbial-faunal interactions in the rhizosphere should be considered as important factors that probably affect diversity at much larger scales. We explore this by detailing both the direct and indirect interactions of the rhizosphere microfauna, then their interactions with symbionts such as mycorrhiza and finally moving on to below-ground above-ground interactions involving the microfauna.

II. Rhizosphere microfauna – direct effects on carbon and nitrogen flows

A. Direct effects

Previous reviews of the role of microfauna (nematodes and protozoa) in the rhizosphere have tended to concentrate on their contribution to gross flows of carbon and nitrogen (see for example Brimecombe et al. 2001; Ekelund and Rønn 1994; Griffiths 1994; Zwart et al. 1994) or their role in disease suppression (Curl and Harper 1990). These are termed direct effects because the organism directly influences the process, unlike indirect effects which are discussed later in which the organisms affects another organism to indirectly affect the process. In the rhizosphere, bacteria are more important decomposer organisms than fungi, because of the large supply of easily decomposable organic matter (Wardle 2002), so interactions between bacteria and their microfaunal grazers have received more attention than those of fungi and their grazing animals. The activity of microorganisms in soil is generally limited by carbon, but not in the rhizosphere where plants steadily supply microorganisms with easily available carbon (Cheng and Gershenson, this volume). Consequently, a specialized microflora typically consisting of fast growing bacteria results in increased levels of microbial biomass and activity around plant roots (Alphei et al. 1996; Hawkes et al., this volume). There is strong top-down control (i.e. regulated by the activity of organisms of a higher trophic level, as oppose to bottom-up control which means regulation by resource at a lower trophic level, see Moore et al., this volume) of these bacterial populations by the grazing pressure of microbivorous nematodes and protozoa (Ingham et al. 1986; Allen-Morley and Coleman 1989; Wardle 2002). The release of carbon in form of root exudates may account for up to 40% of the dry matter produced by plants (Lynch and Whipps 1990). Even if the C-transfer to exudation was 10-20% of total net fixed carbon (Rovira 1991),

other microbial symbionts such as mycorrhizae (Christensen 1989; Marschner 1992; Söderström 1992; Smith and Read 1997) or N_2-fixing microorganisms (Bezdicek and Kennedy 1979; Ryle et al. 1979) may each consume another 10-20 % of total net fixed carbon, so that plants would still release up to half of their total fixed carbon to fuel microbial interactions in the rhizosphere. We take the view that supporting microbial interactions in the rhizosphere must be of fundamental importance for plants to justify this significant input of carbon, which could otherwise be used to construct light-capturing or defensive structural tissues aboveground. In particular, why are plants providing ample energy in form of exudates to a microbial community that is strongly competing with roots for available nutrients? The answer partly lies in the loop structure of the bacterial energy channel in the rhizosphere.

B. The Microbial Loop I soil and rhizosphere

Nutrients become locked up, immobilised, in bacterial biomass but are liberated by microfaunal grazing (Bonkowski et al. 2000a). This interplay between microorganisms and microfauna, termed the 'microbial loop', determines the rate of nutrient cycling and strongly enhances the availability of mineral nutrients to plants (Clarholm 1984; Ingham et al. 1985, Gerhardson and Clarholm 1986; Ritz and Griffiths 1987; Kuikman et al. 1990; Jentschke et al. 1995; Alphei et al. 1996; Bonkowski et al. 2000b, 2001b). Microfaunal grazing is particularly important because plant available nutrients will be strongly sequestered during microbial growth (Kaye and Hart 1997; Wang and Bakken 1997) and would remain locked up in bacterial biomass if consumption by nematodes and protozoa did not constantly re-mobilise essential nutrients for plant uptake (Christensen

