REVIEW ARTICLE

Rhizosphere fauna: the functional and structural diversity of intimate interactions of soil fauna with plant roots

Michael Bonkowski · Cécile Villenave · Bryan Griffiths

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Abstract For decades, the term "rhizosphere fauna" has been used as a synonym to denote agricultural pests among root herbivores, mainly nematodes and insect larvae. We want to break with this constrictive view, since the connection between plants and rhizosphere fauna is far more complex than simply that of resource and consumer. For example, plant roots have been shown to be neither defenceless victims of root feeders, nor passive recipients of nutrients, but instead play a much more active role in defending themselves and in attracting beneficial soil microorganisms and soil fauna. Most importantly, significant indirect feed-backs exist between consumers of rhizosphere microorganisms and plant roots. In fact, the majority of soil invertebrates have been shown to rely profoundly on the carbon inputs from

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M. Bonkowski (⊠) Department of Terrestrial Ecology, University of Cologne, Zoological Institute, Weyertal 119, 50931 Cologne, Germany e-mail: bonkowski@rhizosphere.de

C. Villenave Research Institute for Development, IRD-SeqBio/SupAgro, 2 place Viala, Bât. 12, 34060 Montpellier cedex 1, France

B. Griffiths Teagasc, Environment Research Centre, Johnstown Castle, Wexford, Co., Wexford, Ireland roots, breaking with the dogma of soil food webs being mainly fueled by plant litter input from aboveground. In this review we will highlight areas of recent exciting progress and point out the black boxes that still need to be illuminated by rhizosphere zoologists and ecologists.

Keywords Rhizosphere food web · Root herbivores · Signalling · Microbial vectors · Root growth · Energy channel

Introduction

For decades, the term "rhizosphere fauna" has been used as a synonym to denote agricultural pests among root herbivores, mainly nematodes and insect larvae. We want to break with this constrictive view, since the connection between plants and rhizosphere fauna is far more complex than simply that of resource and consumer. For example, plant roots have been shown to be neither defenceless victims of root feeders, nor passive recipients of nutrients, but instead play a much more active role in defending themselves and in attracting beneficial soil microorganisms and soil fauna. Most importantly, significant indirect feedbacks exist between consumers of rhizosphere microorganisms and plant roots. In fact, the majority of soil invertebrates have been shown to rely profoundly on the carbon inputs from roots, breaking with the dogma of soil food webs being mainly fueled by plant litter input from aboveground. In this review we will highlight areas of recent exciting progress and point out the black boxes that still need to be illuminated by rhizosphere zoologists and ecologists.

The consumers of plant roots: direct impacts, re-programming of plant cells and indirect plant feed-back

Roots anchor the plant in soil, but most importantly, the whole nutrient transfer from soil to aboveground plant parts is channeled through the roots, and roots are important storage organs in perennial plants. This makes roots attractive to herbivores. However, plant roots are no passive victims of attacking herbivores and microorganisms. In fact, they have evolved a whole arsenal of direct defence compounds, such as terpenoids, and also indirect defenses, involving communication strategies to interact with soil fauna, soil microorganisms and other plant roots to ward off attack (Huber-Sannwald et al. 1997; Boff et al. 2001; van Tol et al. 2001; Mathesius et al. 2003; Bais et al. 2004, 2006; Rasmann et al. 2005; Dudley and File 2007). Therefore, successful root feeders are expected to employ highly coevolved strategies to counter root defence systems. The most important root feeders are considered to be root-feeding nematodes and insect larvae.

Root-feeding nematodes

All plant-parasitic nematodes have a stylet; a strong, hollow, needle-like structure that is used to pierce plant cells, inject nematode secretions and to feed on plant cell contents. Stylets vary in shape and size according to the feeding strategy of the nematode; for example, nematodes such as *Trichodorus* that feed on epidermal cells have short stylets, whereas those such as *Xiphinema* or *Longidorus* have considerably longer stylets and can feed on cells deeper within the plant (Gheysen and Jones 2006) (Fig. 1). To find the root, invade the root and induce a feeding site nematodes rely on an arsenal of secreted molecules and signaling pathways (see reviews by: Williamson and Gleason 2003; McKenzie Bird 2004; Gheysen and Jones 2006).

Migrating nematodes can locate their target by sensing chemical gradients (Robinson 2003), plant cell—specific surface determinants or electrical sig-



Fig. 1 A plant-parasitic nematode (Xiphinema sp.) piercing root cells

nals (Riga 2004). However, only a narrow part of roots, between the tip and the root hair zone is vulnerable to nematode attack. Detached root border cells, secreted from root tips are suggested to play a significant role to misdirect plant-parasitic nematodes until the vulnerable part of the root has outgrown its attackers (Rodger et al. 2003) (Fig. 2). If a suitable cell is located, endoparasitic nematodes then enter into the root (as opposed to ectoparasites that simply use their stylet to feed on cells without entering the root themselves), secreting a wide range of enzymes (including cellulases, chitinases and extensins) that are specifically targeted to degrade or modify host tissues, during their migration through the root (Davis et al. 2000). Many nematodes induce the plant to make specialized cells, or feeding sites, which are metabolically active and provide a source of sustained nutrition for the nematode (Fig. 2). Nematode feeding sites tend to have structural characteristics of metabolically active tissues including: cytoplasm highly enriched in sub-cellular organelles; signs of DNA replication and enlarged or multiple nuclei (Wyss 2002). It has been hypothesized that some of the nematode genes encoding these enzymes were acquired from soil bacteria via horizontal gene transfer (Popeijus et al. 2000; Veronico et al. 2001). Comparisons of host transcription patterns using a variety of techniques have indicated that nematode infection initiates complex changes in plant gene expression (Gheysen and Jones 2006). Genes that are induced in defence responses against other pathogens are upregulated by nematode infection. Thus the plants are not passive in the face of nematode invasion but have



