

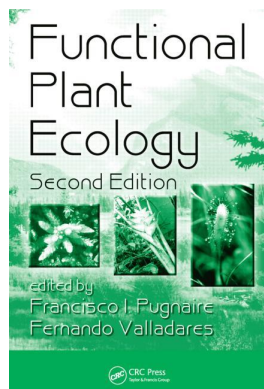
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19 Biodiversity and Interactions in the Rhizosphere: Effects on Ecosystem Functioning

Susana Rodríguez-Echeverría, Sofia R. Costa, and Helena Freitas

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INTRODUCTION

Understanding the implications for ecosystem function of soil biodiversity and processes is the last frontier in terrestrial ecology. Research on this field is lagging behind aboveground studies mainly because soil is such a complex matrix. Some soil processes, such as decomposition and mineralization of organic matter and biogeochemical cycles, have long been recognized as key components of ecosystems. In addition, recent studies in natural ecosystems have revealed that organisms from the rhizosphere—plant pathogens, parasites, herbivores, and mutualists—have a significant impact on natural plant communities (Van der Putten and Peters 1997, Klironomos 2002, De Deyn et al. 2004). The rhizosphere is a hot spot of soil biodiversity driven primarily by plant roots. The exudations of these roots provide nutrients for microbes, and may also attract or repel some organisms (van Tol et al. 2001, Rasmann et al. 2005). The interactions between plants and rhizosphere organisms can range from mutualistic to pathogenic, including direct competition for resources. In general, nitrogen-fixers and mycorrhizal fungi enhance plant growth and survival, and pathogenic fungi and root-feeders

decrease plant fitness. These and other interactions with nonmycorrhizal fungi, rhizosphere bacteria, protozoa, and viruses can also modify the effect of soil-borne pathogens, herbivores, and mutualists in plant populations.

In this chapter, we briefly describe the main groups of organisms that are closely associated with plant roots and their effect on plant growth and survival. We also review the biological and chemical interactions that occur in the rhizosphere and how this changes the outcome for the associated plant. The last part of the chapter is devoted to the implications of these interactions for ecosystem functioning.

MAJOR GROUPS OF ORGANISMS AND DIRECT INTERACTIONS WITH PLANTS

This section focuses on four groups of organisms that live in very close association with plant roots and are thought to have the greatest impact on plant performance and ecosystem processes (Figure 19.1). In focusing on particular groups of organisms, others are necessarily left out, even though they may play an important role. We, however, refer to these when appropriate throughout this chapter. Certainly, a plant is exposed to more than one of these groups at any time and the interactions between them can change the outcome for the plant. This is also discussed in the following section.

SYMBIOTIC NITROGEN-FIXERS

Nitrogen is the most limiting nutrient for plant growth in terrestrial ecosystems. Although molecular nitrogen is very abundant in the atmosphere, eukaryotes have not evolved the ability to fix atmospheric nitrogen into ammonia (Eady 1991). In fact, this capacity is limited to a number of bacteria and archaea species with very different life strategies. Some of them are free-living in soil and water (i.e., *Azotobacter*, *Clostridium*), others occupy the rhizosphere, phyllosphere, or intercellular spaces of plants (i.e., *Azospirillum*, *Azoarcus*, *Gluconacetobacter*), and still others are highly specialized symbionts (like *Frankia*, associated with species of *Alnus*, *Myrica*, *Ceanothus*, *Eleagnus*, and *Casuarina*; and legume symbionts collectively known as rhizobia).