et al. 1992; Griffiths and Caul 1993; Griffiths et al. 1993). For example, Bonkowski et al. (2000b) added labelled plant litter to a soil poor in organic carbon to create hotspots of microbial activity. The simultaneous action of root foraging and microfaunal activity led to a complex pattern of nutrient liberation in space and time. While root foraging in organic hotspots enhanced the spatial coupling of mineralization and plant uptake, microfaunal grazing increased the temporal coupling of nutrient release and plant uptake. The biomass of a ryegrass (*Lolium perenne*) doubled in protozoan treatments, and plant N-uptake and incorporation of ^{15}N from the labeled plant litter increased by factors of x2 and x3, respectively. It is important to note, that the energy supporting microbial growth and mineralization dynamics did not originate from exudation, but was inherently provided with the added plant debris. Root foraging and presence of microfauna respectively accounted for 34 and 47% of variation in plant biomass, indicating that nutrient liberation by microbial-faunal interactions, i.e. the microbial loop, were a major determinant of plant growth. The subsequent increase in plant N uptake in the presence of microbial-feeding nematodes and protozoa is well documented in experimental systems (see previous references plus; Vreeken-Buijs et al. 1997; Mikola and Setälä 1999; Okada and Ferris 2001; Anderson et al. 1983; Ingham et al. 1985; Freckman 1988; Elliott et al. 1979; Verhagen et al. 1995) as well as the field (Ingham et al., 1986; de Ruiter et al., 1993). In the rhizosphere a 'microbial loop' is triggered by the release of root exudates from plants, which increases bacterial growth in the rhizosphere and subsequent microfaunal grazing liberates immobilised N. It had been speculated that this rhizosphere microbial loop would lead to the mineralization of soil organic N (Clarholm 1985), so called root induced nitrogen mineralization. However, the quantifiable benefit of root

induced nitrogen mineralization to the gross N nutrition of plants in the field is slight. Nitrogen balance models indicate that this activity is only sufficient to allow for recycling of the N lost from the plant by exudation rather than to mineralize N from soil organic matter, and could only supply a small proportion of the measured uptake rates of N (Robinson et al. 1989; Griffiths and Robinson 1992).

C. Spatial and temporal variation

Root derived carbon leads to a general increase in the populations of microfauna in the rhizosphere, compared to bulk soil, upto 27-fold for free-living nematodes (Griffiths 1990) and 35-fold for protozoa (Zwart et al. 1994). Microfaunal populations in the rhizosphere often reach a maximum on the older portions of the root system rather than the root-tip itself. On barley roots nematode populations reached a maximum on roots that were 10 days old (Griffiths et al. 1991), although large numbers of active amoebae occurred near the root-tip of plants growing on agar (Coûteaux et al. 1988; Bonkowski and Brandt 2002). The likely maximum effects of the microfauna can, therefore, be spatially (and temporally) removed from the location of exudation at the root-tip, even though bacterial biosensors indicate that root exudation occurs mainly at the root tip (Darwent et al. 2003). The observation that bacterial populations oscillate as a kind of moving wave along a root (Semenov et al. 1999) maybe related to predator-prey dynamics induced by the grazing of microfauna on bacteria, although the periodicity of the waves indicated that bacterial succession was more likely. Increases in rhizosphere protozoa occur mainly early in the life of an annual plant, during the nutrient acquisition

phase before flowering (Rønn et al. 2002; Wamberg et al. 2003a), further emphasising temporal dynamics.

D. Effects of root–feeding microfauna

Microfauna do have significant, direct, effects on rhizosphere C and N-flow through the action of plant-parasitic nematodes. Low amounts of root infestation (typical of natural field densities) by the clover cyst nematode (*Heterodera trifolii*) on white clover (*Trifolium repens*) increased the translocation of photoassimilate to the roots, increased leakage of carbon from the roots and increased microbial biomass in the rhizosphere (Yeates et al. 1998). This increased flow of C was confirmed with subsequent studies on a further four species of root-feeding nematodes (Yeates et al. 1999). While clover root production was increased in response to low levels of infestation by clover cyst nematode, root biomass of a companion species not attacked by the nematode, perennial ryegrass (*Lolium perenne*), was also increased (Bardgett et al. 1999). This was due to increased fluxes of N from the clover being recycled and taken up by the ryegrass.

E. Summary of direct effects

The direct effects of microbial-feeding nematodes and protozoa in the rhizosphere are to effectively recycle nutrients that would otherwise remain immobilized in the microbial biomass. Quantitatively however, this only liberates as much N as the plant would loose through root exudation and does not represent a significant flow of N to the growing plant. If additional carbon is provided, e.g. in form of easily degradable organic matter, microfaunal grazing on the abundantly developing microbial biomass will significantly

stimulate microbial decomposition and mineralization activity, leading to strongly enhanced uptake rates of the liberated nutrients. The effects of low-levels of root herbivory by plant-feeding nematodes directly contribute to rhizosphere C-flows and can also, in some circumstances, enhance N-availability.