Fig. 2 What is known on signalling between rhizosphere fauna, microorganisms and plant roots? (1) Migrating rootfeeding nematodes locate roots by chemical gradients of rootspecific signals (Williamson and Gleason 2003). Root border cells (RBCs) can misdirect root feeding nematodes until the vulnerable part of the root tip has outgrown its attackers (Rodger et al. 2003). (2) Once targeted, root invading nematodes secrete a wide array of enzymes and signal molecules specifically targeted to downregulate host defense responses and to modify host tissues (McKenzie Bird 2004), e.g. root knot nematodes secrete signal molecules to induce cell growth of specific feeding sites. (3) Upon attack by root-feeding insect larvae, roots emit specific volatiles attracting entomopathogenic nematodes to kill the herbivore (Rasmann et al. 2005). (4) Legume roots emit specific volatiles to attract bacterivorous nematodes that carry symbiotic rhizobia on their cuticula to inoculate the roots (Horiuchi et al. 2005). (5) Fungivores affect the balance between mycorrhizal (MF) and saprophytic (SF) fungi in a density dependant manner.

a battery of defences that they employ to try to repel nematodes once they have been detected within the roots. Plant-parasitic nematodes have responded to this by evolving a series of physical and biochemical adaptations that help them either avoid eliciting a host response or to reduce the toxic effects of any plant Some ectomycorrhiza species have been shown to use collembola as nutrient source (Klironomos and Hart 2001). (6) Predatory mites are attracted by volatile signals to the fungal food sources of their collembolan prey (Hall and Hedlund 1999), and injured collembola emit warning signals to alert conspecifics (Pfander and Zettel 2004). (7) Roots interfere with bacterial communication by emitting quorum sensing mimic compounds (Mathesius et al. 2003). (8) Bacterivores, such as amoebae and nematodes regulate rhizosphere bacterial community composition (Rosenberg et al. 2009), they affect the production of bacterial metabolites (see Fig. 3) and release NH₄-N from consumed bacterial biomass (Griffiths 1994). (9) Grazing resistant bacteria benefit from bacterivores (Jousset et al. 2008) and stimulate exudation (see text). (10) Grazing-induced changes in the composition of rhizosphere bacteria lead to enhanced production of lateral roots (Mao et al. 2007), thereby favouring a positive feedback on steps (8) and (9) (Bonkowski 2004)

defence response. A large number of the genes that are induced by nematode infection are likely to contribute to establishing the parasitic interaction (Puthoff et al. 2003). Thus, while nematodes themselves will inject cell-wall degrading enzymes via the stylet, they also stimulate the plant to upregulate genes that encode host cell-wall degrading enzymes such as endoglucanase and polygalacturonase (Goellner et al. 2001; Vercauteren et al. 2002). Analysis of mutants and reporter-gene constructs indicate that auxinresponse genes are also induced in the formation of nematode feeding sites (Goverse et al. 2000). There are remarkable similarities in the signaling pathways between the formation of nematode feeding sites, root nodules induced by Rhizobium, mycorrhizal infections of roots and lateral root formation (Mathesius 2003). In all cases, it is possible that the perturbance of the root auxin balance is mediated by plant flavonoids, the only plant derived auxin transport inhibitors known (Jacobs and Rubery 1988). The specificity of each interaction might be determined by temporal and spatial patterns of expression and by the induction of specific isoforms of enzyme classes. Overall, the web of interactions between internal and external signals regulating plant responses to microbial signals shows that the plant is actively orchestrating its interactions with microorganisms (Mathesius et al. 2003).

Root feeding invertebrates can have major direct effects by reducing plant performance and so facilitating ecological succession or invasion. Phytophagous nematodes have been estimated to take up as much as one quarter of the net primary production of grassland vegetation (Stanton 1988), and they affect plant quality (Troelstra et al. 2001), plant diversity, and vegetation succession (De Deyn et al. 2003a). By focusing on agricultural systems, important and beneficial functions of root feeders, such as plant-parasitic nematodes, in natural systems are frequently overlooked. Organisms that derive their energy from living roots, such as nematodes, affect rhizodeposition and thereby influence the supply of root C to rhizosphere microorganisms (Yeates et al. 1998, 1999a, b; Bardgett et al. 1999a; Bardgett and Wardle 2003; Ayres et al. 2007; Haase et al. 2007; Poll et al. 2007). The activities of root feeders affect the turnover rate of root tissue (Dawson et al. 2002; Treonis et al. 2005), enhance rhizodeposition of organic compounds (Murray et al. 1996; Yeates et al. 1998; Treonis et al. 2005) and alter root architecture (Treonis et al. 2007). This has important consequences for micro-food webs of free-living bacteria and their consumers on plant roots (see below).

At low levels of nematode infestation, losses of C from the plant have been shown to be offset by changes in the root architecture that reduce rhizode-

position (Treonis et al. 2007). N fluxes in the soil may also be affected. For example, clover-cyst nematodes have been shown to stimulate the transfer of N from clover to neighbouring grasses (Hatch and Murray 1994; Bardgett et al. 1999b; Denton et al. 1999; Yeates et al. 1999a), potentially affecting plant succession in grasslands. Thus, root herbivores in natural communities can have net positive effects on nutrient mineralization, and soil microbial community structure and functioning (Denton et al. 1999; Grayston et al. 2001; Bardgett and Wardle 2003; Treonis et al. 2005).

Root-feeding insect larvae

Plant interactions with root-feeding insect larvae are as complex as plant-nematode interactions. According to the proverb "the enemy of my enemy is my friend", roots have been shown to actively attract pathogens of insect root herbivores. This mechanism has been demonstrated for the roots of very distantly related plant species, such as the evergreen shrub Thuja (Cupressaceae) (van Tol et al. 2001) and the monocotyledenous Zea mays (Poaceae) (Rasmann et al. 2005), suggesting a wide occurrence among plants. Upon attack by insect larvae, plant roots have been shown to release (E)- β -caryophyllene, a specific volatile that attracts entomopathogenic nematodes of the genus Heterorhabditis (Rhabditidae) (Boff et al. 2001; Rasmann et al. 2005). The nematodes themselves exist in a further obligate symbiosis and employ bacteria of the genus Photorhabdus (Enterobacteriaceae) to kill the insect hosts and to protect the insect corpse against competitors, such as saprophytic microorganisms, bacteriovorous nematodes and scavenging insects. The bacterial symbionts also serve as substrate for growth and reproduction of the nematode. In turn, the Photorhabdus bacteria utilize the nematode as a vector for delivery into another insect hemocoel and to persist outside the insect host (Ciche et al. 2006). This example of a positive feedback interaction vividly illustrates the complexity and high degree of multitrophic coevolution between plant roots, soil fauna and microorganisms.