The symbiotic diazotrophs are the main contributors to biological nitrogen fixation in terrestrial ecosystems. Research has focused mainly in the legume symbionts because of the importance of this plant family in agriculture. However, they also play a key role in natural

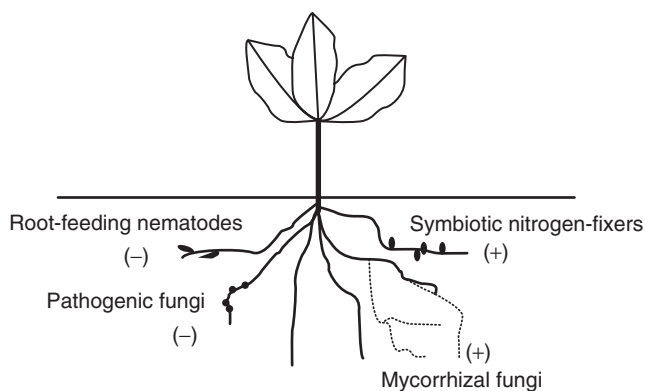


FIGURE 19.1 Rhizosphere organisms that have the greatest impact on plant performance. Positive interactions are indicated by (+); negative interactions are indicated with (-).

ecosystems because of the wide distribution of legumes in temperate, tropical, and arid regions (Lafay and Burdon 1998, Ulrich and Zaspel 2000, Rodríguez-Echeverría et al. 2003). Most of the known legume symbionts belong to the order Rhizobiales, but there are also some species that nodulate legumes in the order Burkholderiales. Currently all the species within the genera *Rhizobium*, *Sinorhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium*, and *Allorhizobium* have the ability to nodulate legumes and fix nitrogen. Some other genera, like *Ensifer*, *Blastobacter*, *Burkholderia*, and *Ralstonia*, contain both legume symbionts and nonsymbiotic species (Sawada et al. 2003). Nevertheless, the taxonomy of the bacterial symbionts of legumes is under revision and could result in the amalgamation of some genera. The ability to nodulate legumes and to fix nitrogen is encoded in mobile genetic elements such as transmissible plasmids or conjugative transposon-like sequences. The taxonomical diversity of legume symbionts might therefore be explained by the horizontal transfer of those elements between soil bacteria.

The specificity of the association between legumes and their bacterial symbionts depends on a very fine molecular communication between the plants and the rhizobia. Nodulating bacteria respond to the flavonoids produced by legume roots by producing *N*-acylated oligomers of *N*-acetyl-D-glucosamine, known as Nod-factors, which initiate the physiological changes in the host roots leading to nodulation. The basic structure of Nod-factors has variations that are dependent on each strain or species and determine the host-specificity (Perret et al. 2000). Although the symbiotic association between legumes and their symbionts was considered to be highly specific, it is now believed that this only applies to the tribes Trifolieae, Viceae, and Cicereae (Perret et al. 2000). Symbiotic promiscuity is common in nature and could be an advantage for colonizing new soils. In fact, some studies suggest that highly promiscuous legumes are successful invasive species (Richardson et al. 2000, Ulrich and Zaspel 2000). The association is crucial for the establishment and growth of many pioneer leguminous species. Soil enrichment in nitrogen due to these associations subsequently facilitates the growth of other plant species, thus promoting plant succession. In turn, increasing levels of nitrogen can also lead to the displacement of other species promoting spatial heterogeneity. This is, therefore, a key symbiosis for the functioning of terrestrial ecosystems.

MYCORRHIZAL FUNGI

A mycorrhiza is a symbiotic, nonpathogenic, permanent association between a plant root and a specialized fungus, both in the natural environment and in cultivation. This is the most common and ancient symbiotic association to be found in plants and evolved with the colonization of land by primitive plants (Brundrett 2002). In this symbiosis, plants exchange carbohydrates for mineral nutrients—mainly phosphorus, nitrogen, potassium, calcium, and zinc—retrieved by the fungal mycelium from large soil volumes. Mycorrhizal fungi are also involved in many other processes such as plant protection against abiotic stresses (Allen and Allen 1986) or root pathogens and herbivores (Newsham et al. 1995, de la Peña et al. 2006); the degradation of complex and organic molecules, making essential nutrients available to the plant (Cairney and Meharg 2003); and the synthesis or stimulation of plant-growth hormones like auxins, cytokinins, and gibberellins. However, not all mycorrhizal associations are positive. When one of the partners does not receive a quantitative benefit, they can become exploitative. In fact, the mycorrhizal symbiosis is in the mutualism–parasitism continuum, depending on the identity of plant and fungus species and abiotic factors (Johnson et al. 1997).