III. Rhizosphere microfauna – indirect effects on plant growth

A. Signalling in the rhizosphere

Indirect interactions of microfaunal grazing in the rhizosphere are even more important than their direct effects (Bonkowski and Brandt 2002). Protozoa have, for example, been found to increase plant biomass independently of nutrient contents in the plant tissue (Alphei et al. 1996). Thus, in a laboratory experiment with a constant supply of excess nutrients protozoa increased the biomass of spruce (*Picea abies*) seedlings up to 60% (Jentschke et al. 1995 - Table 1).

Table 1. The biomass and root development of spruce (*Picea abies*) seedlings, grown in the presence or absence of protozoa (either a natural community of soil protozoa or a limited number of species from laboratory culture), but with a non-limiting supply of nutrients. Means followed by different letters are significantly different ($P<0.05$), data from Jentschke et al. 1995.

	No protozoa	Mixed soil protozoa	Protozoa from culture
Shoot wt (mg)	278[a]	493[b]	406[b]
Root wt (mg)	401	571	572
Root tips (000's)	4.3[b]	13.3[a]	9.8[ab]

Root length (m)   11 [b]   31 [a]   26 [a]

Plants are not simply passive recipients of nutrients, but information from the environment affects their belowground allocations such as: root proliferation (Huber-Sannwald et al. 1997; Hodge et al. 1998; 1999); formation of symbiotic relationships (e.g. mycorrhizal fungi, Fitter and Merryweather 1992; Smith and Read 1997; or N_2-fixing bacteria, Ryle et al. 1979); alteration in exudation rates (Kraffczyk et al. 1984; Jones and Darrah 1995; Bonkowski et al. 2001b; Wamberg et al. 2003b); interactions with free-living bacteria (Mathesius et al. 2003; Joseph and Phillips 2003) or production of secondary defence compounds against herbivores (Baldwin and Hamilton 2000; Cipollini et al. 2003). Since root morphology is both genetically programmed and environmentally determined (Rolfe et al. 1997), there must be signal transduction pathways that interpret complex environmental conditions and activate genes to enter a particular symbiosis or to form a lateral root at a particular time and place, for example. The exchange of signals between plants and microorganisms is reciprocal and in case of root-infecting plant symbionts and pathogens an area of intense research (Alfano and Collmer 1996; Long 1996; Barker et al. 1998; McKenzie Bird and Koltai 2000). Recently, Phillips and Strong (2003) introduced the concept of 'rhizosphere control points' to emphasize the importance of information exchange between plants and microorganisms. These control points link signals to genes in the rhizosphere and it is proposed that identification of control points will allow hypothesis testing through, for example, the use of defined mutants to quantify effects of known genes.

B. Effects on rhizosphere microbial community structure.

The strong top-down regulation of rhizosphere bacteria by grazing gives a central role to nematode and protozoan in the interactions between plant roots and their colonizing microorganisms. Such food web interactions are explored in greater detail by Moore et al. (this volume). Protozoa seem quite selective in their bacterial food choice (Boenigk and Arndt 2002) and significant changes in bacterial community composition due to protozoan grazing have been confirmed in freshwater systems (Pernthaler et al. 1997; Jürgens et al. 1999; Posch et al. 1999) as well as in the rhizosphere of plants (Griffiths et al. 1999; Bonkowski and Brandt 2002; Rønn et al. 2003). These grazing-induced changes in microbial composition affect fundamental ecosystem properties because soil bacteria occupy some of the most important control points for nutrient cycling and plant growth. For instance, N_2-fixing, nitrifying and denitrifying bacteria dominate the nitrogen cycle (Mengel 1996). A strong stimulation of nitrifying bacteria is commonly observed in presence of protozoan grazers, presumably through predation on their faster-growing bacterial competitors, resulting in high concentrations of NO_3^- in culture liquid and rhizosphere soil (Griffiths 1989; Verhagen et al. 1995; Alphei et al. 1996; Bonkowski et al. 2000a). Introduced bacteria also interact with rhizosphere microfauna. Inoculation of pea (*Pisum sativum*) seeds with strains of the bacterium *Pseudomonas fluorescens* increased the abundance of nematodes and protozoa in the rhizosphere, non-inoculated germinating pea seedlings exerted a nematicidal effect that was thought to be metabolized and inactivated by the introduced bacteria (Brimecombe et al. 1999). Conversely, inoculation of wheat (*Triticum aestivum*) with the same bacteria increased rhizosphere populations of nematodes but not protozoa, showing that the outcome of the plant –

microfauna interaction depends on plant characteristics such as root exudation patterns (Brimecombe et al. 1999).