Thus, roots produce specific volatile signals to attract entomopathogenic nematodes in much the same way as attacked plant leaves have been shown to release volatiles to attract the parasitoids of insect leaf herbivores (Erb et al. 2008; Rasmann and

Agrawal 2008; Dicke 2009). Since plants have to integrate and coordinate the signals and activities from both the below- and aboveground parts, it is not surprising that consumers of plant roots also influence aboveground food webs and plant signaling pathways. In fact, belowground interactions do not stop at the soil surface, but may significantly affect plant performance and food webs of herbivores and their consumers aboveground (Gange and Brown 1997; Tscharntke and Hawkins 2002). Rasmann and Turlings (2007) exposed young maize plants to either root herbivores (Diabrotica virgifera (beetle) larvae) or leaf herbivores (Spodoptera littoralis larvae), or to both herbivores, in the presence of their predators. They found that the parasitic wasp Cotesia marginiventris and the entomopathogenic nematode H. megidis were strongly attracted if their respective host was feeding on a plant, but the attraction was significantly reduced if both insect herbivores occurred together on a plant (Rasmann and Turlings 2007). The emission of root volatile signals was reduced by the double infestation. Although leaf volatiles did not change, the parasitoid wasp was able to learn the differences in odour emissions and showed reduced attraction to the odour of a doubly infested plant (Rasmann and Turlings 2007). Similarly, in a semi-field experiment with mustard plants (Brassica nigra), Soler et al. (2007) demonstrated that root herbivory by the dipteran larvae Delia radicum (Anthomyiidae) affected the behaviour of Cotesia glomerata, a parasitoid wasp on caterpillars of the leaf herbivore Pieris brassicae (Lepidoptera), mediated by changes in plant volatiles. Plants exposed to root herbivory were shown to emit high levels of specific sulphur volatile compounds with known toxicity for insects, combined with low levels of several compounds, i.e. beta-farnesene, reported to act as attractants for insect herbivores. By exploiting root-induced signals to evaluate and select the most suitable host for their offspring, females of the parasitoid C. glomerata preferred to search for hosts and to oviposit in hosts feeding on plants with no root herbivory. Root herbivory on neighbouring plants significantly affected search efficiency of aboveground parasitoids (Soler et al. 2007). Biocontrol activity of parasitoids on aboveground herbivores can, therefore, be influenced by belowground herbivores through changes in the composition of plant volatiles. These studies shed light on the importance of volatile signals in orchestrating above- and belowground plant defences and clearly demonstrate how root herbivory can influence aboveground tritrophic signalling and parasitoid feed-back (van Dam et al. 2003; Bezemer and Van Dam 2005). A review on plant responses to below- and aboveground herbivory is given by van Dam et al. (2003).

Direct plant defence compounds can also be induced by root herbivory. Bezemer et al. (2003) demonstrated that the relative growth rate and food consumption of the herbivorous caterpillar Spodoptera exigua was reduced by more than 50%, on cotton plants exposed to previous root damage by larvae of the beetle Agriotes lineatus, even though plant growth and foliar nitrogen levels were not affected by root herbivory. Exposure to root herbivores resulted in an increase in terpenoid levels in both roots and foliage, demonstrating that root herbivores may change the level and distribution of plant secondary chemistry and thus direct plant defences aboveground (Bezemer et al. 2003). A meta-analysis (Kaplan et al. 2008) indicated that root feeders generally induce strong responses in roots as well as in shoots, whereas leaf feeders tend to induce responses only in the aboveground parts of the plants.

Root herbivores have been shown to affect plant performance both directly and indirectly by their influence on bottom-up and top-down control of aboveground invertebrate herbivores Bezemer et al. 2005) with important consequences for plant community composition (Brown and Gange 1989; De Deyn et al. 2003b; Schädler et al. 2004; van Ruijven et al. 2005). The relationship between plants, their belowground herbivores, and the soil microbial community is likely to be dynamic, depending on plant growth stage, the degree of herbivory and the life-cycle of the herbivore. An overview of the interactions between above- and below-ground plant associated organisms and their biodiversity is given by Bardgett et al. (1998); Wardle (2002); Bardgett and Wardle (2003); De Deyn and Van der Putten (2005).

Rhizodeposition and interactions of rhizosphere fauna with microorganisms on plant roots

In contrast to conventional wisdom, recent evidence suggest that a major part of the soil animal food web strongly relies on the C-inputs from plant roots and less so on the carbon and nutrient inputs via leaf litter (Albers et al. 2006; Larsen et al. 2007; Pollierer et al. 2007), but see Elfstrand et al. (2008). Therefore special attention must be given to the consumers of microorganisms in the rhizosphere, because they are at the base of the soil food web channeling the energy to the higher trophic levels via two distinct routes, the fungal and the bacterial energy channel (Moore and Hunt 1988) and determine the rates of nutrient cycling and the availability of mineral nutrients to plants (Clarholm 1985; Kuikman et al. 1990; Ekelund and Rønn 1994; Laakso and Setälä 1999; Bonkowski 2004).

Interactions of fauna with fungi in the plant rhizosphere

A considerable amount of microbial biomass in soil is contained within the extensive hyphal network of soil fungi. In arable and forest ecosystems fungal hyphae may gain a length of up to 400 and 2,000 m per gram of soil, respectively (Christensen 1989). Not surprisingly fungal feeders are found among all soil animal taxa and have been shown to play a significant role in the release of nutrients to plants (Beare et al. 1995; Bardgett and Chan 1999; Chen and Ferris 1999; Bonkowski et al. 2000a; Gange 2000). Rhizosphere fauna may even serve as a source of nutrients for mycorrhiza (Fig. 2) (Klironomos and Hart 2001; Wilkinson 2008). Some of the most important root symbionts and pathogens are fungi, and apart from the liberation of nutrients soil fauna plays an important role in shaping plant-fungus interactions.