The classification of mycorrhizas is primarily based on the morphology and physiology of the association. There are three main morphological groups of mycorrhizas: (i) the ectomycorrhizas, with fungal mycelia surrounding the root and penetrating the intercellular spaces; (ii) the endomycorrhizas (which can be either arbuscular or ericoid mycorrhizas), in which the

mycelium does not coat the root, yet there is an intimate contact between the fungi and the root through structures inside the root cells that are specialized for nutrient exchange and storage; and (iii) the intermediate types that share characteristics with both ecto- and endomycorrhizas, and include the ectendo-, arbutoid, monotropoid, and orchid mycorrhizas. The most widespread mycorrhizal associations by far are the ectomycorrhizas and the arbuscular mycorrhizas.

The ectomycorrhizal association occurs in 140 genera of seed plants belonging to the families Betulaceae, Fagaceae, Pinaceae, Rosaceae, Myrtaceae, Mimosaceae, and Salicaceae. Although there are much fewer species of ectomycorrhizal plants than of endomycorrhizal plants, the association is ecologically significant, as it involves the dominant species of boreal, temperate, and many subtropical forests. The fungi involved in this symbiosis are almost exclusively basidiomycetes and ascomycetes. Common genera of Basidiomycetous fungi include both hypogeous and epigeous genera such as *Amanita*, *Boletus*, *Leccinium*, *Suillus*, *Hebeloma*, *Gomphidius*, *Paxillus*, *Clitopilus*, *Lactarius*, *Russula*, *Laccaria*, *Thelephora*, *Rhizopogon*, *Pisolithus*, and *Scleroderma* (Smith and Read 1997).

The arbuscular mycorrhizas are ubiquitous, occurring over a broad ecological range with almost all natural and cultivated plant species. With few exceptions, species from all angiosperm families can form endomycorrhizal associations. A few gymnosperms such as species of *Taxus* and *Sequoia* also show infection. Phylogenetically, these fungi are the oldest symbionts infecting also bryophytes and pteridophytes. The fungi that form these associations (arbuscular mycorrhizal fungi or AMF) belong to the Glomeromycota phylum (Schüßler et al. 2001) and are obligate symbionts. Little specificity has traditionally been recognized in this association, but more recent studies have shown a higher genetic and functional diversity than previously estimated (Sanders et al. 1996, Helgason et al. 2002, Munkvold et al. 2004). The presence of AMF can increase plant diversity and ecosystem productivity (Grime et al. 1987, van der Heijden et al. 1998). This could be explained by the high functional diversity of AMF and the specificity of the outcome of the interaction with different plant species. A rich AMF community is more competent at exploiting soil resources and it is more likely to benefit a wider range of plant species (van der Heijden et al. 1998). There is, however, an alternative explanation for the positive correlation between AMF and plant diversity, and that comes from the observation that AMF can also have a detrimental effect on plant growth. According to this hypothesis, a richer fungal community increases plant diversity because no plant has a greater advantage with all AMF at the site (Klironomos 2003).

In some circumstances, the absence of mycorrhizal fungi can lead to an increase in plant diversity. This is the case with plant communities that are dominated by highly mycotrophic species, or by one mycorrhizal type, that is, ectomycorrhizal species. The removal of mycorrhizal fungi leads to a decrease of the dominant species and the consequent competitive release of the subordinate species (Connell and Lowman 1989, Hartnett and Wilson 1999).