C. Effects on root architecture and plant growth hormones

From a microbial perspective, the evolution of strategies capable of enhancing energy transfer to the roots would lead to a strong increase in fitness of those microorganisms that influence gene regulation in plants by sending the right signals. Specialized bacteria are the dominant colonizers of plant roots (Marilley and Aragno 1999) and indeed many of the rhizosphere bacteria have the potential to affect plant performance by producing hormones (Brown 1972; Costacurta and Vanderleyden 1995; Arshad and Frankenberger 1998; Lambrecht et al. 2000). Up to 80% of the bacteria isolated from plant rhizospheres are considered to produce auxins (Barea 1976; Patten and Glick 1996), and the widespread ability of both beneficial and deleterious rhizosphere microorganisms to produce plant hormones suggests that rhizosphere bacteria play an important role in manipulating root and plant growth (Shishido et al. 1996; Rolfe et al. 1997). Recent molecular evidence points to the role of phytohormones in the induction of giant cells by root-knot nematodes (*Meloidogyne* spp.), and that the nematodes acquire the genes to synthesize or modulate phytohormones by horizontal gene transfer (McKenzie Bird and Koltai, 2000).

More importantly, the effects of rhizobacteria on root architecture seem to be controlled to a great extent by protozoan grazing (Bonkowski and Brandt 2002). Plants develop an extensive and more highly branched root system in presence of protozoa (Jentschke et al. 1995) than when grown in the absence of protozoa, corresponding to

hormonal effects on root growth by beneficial rhizobacteria (Chanway et al. 1988; Petersen et al. 1996; Rolfe et al. 1997). Thus, in addition to the stimulation of gross nutrient flows, protozoa promote a loosely mutualistic interaction between plant roots and rhizobacteria (Bonkowski and Brandt 2002). Protozoan grazing has been found to promote auxin-producing rhizobacteria, which stimulates the growth of the root system, allows more nutrients to be absorbed, but will also increase exudation rates thereby further stimulating bacterial-protozoan interactions (Bonkowski and Brandt 2002). These observations have been substantially supported by the experimental study of protozoan effects on *Arabidopsis thaliana* plants transformed by the cytokinin-inducible ARR5-promoter-GUS construct (Dickler and Kreuzer, unpublished). As expected, root elongation and root branching nearly doubled in plants grown in presence of a naked amoeba (*Acanthamoeba castellanii*), compared to control plants grown solely in soil inoculated with a filtered microbial inoculum. Simultaneously, GUS-reporter gene activity strongly increased in treatments with protozoa. The dramatic change in root architecture of *Arabidopsis* suggests a strong auxin effect, which presumably had to be down-regulated in the root by the auxin-antagonist cytokinin. These findings have been summarised in a conceptual model of microfaunal-induced hormonal effects on root growth (Fig. 1).

D. Signalling in the rhizosphere

Recently the role of other signal molecules, apart from hormones, in microbe-root communication has been established. Phillips et al. (1999) found that *Sinorhizobium meliloti* bacteria produce a signal molecule that enhances root respiration and triggers a

compensatory increase in whole-plant net carbon assimilation in alfalfa (*Medicago sativa*). They identified the signal as lumichrome, a common breakdown product of riboflavin. In addition, a large proportion of the bacteria colonizing the roots of plants are capable of producing N-acyl homoserine lactone (AHL) signals to coordinate their behaviour in local rhizosphere populations. Specific interactions of bacteria with plant hosts, like nodulation (Wisniewski-Dyé and Downie 2002) or the successful infection of plants by deleterious bacteria seem to depend on such AHL-mediated "quorum-sensing" regulation. Recently, Mathesius et al. (2003) demonstrated that auxin responses and investment in defence by the legume *Medicago truncatula* were directly affected by AHLs from both, free-living beneficial and deleterious bacteria. Additionally, Joseph and Phillips (2003) showed that homoserine lactone, the breakdown product of AHL, leads to a strong increase of water transpiration in bean (*Phaseolus vulgaris*) and speculated that the microorganisms would benefit from enhanced transpiration when soil moisture carries mineral nutrients towards the root. These examples demonstrate the presence of several, indirect, plant – microorganism interactions that could potentially be significantly affected by the action of rhizosphere microfauna.