Unfortunately, we know little about fungal defence strategies against fungivores which are probably as complex as bacteria-predator relationships (Kampichler et al. 2004; Scheu and Folger 2004; Scheu and Simmerling 2004; Harold et al. 2005; Bretherton et al. 2006; Tordoff et al. 2006, 2008; Wood et al. 2006).

In multiple choice feeding experiments, fungivores have shown surprisingly similar feeding preferences over a broad range of animal taxa with plant pathogens being among the most preferred fungal diet (Bonkowski et al. 2000c), and mycorrhizal fungi being less attractive (Thimm and Larink 1995; Klironomos and Kendrick 1996; Gange 2000; Sabatini and Innocenti 2001; Bracht Jørgensen et al. 2005). In correspondence with these findings collembola were important for shifting competition between arbuscular mycorrhizal and saprophytic fungi in the rhizosphere of the invasive grass *Cynodon dactylon* (Fig. 2) (Tiunov and Scheu 2005) and significant reductions of fungal plant pathogens have been reported in both laboratory and field studies for protozoa (Tapilskaja 1967; Chakraborty 1983), collembola (Sabatini and Innocenti 2001; Shiraishi et al. 2003) and earthworms (Stephens and Davoren 1997; Clapperton et al. 2001).

There is increasing evidence that fungivores and higher trophic levels in the food web depend in large part on root-derived carbon. This is convincingly exemplified for the best studied group of soil fungivores, the Collembola (Larsen et al. 2007; Ostle et al. 2007). By tracing ¹³C-signatures of grasses in grassland soil Jonas et al. (2007) have shown that depending on soil type and plant species, saprophytic fungi made up between 40-80%, while arbuscular mycorrhizal fungi constituted up to 60% of the collembolan diet, respectively. Similarly, by investigating the stable isotope composition of soil fauna under a C4-plant (maize) growing in an arable field with C3-plant derived organic matter Albers et al. (2006) demonstrated that 40-50% collembolan body carbon was root-derived within a growing season.

It is an important fact that the effects of fungivores on plant performance are strongly density dependent (Harris and Boerner 1990; Klironomos and Ursic 1998; Bakonyi et al. 2002). The fungivores themselves seem to be regulated mainly by resource levels. Steinaker and Wilson (2008) made a detailed field study on the relationships between roots, mycorrhiza and collembola by using a noninvasive minirhizotron camera technique. Collembola correlated well with root production over the whole growing season in grasslands and forests, suggesting a general dependence of fungivores on plant belowground allocation. Strongly negative exponential relationships between both root and mycorrhizal growth with collembola over short sampling intervals indicated that consumers were driving rhizosphere resource levels at short time scales. By severing the hyphal mycorrhizal network from plant roots collembola have been shown to significantly reduce plant carbon allocation belowground and may impair mycorrhizal function (Johnson et al. 2005), but this may not ultimately result in negative effects on plant growth (Setälä 1995). In fact Steinaker and Wilson (2008) demonstrated that annual root and mycorrhizal production were at

a maximum at intermediate collembolan densities with 300–700 and 600–1,500 ind. m^{-2} , in grassland and forest soils, respectively. Predators at higher trophic levels have been shown to regulate population densities of fungivores, thus channelling rootderived energy higher up the food chain. The predatory mite Hypoaspis aculeifer which is attracted to the fungal food sources of their collembolan prey by volatiles of the fungus Alternaria alternata (Hall and Hedlund 1999) was shown to regulate population densities of collembola to levels which resulted in maximum microbial respiration (Hedlund and Sjögren Öhrn 2000, Fig. 2). In fact, (Pollierer et al. 2007) demonstrated in a stable isotope labelling study of forest trees that rootderived C was quickly incorporated in high amounts into virtually all decomposer species. These studies suggest that the fungal energy channel in fact consists of two distinct routes: a fast energy pathway linked to plant roots and a slower pathway linked to decomposing organic matter.

Root-derived carbon rapidly enters the soil food web (Fitter et al. 2005; Leake et al. 2006) and since coupling of the fungal and bacterial energy channels via top predators is thought to confer the extraordinary stability of soil food webs (Rooney et al. 2006), the food webs connected with both, mycorrhizal fungi and rhizosphere bacteria seem crucial for soil food web functioning.

Effects of collembola on root growth

Soil zoologists have recently begun to pay attention to fauna-induced changes in root architecture. Endlweber and Scheu (2006) investigated the effect of the collembola Protaphorura fimata on growth and competition between Cirsium arvense (creeping thistle) and Epilobium adnatum (willow herb) in a laboratory experiment. Although Collembola did not affect total root biomass they influenced root morphology of both plant species. Roots grew longer and thinner and had more root tips in presence of Collembola. Comparable effects were shown in a subsequent experiment studying competition between clover (Trifolium repens) and the grass Lolium perenne (Endlweber and Scheu 2007). The authors hypothesized that changes in root morphology in presence of collembola were due to collembola-mediated changes in nutrient availability and distribution.

Interactions between bacterivores and bacteria in the rhizosphere

In the rhizosphere of plants, pulses of root-derived carbon (exudates) fuel bacterial growth and activity on and around roots (Kuzyakov et al. 2000; Paterson 2003). Protozoa and bacterivorous nematodes are the major consumers of bacterial production in the rhizosphere, forming the basis of the heterotrophic eukaryotic food web that channels the energy flow via the bacterial energy channel to higher trophic levels in soil.