The external mycelium of mycorrhizal fungi establishes an underground network that links different plants. This fungal network also reduces nutrient losses by sequestering nitrogen, phosphorus, and carbon within their biomass (Simard et al. 2002). Nutrients move within the external mycelium according to fungal needs, but there is also a nutrient transfer between plants through the hyphal network (Simard et al. 2002). Carbon transfers between plants are better known in ectomycorrhizas (Smith and Read 1997), but they also occur through arbuscular mycorrhizas (Carey et al. 2004). The transfer of N and P between live, intact plants has been documented mainly for arbuscular mycorrhizal plants (Simard et al. 2002). The net transfer of nutrients between plants varies with mycorrhizal colonization, soil nutrient content, and the plant physiological status. Therefore, the results obtained in greenhouse studies have been very variable. A high rate of nutrient transfer between plants through the external hyphae of mycorrhizal fungi would have important ecological consequences. For example, nutrient transfer can enhance the establishment and growth of new

seedlings of mycorrhizal plants, allowing a quick recovery after disturbance and also affecting plant competition. Little is known about the specificity of this mechanism in natural systems, whether some plants species are mainly donors or sinks of nutrients, or whether the transfer is species-specific.

PATHOGENIC FUNGI

The research about soil fungi that have deleterious effect on plant growth has historically focused on agricultural systems for obvious economic reasons. Only in the last two decades have ecologists started to explore the diversity and the role of pathogenic fungi in natural ecosystems.

The majority of soil fungal pathogens that attack plants are ascomycetes. There are many genera of pathogenic ascomycetes that have been identified from plants in agricultural systems and later isolated from natural systems. In coastal sand dune studies that focused on the degeneration of pioneer plant species, *Verticillium* and *Fusarium* species were isolated from declining stands of the dune grass *Ammophila arenaria* in The Netherlands (Van der Putten et al. 1990); and species of *Fusarium*, *Cladosporium*, *Phoma*, and *Sporothrix* were involved in the degeneration of *Leymus arenarius* in Iceland (Greipsson and El-Mayas 2002). Another example is the dieback of the endemic Hawaiian tree koa (*Acacia koa*), a keystone species in upper-elevation forests, caused by the systemic wilt pathogen *Fusarium oxysporum* f. sp. *koae* (Anderson et al. 2002). Other root rot fungi play a significant role in the dynamics of temperate forests by killing big trees and opening gaps in the forest. A well-studied example is the basidiomycete *Phellinus weirii* that attacks specifically *Pseudotsuga menziesii* in temperate forests of North America (Hansen 2000).

There is also a fungal-related group of organisms that attacks plant species in both natural and agricultural systems: the oomycotan genera *Pythium* and *Phytophthora*. Species of *Pythium* are responsible for the mortality of seedlings in tropical and temperate forests (Augsburger 1983, Packer and Clay 2000, Reinhart et al. 2005, Bell et al. 2006). The proximity to parent trees causes a high mortality of new seedlings, which is correlated with the build-up of pathogenic *Pythium* spp. on the rhizosphere of the parent trees.

Among the *Phytophthora* species isolated in natural systems, we would highlight *Phytophthora cinnamomi*, identified as the cause of die-backs of native tree species in North America (Zentmyer 1980), Australia (Wills and Kinnear 1993), and Southern Europe (Brasier et al. 1993). In North America, the most affected species were *Pinus echinata*, *Abies fraseri*, and *Castanea dentata*. In Australia, it has caused the sudden death of plants belonging to more than 20 genera including *Acacia*, *Banksia*, *Eucalyptus*, and *Grevillea* species. In Southern Europe, this species, in combination with other *Phytophthora* spp., has been suggested to contribute to oak decline since the beginning of the twentieth century.

The impact of pathogenic fungi and oomycetes depends not only on the life-stage of the plants, but also on the specificity, virulence, and overall life history of the pathogen. Gilbert (2002) classifies the fungal pathogens of noncrop plants as (a) seed decay, (b) seedling diseases, (c) foliage diseases, (d) systemic infections, (e) cankers, wilts, and diebacks, (f) root and butt rots, and (g) floral diseases, and these are good descriptors of the many ways these organisms can interfere (and interact) with plants. The impact that fungal pathogens can have on plant populations is thought to contribute to plant genetic diversity, species diversity, and succession in natural systems (Gilbert 2002, Van der Putten 2003).