IV. Rhizosphere microfauna – interactions with mycorrhizal and other symbionts

The outcome of the symbiosis between mycorrhizal fungi and the plant is normally regarded as positive for the plant, as it is supplied with nutrients from the mycorrhiza (Smith and Read 1997; Johnson and Gehring, this volume). But different arbuscular-mycorrhizal (AM) fungi affect the growth of individual plants differently (Jakobsen

1992) and at high mycorrhizal infection the AM can be harmful to the plant (Gange and Ayres 1999). The interaction of AM and aboveground plant parasites can be beneficial or detrimental to the plant, probably dependent on the availability of phosphorus in the soil (West 1995). Actually, it is possible that the problems often seen with establishment of AM in agricultural crops (Iver Jakobsen, pers. comm.) is to a large extent caused by the dual effect of AM fungi that switch between symbionts and parasites (Gange and Ayres 1999). We will deal here only with interactions between mycorrhiza and microfauna, the wider issues of mycorrhizae are covered in depth by Johnson and Gehring (this volume).

Root infection by symbiotic rhizosphere organisms often affects populations of rhizosphere protozoa, especially if the plant is also stressed by environmental factors including elevated concentrations of atmospheric CO_2 (Rønn et al 2002) or herbivory (Wamberg et al. 2003b – see Table 2). A likely explanation is that the mycorrhizal fungus can directly access photo-assimilate C from the roots, thereby reducing the flow of C into the rhizosphere as exudates. Differences between mycorrhizal and non-mycorrhizal plants are likely to be exaggerated under conditions increasing C-allocation below-ground. Bonkowski et al. (2001b), in an experiment with ecto-mycorrhizae and protozoa in soil, saw a reduction of bacteria and protozoa in the presence of mycorrhizae, and a reduction of fungal mycelium in the presence of protozoa, suggesting a trade-off in C-allocation (Fig. 2).

Grazing by soil fauna is known to affect mycorrhizal fungi, although most work concerns microarthropods (Warnock et al. 1982; Sëtala 1995) and microfaunal effects on mycorrhizal fungi have received less attention. Fungal-feeding nematodes (Yeates et al. 1993) and protozoa (Petz et al. 1985; Hekman et al. 1992) are common in soils so an

interaction between microfauna and fungi, including mycorrhiza, is probable. Háněl and Šimek (1993) observed a significant positive correlation between seasonal changes in plant-feeding nematodes and nitrogen-fixing nodules on red clover (*Trifolium pratense*) roots, and also between bacterial-feeding nematodes and root nitrogenase activity. That soil microfauna reproduce more effectively on some microbial species as food than others is well documented (e.g. Grewal 1991) but the observation that bacterial-feeding nematodes isolated from the potato (*Solanum tuberosum*) rhizosphere reproduced better on a *Comomonas* bacteria, than eight other bacterial strains isolated from the potato rhizosphere, and that *Comomonas* is a growth promoting rhizobacterium opens the possibility of a specific relationship such that the nematode is favoured by and moves the bacterium around the rhizosphere, the bacterium in turn enhances plant growth which stimulates growth of the both bacterium and nematode (Kimpinski and Sturtz 1996). Interactions between rhizosphere microfauna and plant symbionts other than mycorrhizae are probably more widespread than published studies suggest.

V. Plant response to above- and below-ground herbivory

The interactions between rhizosphere organisms and foliar herbivores must be mediated by plant responses. Foliar-feeding insects have a variable effect on above- and below-ground plant biomass (Wardle 2002), but usually induce an increased carbon flow to the plant roots (Bardgett et al. 1998; Dyer et al. 1991) and a higher root respiration (Holland et al. 1996). Defoliation can result in an increased number of bacterial-feeding nematodes in the rhizosphere (Mikola et al. 2001), which was taken to indicate increased allocation of plant carbon to the soil, leading to enhanced bacterial production and thus

more bacterial grazers. Defoliation does not necessarily increase C availability in the rhizosphere though (Mikola and Kytöviita, 2002). The allocation of plant-C to different microbial interactions varies with the growth stage of the plant and the presence of both foliar herbivores and symbiotic mycorrhiza (Bonkowski et al. 2001a; Wamberg et al. 2003b; Vestergård et al. 2004). The example shown in Table 2 shows that in the vegetative, pre-flowering stage, when plants are actively investing C below-ground, leaf chewing herbivores induced increases in C-transfer are used mainly for the production of mycorrhizal fungal biomass (seen by the increases in soil respiration and rhizosphere protozoa if no mycorrhizae are present, and the increase in mycorrhizal infection with foliar-herbivory). In the post-flowering stage, when C-transfer to developing seeds is important, herbivory does not increase C-transfer below-ground. With leaf sucking herbivores the opposite effect has been noted belowground, i.e. a decrease in belowground respiration and the bacterivorous fauna (Vestergård et al. 2004).