Although bacterivores are usually small, their abundance, biomass and in particular their turnover in soil is high, suggesting a significant impact on bacterial turnover in the rhizosphere (Venette and Ferris 1998; Christensen et al. 2007). In a comparison of Dutch farming systems, the average biomass and annual production rates of bacterivores under winter wheat (0–25 cm soil depth) were estimated as 16 kg C ha $^{-1}$ and 105 kg C ha $^{-1}$ yr-1, respectively for protozoa and 0.33 kg C ha⁻¹ and 11.6 kg C ha⁻¹ yr⁻¹ for nematodes (Bouwman and Zwart 1994). Consequently, bacteria in the rhizosphere are strongly top-down regulated via grazing by protozoa and nematodes (Wardle and Yeates 1993). From a gross nutrient perspective, the interactions between plants, bacteria and protozoan grazers in the rhizosphere have been described to form a loop: plant exudates stimulate bacterial growth and through grazing on bacteria protozoa liberate nutrients which in turn stimulate plant growth ("microbial loop in soil", Clarholm 1985). In fact, bacterivores have been well known for their plant growth-promoting properties (Ingham et al. 1985; Clarholm 1994; Ekelund and Rønn 1994; Griffiths 1994; Zwart et al. 1994). Recent investigations indicate that the nutrients released from microbial biomass are only a small part of an intimate, but indirect symbiosis of bacterivores with plant roots (Fig. 2). To understand these complex multitrophic interactions between plant roots, bacteria and bacterivore soil fauna we will focus on mechanisms of selective grazing of bacterivores, bacterial defence and resulting changes in microbial community composition with subsequent feed-backs on root growth.

Grazing of bacterivores is not random

Although the interactions between bacteria and protozoa form one of the oldest and most highly

evolved predator-prey systems on earth, predation is a factor rarely included for understanding microbial community structure. In fact, there exists a great diversity of feeding modes of protozoa and nematodes on bacteria, suggesting high competition and distinct niche partitioning of bacterivores (Weisse 2002; Bjørnlund et al. 2006; Blanc et al. 2006) and bacteria evolved sophisticated physical and chemical defence strategies to escape consumption by bacterivores which in their diversity are comparable to the strategies of plants to escape herbivore grazers aboveground (Bonkowski 2004; Huber et al. 2005; Young 2006; Montagnes et al. 2007).

In general, size-selection has been shown to play an important role for predation on bacteria, resulting in distinct shifts in the size and morphology of grazed suspended planktonic cells (Pernthaler 2005; Young 2006). Bacteria in the rhizosphere, however, are organized in surface associated biofilms (Rudrappa et al. 2008). These biofilms are regulated in a population density dependent manner by quorum sensing (Shapiro 1998; Matz et al. 2004a) where chemical defence is probably most important.

It is well known that both, protozoa and nematodes show distinct feeding preferences and different growth rates according to bacterial prey quality (Weekers et al. 1993; Venette and Ferris 1998; Arndt et al. 2003; Newsham et al. 2004; Blanc et al. 2006; Pickup et al. 2007), but only recently have studies begun to reveal the different roles of bacterial toxin production in defence of predators (Köthe et al. 2003; Matz et al. 2004b; Matz and Kjelleberg 2005; Jousset et al. 2006). Species-specific differences in bacterial consumption depend on the general feeding mode and size of the buccal cavity, the numbers of bacteria ingested, and the ability of bacterivores to digest the prey. For example, high food selectivity appears imperative for small flagellates which successively ingest only single bacteria, (Boenigk and Arndt 2002). Some nematodes have been shown to sense bacterial quorum sensing signals and learn to avoid well-defended colonies (Beale et al. 2006; Köthe et al. 2003), while some species of bacteria-feeding nematodes exhibit stronger food preferences (e.g. monhysterids) than others (e.g. Panagrolaimus) (De Mesel et al. 2004). In certain nematode taxa a sclerotized culticular lining of the terminal bulb serves to grind food particles (Munn and Munn 2002). Due to this mechanical comminution, nematodes seem able to thrive on bacteria undigestible for protozoa (Bjørnlund et al. 2006). However, non-selective feeding bears a cost. In a study using antibiotic-producing Pseudomonas fluorescens and non-toxic mutants in rhizosphere systems, Jousset et al. (2009) found that the amoeba Acanthamoeba castellanii was able to keep up high population densities even at high densities of toxinproducing bacteria by selectively preying on the mutants. The nematode C. elegans in contrast showed high consumption rates of all bacterial strains, even at high densities of toxin-producing bacteria, which produced strongly negative effects on nematode reproduction (Jousset et al. 2009). In more diverse bacterial communities, nematode predators may even benefit from P. fluorescens in the rhizosphere. Germinating pea seedlings had a nematicidal effect on C. elegans which was reversed by inoculation with P. fluorescens strains, suggesting that the nematicidal compounds were metabolised by the introduced bacteria (Brimecombe et al. 2000).

Grazing-induced shifts in rhizosphere bacterial community structure and feed backs on root architecture

Predation is a major factor influencing rhizosphere bacterial community structure and function (Blanc et al. 2006; Murase et al. 2006). Microbivores enhance microbial turnover, carbon transfer and nutrient recycling in soils out of proportion to their own biomass with significant feedbacks on root growth and plant performance. Predators will affect the fitness of bacteria at the individual level by selective feeding on non-toxic cells, and at the group level by preferentially consuming bacteria from populations containing few toxin producing bacteria.

More detailed studies have now shed light on the complex mechanisms by which certain bacteria thrive under grazing and have identified some of the key traits.

The formation of biofilms is a quorum-sensing regulated key trait in the defence against bacterivores and it is interesting to note that plant roots have been shown to interfere with bacterial communication in the rhizosphere (Bauer and Mathesius 2004). A well described example is the formation of biofilm by *P. aeruginosa* in response to protozoan grazing. Within the first 3 days, the bacteria form microcolonies that

are physically protected from flagellate predators. At a later state, a mature biofilm forms and quorum sensing regulated toxins are released. These toxins are possibly targeting amoebae that often arrive to the scene later than flagellates in the course of a natural decomposer succession (Matz et al. 2004a; Weitere et al. 2005). This pattern indicates that protection against grazers for individual strains of bacteria may have developed to match the most likely succession of bacterial feeders. The experimental results suggested that the competitive success of a bacterial strain depended on its ability to cope with the prevailing bacterial predator.