NEMATODES

Nematodes are the most abundant metazoans. Some 20,000 species of nematodes have been described, a small proportion of the estimated 10^5 or 10^6 likely to exist, and they can be found in

any environment where decomposition occurs. In ecological studies, they are usually classified by their feeding habit. Nematodes can be bacterial feeders, fungal feeders, omnivores, or plant feeders (Bongers and Bongers 1998). This is a relatively simplified classification, as other authors consider nematodes to be functionally divided into eight groups (Yeates et al. 1993). In this section, we focus on the plant feeders, a group of nematodes that have specialized mouth structures (stylet) to feed on plant roots. Plant-feeding nematodes are highly specialized obligate parasites that have evolved through close interactions with plants, and this explains the high impacts on the plant populations they attack. According to Stirling (1991), the belowground plant–parasitic nematodes can be subdivided into four different groups: sedentary endoparasites, sedentary semiendoparasites, migratory endoparasites, and ectoparasites.

- Sedentary endoparasites (e.g., *Meloidogyne* spp., *Heterodera* spp.) are completely surrounded and protected by their host's root tissue for most of their life cycle (Stirling 1991). They interact with the plant root to develop permanent and highly specialized feeding sites within the root tissues that act as nutrient sinks (Zacheo 1993).
- Sedentary semiendoparasites (e.g., *Rotylenchulus* spp.) are partially exposed in the root tissue for part of their life cycles, and juveniles and young females feed ectoparasitically, spending much time in the rhizosphere.
- Migratory endoparasites (e.g., *Pratylenchus* spp.) can hatch and develop to maturity inside the root tissue of their hosts, and are rarely found in soil unless their host plant is under stress (Stirling 1991). They do not establish a permanent feeding site, but migrate within roots, causing extensive damage. *Pratylenchus* nematodes have been reported to feed ectoparasitically on some grasses (Timper, personal communication).
- Ectoparasites (e.g., *Xiphinema* spp.) only penetrate root tissue with the stylet; their body is outside the root tissue at all times. Ectoparasites are not protected by roots and feed on epidermal and cortical root tissues (Zacheo 1993).

Sedentary endoparasites and migratory endoparasites are the main nematode groups implicated in disease complexes, or additive effects on disease incidence or severity on the host plant by association with bacteria or fungi (Hillocks 2001). Plant-feeding nematodes can also develop additive and synergistic interactions with pathogenic fungi and bacteria and some (e.g., *Xiphinema*, *Longidorus*) are vectors of plant viruses.

Plant-feeding nematodes and their host plants are involved in a coevolutionary arms race. One of the classical examples of nematode resistance in plants is that of *Tagetes erecta* and *Tagetes patula* (Goff 1936). The research to discover the causes of resistance led to the isolation of various nematocidal polythienyl compounds from *Tagetes* plants, the first of which is thiphene R—terthienyl (Ulenbroek and Brijlloo 1958). It was later discovered that endoroot bacteria in both *T. patula* and *T. erecta* roots produced nematotoxic compounds that reduced nematode populations in soil. These bacteria were successfully transferred to potato, *Solanum tuberosum*, and effectively reduced the numbers of nematode parasites of this plant (Sturz and Kimpinski 2004).

Nematodes can detect (and react to) chemical gradients in soil, and plant metabolites in roots, through their chemoreceptors. A well-illustrated example is that of *Globodera rostochiensis*, an obligate parasite of potato. Nematode eggs exposed to the potato root exudates are stimulated to hatch (Jones et al. 1997). These juveniles increase their activity in response to the exudates, and orientate themselves, following the exudation gradient, to the roots (Perry 1997). Then they invade the roots and alter the physiology of the root cells to form a syncytium on which the nematode feeds.