Table 2. Combined affects of foliar herbivory (by the weevil *Sitona lineatus*) and mycorrhizal root infection (by *Glomus intraradices*) on below-ground carbon allocation in pea (*Pisum sativum*) plant pre- and post-flowering. Means followed by different letters are significantly different (*P*<0.05), data from Wamberg et al. (2003b).

		Mycorrhizae Present		Mycorrhizae Absent	
		Herbivory Present	Herbivory Absent	Herbivory Present	Herbivory Absent
Pre-flowering	Plant dry wt. (g)	1.1	1.2	1.2	1.2

	Relative herbivory	2.7	-	2.0	-
	Mycorrhizal roots (%)	58[a]	28[b]	-	-
	Soil + root respiration (μg C g^{-1} d^{-1})	14[a]	18[a]	40[b]	16[a]
	Protozoa (000's g^{-1})	18[a]	21[a]	53[b]	25[a]
	Plant dry wt. (g)	1.2	1.2	1.0	1.2
Post-flowering	Relative herbivory	0.5[a]	-	2.3[b]	-
	Mycorrhizal roots (%)	42[a]	68[b]	-	-
	Soil + root respiration (μg C g^{-1} d^{-1})	23	26	29	18
	Protozoa (000's g^{-1})	34	20	38	39

Mycorrhizal fungi are known to stimulate leaf sucking insects, probably because of an increased nutrient content in the sap (Gange et al. 1999), but these fungi also reduce the activity of leaf chewing insects, possibly due to an increased content of structural compounds in the leaves (Gange and West 1994). Foliar herbivory is reported to inhibit mycorrhizal fungi in most cases (Gehring and Whitham 1994). There is a significant interaction with the growth phase of the plant, however, since leaf-chewing insects stimulate mycorrhiza and free-living rhizosphere microorganisms in the early nutrient acquisition phase of the plant, but not during flowering when herbivory did not affect belowground organisms (Wamberg et al. 2003b – Table 2). The connection between the above- and below-ground food webs has been formalized mathematically by Moore et al. (this volume).

Root-feeding insects with different specificity towards crops and weeds (House et al. 1984) can have a beneficial or detrimental effect on the growth of a single plant (Gange

and Brown 1989; Wardle 2002). In a plant community these insects can increase the N transport from clover to grasses (Hatch and Murray 1994), as detailed for root-feeding nematodes above, and even increase shoot growth for both plant species (Bardgett et al. 1999). Root-feeding by other invertebrates has been shown to stimulate plant defense chemicals in the leaves, and so reduce populations of foliar-feeding insects (Bezemer et al. 2003). It is not known whether root feeding by nematodes similarly impacts upon foliar plant defenses.

Host-specific root pathogenic nematodes can strongly influence when one plant out competes another and so influence plant succession via rhizosphere effects (Van der Putten et al. 2001, Wardle 2002). The presence of root herbivorous nematodes to a large extent depends on plant nutrient status (Verschooer et al. 2001) and an increase in number of endoparasitic over ectoparasitic nematodes has been observed in barley grown at low N and P as opposed to fully fertilised barley (Vestergård et al., 2004.). Different types of plant parasites may therefore indicate the nutrient status of the host plants.

VI. Conclusions and directions for future research

The interactions between plants and microfauna in the rhizosphere are clearly not simply limited to the mineralising activities of the fauna, nor are they unidirectional with the fauna impactingly solely on the plant. Rather, there are a complex series of interactions between plants, symbiotic flora, fauna and soil nutrient status with the microfauna affecting, and being affected by, both the shoot and root portions of the plant. These interactions are also evident at the level of the individual plant as well as the plant community. It is well known that the plants respond to differences in soil nutrient

content. Thus, root growth is stimulated in portions of soil with elevated nutrients (Fransen et al. 1999; Hodge et al. 1999) and the root system can also benefit from nutrient pulses of a few hours duration (Campbell and Grime 1989). It is an open question to what extent there has been an evolutionary benefit for the plant of being able to direct its carbohydrates towards the different consumers in direct response to the needs of the plant. The soil, fauna, flora, root, shoot, herbivores, predators in many ways act like a single, connected organism. Rhizosphere microfauna provide a useful focus in the study of the complex interactions. Future significant advances in understanding and management will come from a holistic approach to the 'rhizo-organism'.

Acknowledgements

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