In the rhizosphere, fluorescent pseudomonads are important and common root colonizers which increase their competitiveness by producing a broad array of secondary metabolites which inhibit competitors and repel predators (Haas and Keel 2003; Jousset et al. 2006, 2008). These toxins often also inhibit plant pathogens, making pseudomonads potent biological control agents in agricultural systems (Haas and Defago 2005; Siddiqui et al. 2005). P. fluorescens produces the phenolic antifungal metabolite 2,4diacetylphloroglucinol (DAPG) (Keel et al. 1992; Maurhofer et al. 2004), which Jousset et al. (2006) identified as being also the most potent toxin conferring grazing resistance against protozoan predators. Recently we have shown that P. fluorescens Q2-87 responded to the addition of A. castellanii by increasing DAPG production (Fox, Bonkowski and Phillips, unpublished) (Fig. 3). A sterile-filtered rinse of an overnight culture of amoebae in mineral water also stimulated *P. fluorescens* Q2-87 to significantly increase its toxin production. These results demonstrate that P. fluorescens Q2-87 was able to sense the presence of the amoebae and up-regulate DAPG production in anticipation of the predators (Fig. 4).

Toxic exoproducts not only protect bacteria by repelling grazers, but result in prey-switching of predators towards more palatable prey (Jezbera et al. 2006; Liu et al. 2006). For example, Jousset et al. (2008) introduced *gfp*-tagged *P. fluorescens* CHA0 or an isogenic bacterial mutant defective in secondary metabolite production to a complex bacterial community in the rhizosphere of rice. Comparing the competitive outcomes between *P. fluorescens* CHA0, a biocontrol strain with antifungal activity, and its mutants in absence and presence of the amoeba *Acanthamoeba castellanii* clearly demonstrated that



Fig. 3 Numbers of bacteria (cfu / ml) (a) and parallel production of the metabolite 2,4-diacetylphloroglucinol (DAPG) (both amount per bacterial cell (b) and total amount produced (c)) by the bacterial strain *Pseudomonas fluorescens* Q2-87 during 20 h of growth (Control) or in response to the addition of 1×10^4 *Acanthamoeba castellanii* ml⁻¹ (10 K amoebae/ml). Note that numbers of bacteria generally did not significantly change in the presence of amoebae. Asterisks indicate significant differences between bacteria and bacteria + amoeba treatments (**P*<0.05; ***P*<0.01) (Phillips, Fox and Bonkowski, unpublished)

the biocontrol strain *P. fluorescens* CHA0 was not only rejected by the protozoan predator but doubled in numbers because their bacterial competitors were preferentially consumed. In addition, growth-limiting



Fig. 4 Production of the metabolite 2,4-diacetylphloroglucinol (DAPG) by the bacterial strain *Pseudomonas fluorescens* Q2-87 after 20 h growth in treatments with (**a**) bacteria only (Bacteria), (**b**) in response to a sterile-filtered supernatant (rinse) of an axenic culture of *Acanthamoeba castellanii* kept for 24 h in mineral water (Bacteria + Amo Rinse), (**c**) in response to the addition of $1 \times 10^3 A$. *castellanii* ml⁻¹ and (**d**) in response to the addition of $1 \times 10^4 A$. *castellanii* ml⁻¹. Asterisks indicate significant differences between bacteria and amoeba treatments (*P<0.05; **P<0.01) (Phillips, Fox and Bonkowski, unpublished)

nutrients released from the protozoa will further benefit growth of the toxin producing strain (Griffiths 1994). Thus grazing-resistant bacteria will gain a threefold benefit by avoiding predation losses, elimination of competitors and by having more resources at their disposal. These results reveal a basic principle how specific rhizosphere bacteria consistently gain a competitive edge over less defended bacterial taxa in the presence of bacterivores.

Microorganisms in soil are generally limited by the availability of low-molecular weight carbon compounds and rhizodeposition plays a crucial role as energy source in the coupling of plant and microbial productivity (Paterson 2003). With this in mind let us consider that *P. fluorescence* has also been noted to stimulate root branching (Beyeler et al. 1999; De Leij et al. 2002). Since root tips are the major sites of root exudation, grazing-resistant bacteria might have evolved mechanisms to gain carbon from plant roots and nutrients via their interaction with bacterivores at the same time.

This view corresponds well with contemporary theory on rhizosphere interactions. In their conceptual review Phillips et al. (2003) introduced an evolutionary view on rhizosphere interactions and assumed that during the colonization of land, plants would have benefited from preexisting associations between soil microorganisms and their consumers. Many rhizosphere bacteria are known to manipulate plant exudation and root branching by the release of hormones (Spaepen et al. 2007) and other signal molecules (Phillips et al. 1999, 2004; Dakora and Phillips 2002; Joseph and Phillips 2003) but rhizosphere bacteria are inextricably linked with their consumers. Therefore interactions with the microbial rhizosphere food web have to be considered to gain a deeper mechanistic understanding of the evolutionary forces shaping microbial rhizosphere interactions. Plant roots can be viewed as a source and receptor of molecular signals for mutualistic organisms (microbes and their consumers) and there are genetic 'control points' at which interactions between organisms (including the plant) determine the outcome of the interaction (Phillips et al. 2003). Such a 'control point' is the signalling between exudates-bacterial grazers-bacteria-plant root growth as has been postulated by Bonkowski (2004).

Bonkowski and Brandt (2002) demonstrated strong growth-stimulating effects of amoebae on the root system of garden cress (Lepidium sativum). The numbers and length of first order lateral roots increased four- and fivefold, respectively in treatments with amoebae. A concomitant proportional increase in auxin-producing bacteria led Bonkowski and Brandt (2002) to suggest that specific plant growth-promoting bacteria were favoured by amoebae and stimulated root growth which allowed more nutrients to be absorbed, but would also increase exudation rates, thereby further stimulating bacteriabacterivore interactions. Thus a mutual feedback exists between plant roots, bacteria and bacterivores. Several studies with grasses, cereals, forbs and tree seedlings have confirmed a strongly stimulating effect of amoebae on the number and length of lateral roots (Jentschke et al. 1995; Kreuzer et al. 2006; Herdler et al. 2008; Somasundaram et al. 2008). The increase in laterals plays a crucial role in plant development because they form the scaffold for the architecture of the branched root system (Malamy and Benfey 1997) and enhance root uptake of nutrients released by protozoa (Bonkowski et al. 2000b; Somasundaram et al. 2008). In line with this concept, it has been found that the presence of bacterial-feeding nematodes increased the total amount of organic-C exuded by



Fig. 5 A perspective on methods in "Rhizosphere Molecular Ecology" to detect molecular control points in rhizosphere food webs. In plants, apart from mapping changes in (root) morphology and physiology, changes in the regulation of gene expression are crucial to uncover the specific pathways involved in plant-microbial-faunal interactions. Subsequently mutants silenced in specific pathways are being used to verify the functional significance of the mechanisms involved. Proteomics and metabolomics in parallel with stable isotope labelling provide means to check for the transcription and expression of specific plant-derived signaling cascades. A broad spectrum of methods allows the analysis of changes in microbial biofilms on roots at different levels of complexity. Denaturing Gradient Gel Electrophoresis (DGGE), Terminal Restriction Fragment Length Polymorphism (T-RFLP) analysis or Phospholipid Fatty Acid (PLFA) profiling are some methods

roots of *Brassica napus* almost 3-fold over bacteria only controls (Sundin et al. 1990). The positive feedback effects of bacterial feeding nematodes on bacterial biomass and activity varies with the nematode species and population size. *Cruznema tripartum*, for example, increased bacterial biomass and activity approximately 4-fold while *Acrobeloides bodenheimeri* was responsible for only a 2-fold increase (Fu et al. 2005). A future goal therefore must lie in the identification of bacterivore taxa most important for plant growth promotion.

In soil with greater populations of bacterial-feeding nematodes, either the native soil population or added *C. elegans*, tomato plants developed a more highly branched root system with longer and thinner roots accompanied by an increase of soil auxin content, such as indole-acetic acid (IAA) and an altered microbial

often used for a global assessment of microbial diversity. Fluorescence in situ Hybridization (FISH) with phylum-specific probes gives quantitative data on the spatial arrangement of micoorganisms on roots, whereas Community Level Physiological Profiles (CLPP), FISH or microarrays on functional genes or reporter bacteria are sensitive methods to monitor functional changes in microbial consortia along roots. Stable isotope studies are increasingly used to quantify trophic interactions with the soil fauna, but model organisms (e.g. the bacterial-feeding nematode *Caenorhabditis elegans*) already allow the testing of more subtle interactions (e.g. attraction or stress responses) of rhizosphere fauna to plant- and microbial signals (metabolites and volatiles) by using mutants (e.g. knock out or *gfp*-reporter) or measuring gene expression (e.g. micro-arrays, quantitative real-time PCR)

community structure. Bacterial-feeding nematodes may have affected plant growth by stimulating hormone production through grazing-induced changes to the soil microbial community (Mao et al. 2006, 2007), suggesting corresponding mechanisms of nematodes and protozoa (Bonkowski and Brandt 2002). The role of IAA in microbial and microbial-plant signaling have been reviewed by Spaepen et al. (2007) but the inclusion of bacterial grazers adds another level of interaction. The feedback between bacterial-feeding fauna and IAA producing bacteria and root growth maybe strongest with young plants, as the interaction with the microbial community seems to diminish with plant age (Vestergård et al. 2007).

We suggest that significant progress will be made in understanding the molecular and genetic basis of the interactions involving signaling compounds in the rhizosphere and how microfauna mediate and even control these outcomes (Fig. 5). However, not all plant cultivars are similarly responsive to bacterivores, Somasundaram et al. (2008) found a general strong growth increase of rice in the presence of *Acanthamoebae*, but some rice cultivars did not respond at all to protozoa. In particular upland and lowland Japonica rice cultivars differed strongly in their response to the presence of amoebae, suggesting that during rice breeding some essential genes involved in the signalling between rhizosphere bacteria or bacterivores with plant roots were lost. Similar findings have been made with maize (R. Koller, personal communication).

Moreover, plants exert species specific effects on the composition of root colonizing bacteria (Chanway et al. 1991; Stephan et al. 2000; Wieland et al. 2001), and rhizosphere populations of bacterial-feeding protozoa and nematodes seem partly dependent on the plant species (Henderson and Katznelson 1961; Geltzer 1963; Griffiths 1990; Brimecombe et al. 2000). Venette et al. (1997), for example, observed significant increases in bacterial-feeding nematode abundance in the rhizosphere of *Crotalaria juncea* (sun hemp) and *Vicia villosa* (vetch) but not *Tagetes patula* (marigold), *Eragrostis curvula* (love grass) or *Sesanum indicum* (sesame) compared with bulk soil in a pot experiment.

In view of these findings, it seems crucial to narrow down specific plant traits, and ultimately genetic rhizospere control points (*sensu* Phillips et al. 2003) interacting with the rhizosphere microbial food web for plant breeding to improve the management of nutrient availability in soils (Phillips and Streit 1998; Rengel and Marschner 2005; Joshi et al. 2007).

Soil fauna as vectors of rhizosphere microorganisms

Since microorganisms are not very mobile in soil, it has been suggested that the soil fauna plays important roles as vectors of microbial symbionts in rhizosphere.

Nematodes seem particularly important in spreading bacteria around the rhizosphere. Nematodes can defaecate 30–60% of ingested bacteria in a viable form (Chantanao and Jensen 1969) and can harbour and protect bacteria from adverse environmental conditions (Caldwell et al. 2003). They are also able to carry bacteria and fungal spores externally, adhering to their cuticular mucilage. It is well known that on an agar plate, for example, one can follow the trails of where nematodes have been from the bacterial colonies that subsequently grow there (Young et al. 1996). A recent finding that legume roots, by emitting specific volatile signals, recruit bacterivorous nematodes for their inoculation with rhizobia is again testimony of the so far unnoticed, but fundamental role of signal exchange between roots and soil fauna. Horiuchi et al. (2005) showed the transfer of Sinorhizobium meliloti by C. elegans to the roots of the legume Medicago truncatula in response to the plant-released volatile dimethylsulfide that attracted the nematode to the roots. Bacterialfeeding nematodes therefore, may significantly foster the initiation of the N-fixing symbiosis in legumes, but they have also been repeatedly shown to spread plant growth-promoting bacteria. For example in mushroom cultures, C. elegans has been shown to feed selectively on a biocontrol species of Pseudomonas in preference to plant pathogenic Pseudomonas species and so reduced the incidence of bacterial blotch by spreading the antagonistic species (Grewal 1991). Rhizosphere colonisation of seed applied biocontrol agents was substantially increased by bacterialfeeding nematodes (Knox et al. 2003, 2004) and the bacterial-feeding Diplogaster iheritieri preferred to feed on growth promoting rhizobacteria in laboratory tests and it was suggested that it could move viable cells around plant roots and enhance plant growth in the field (Kimpinski and Sturz 1996).

Microarthropods have been shown to disseminate viable spores of ectomycorrhizal and arbuscular mycorrhizal fungi (Lilleskov and Bruns 2005; Seres et al. 2007), and they are potential vectors of entomopathogenic and saprophytic fungi (Dromph 2003; Renker et al. 2005). But Gormsen et al. (2004) showed that earthworms and collembola did not affect the spread of AM fungi over a distance greater than 20 cm. Although the dispersal range of microbes by soil fauna might be quite limited, this distance seems not without significance in respect to the tiny size of microorganisms and microbial competition within the tight network of roots in dense stands of established vegetation. Similarly Rantalainen et al. (2004) demonstrated in a laboratory study an important role of enchytraeids in spreading saprophytic fungi between habitat patches through corridors, but in a successive field study it was shown that most fungi had quite good dispersal abilities via hyphal growth independent of soil faunal activity (Rantalainen et al. 2005). At present, evidence suggests nematodes as being important vectors of bacteria, whereas fungivores appear to have more important roles as consumers than as vectors of fungi in the rhizosphere.

Rhizosphere macrofauna: new functional roles of earthworms

Due to their important function in the acceleration of decomposition by physicochemical processes, the role of earthworms is usually considered important in long-term processes such as decomposition of litter materials (Scheu 1993; Brussaard 1998; Schulman and Tiunov 1999). It would be incorrect, however, to assume that earthworms solely affect plant performance by enhanced liberation of nutrients. For example, humus compounds released from earthworm worked soils have been shown to exert hormone-like effects (Nardi et al. 1994; Muscolo et al. 1999; Zandonadi et al. 2007) and recent studies provide convincing evidence that earthworms can induce subtle host-mediated changes that determine the disposition of plants to herbivore attack (Scheu et al. 1999; Wurst and Jones 2003).

For example, Blouin et al. (2005) found that presence of earthworms strongly increased the tolerance of rice to root-feeding nematodes. Although earthworms had no direct effect on nematode population size, the detrimental effects of nematodes on root biomass and photosynthesis of rice disappeared in the presence of earthworms. Since the expression of three stress-responsive genes in leaves (coding for lipoxygenase, phospholipase D and cysteine protease) was modulated in presence of earthworm activity, Blouin et al. (2005) convincingly demonstrated that earthworms triggered the induced defense of rice against root parasitic nematodes.

Similarly, Wurst et al. (2003) investigated the effects of *A. caliginosa* and *O. tyrtaeum* on aphid performance on plants of different functional groups (the grass *Lolium perenne*, the forb *Plantago lanceolata*, the legume *Trifolium repens*) that differed in root morphology and N allocation strategies. Earthworm activity generally enhanced nitrogen mobilization

from litter and from soil. However, the earthwormmediated increase in plant nitrogen uptake differed between plant species. Earthworms enhanced N uptake from litter and soil in all plant species but shoot and root growth only in L. perenne and P. lanceolata. Earthworms increased aboveground biomass and contents of total nitrogen and ^{15}N in both L. perenne and P. lanceolata, and root growth in the grass. Due to the increase in plant nitrogen content one would expect positive effects of earthworms on aphid reproduction (Dixon 1985). But reproduction of M. persicae was reduced on P. lanceolata in presence of earthworms (Wurst et al. 2003), most likely as a result of earthworm effects on plant defense compounds. Wurst et al. (2004) subsequently confirmed that earthworms and organic matter distribution strongly affected the contents of phytosterols in P. lanceolata. Phytosterols serve as precursors of moulting hormones in the diet of herbivorous insects, including aphids (Campell and Nes 1983). Phytosterols and iridoid gylcosides were positively correlated with plant nitrogen content, suggesting that the production of defense compounds might be indirectly driven by increased N availability as a result from earthworm activity.

These results demonstrate that plant vigour and susceptibility to insect herbivores are driven by a complexity of interactions with soil macrofauna, reaching far beyond the standard view on nutrient liberation (Bonkowski et al. 2000a; Scheu and Setälä 2002).

Conclusions and directions for future research

This review highlights the importance of the many recent findings on significant indirect interactions between soil fauna, rhizosphere microorganisms and plant roots. Even "direct" feeding relationships between plant roots and herbivores are not as simple and straight forward as seen in the past. The exchange of chemical signals which formerly was only considered important between roots and closely associated microbial symbionts now appears common between all rhizosphere players on all levels of interaction. The arms race between plants and herbivores belowground seems as highly coevolved as plant interactions with the aboveground food web, and both are intricately connected. Bacteria and bacterivores mutually cooperate with significant effects on root architecture, but there is considerable uncertainty to which degree

plants are in control of these processes. Animal behaviour has been intensively studied for decades. Now it becomes apparent that plant roots "behave" in much the same sense (Dudley and File 2007). Upon specific key signals, roots have been shown to emit signal compounds to communicate with soil organisms, including fauna. The signals are used to attract entomopathogenic nematodes against root herbivores, or bacterivores for root inoculation with beneficial rhizosphere bacteria, or to disturb communication among potential harmful soil bacteria, but also to manipulate plant belowground allocation. Undoubtedly more such examples will be discovered soon, and the challenge will be to identify the genetic control points which determine these interactions and to determine how the interactions between multiple plant symbionts are orchestrated (Fig. 5).

In view of the increasing efforts to increase crop resistance to agricultural pests by transformation of crops with foreign genes, the study of natural plant defence systems has a practical application. However, lack of consideration by scientists and plant breeders of root ecology has already led to the loss of genes important in root-fauna communication (Rasmann et al. 2005; Somasundaram et al. 2008). In the light of these results, it seems timely to consider the study of rhizosphere ecology as a multidisciplinary task to improve plant breeding efforts.

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