Entomologists and nematologists have tried to identify semiochemicals (signalling compounds) in the rhizosphere that would help insects and nematodes to locate roots (Perry 1996, Johnson and Gregory 2006). According to the physical soil structure, both volatiles and

water-soluble compounds could be involved, but volatile compounds can potentially travel faster (Young and Ritz 2005). A common molecule to which both nematodes and insects are attracted is CO₂. The main problem with considering CO₂ a semiochemical is that it is ubiquitous in soil, and therefore could only be of potential importance to generalist root herbivores (Johnson and Gregory 2006).

Plant-feeding nematodes are very responsive to changes in vegetation (Korthals et al. 2001), and plant identity greatly influences their population densities (Yeates 1987). Plant-parasitic nematodes can have dramatic effects in agricultural systems, where they cause estimated losses of US\$ 100 billion every year due to yield reductions or overall damage to crops (Oka et al. 2000). There is not much information about this interaction from natural systems (Van der Putten and Van der Stoel 1998). Nevertheless, a disease complex of plant-feeding nematodes and fungal pathogens has been implicated in the degeneration of *A. arenaria* (marram grass) in coastal sand dunes (Van der Putten et al. 1990). If nematode herbivory is low, however, plant growth might be enhanced through changes in the exudation pattern and release of nutrients from damaged roots. These changes promote soil nutrient influx, which increases soil microbial biomass and root growth of the attacked and neighboring plants (Bardgett et al. 1999a,b).

INTERACTIONS IN THE RHIZOSPHERE

In this section, we describe some of the interactions that occur between organisms in the rhizosphere. At this point, it seems important to take a holistic approach, and although we have divided the section into subheadings, all these interactions are likely to occur at the same time, arguably with different ecological importance for different systems. We include here trophic interactions but also other ecological and chemical interactions.

All organisms produce chemicals and respond to chemical release by others, in a vast network of communications (Eisner and Meinwald 1995). Plants themselves are involved in this communication system, although this has only recently been recognized (D'Alessandro and Turlings 2006, Schnee et al. 2006). They constantly release not just primary compounds (CO₂, sugars), but also secondary metabolites through root exudations and leaf volatiles, which are indicative of their physiological state. These can act as cues for their herbivores and for the natural enemies of these herbivores.

The term allelopathy has classically been used to describe strictly plant–plant direct interactions. But these often cannot be dissected out and are very difficult to prove, as the effect of allelochemicals can be modified or influenced by both abiotic and biotic factors (Inderjit and Weiner 2001, Inderjit 2005). Therefore, the allelopathy concept has been extended to encompass microorganism-mediated processes of plant interference (Inderjit and Weiner 2001). An even broader concept is that of the International Allelopathy Society, which includes the effects and activities of not only plants and algae, but also of fungi and bacteria. In this chapter, we refer to the biological, ecological, and behavioral effects of such chemical interactions.

Unfortunately, chemical and biological interactions have mostly been studied separately, despite their intrinsic links. We have tried to reunite them in describing the rhizosphere interactions included in this section, namely belowground plant–plant interactions, the effect of soil organisms on resource availability and uptake in plants, and interactions between the soil organisms previously described.

BELOWGROUND PLANT–PLANT INTERACTIONS

Belowground, plant roots explore the soil heterogeneity and patchiness and compete for nutrient resources (Hodge 2006). This competition effect apparently occurs only between different plants, as recent root physiology studies suggest that plant roots can distinguish

between self and nonself, changing their growth patterns accordingly (Gruntman and Novoplansky 2004). This mechanism should act to avoid competition between roots of the same plant and maximize root exploratory potential.

Plants can interact negatively through the production of phytotoxic compounds. For a recent review on aspects of plant interference see Weston and Duke (2003). As an example, we mention the case of mugwort (*Artemisia vulgaris*), which has been extensively studied. This plant has a range of reported biological activities and its chemical composition has been studied in detail. Mugwort is a ruderal nitrophylic plant, a noxious and highly successful weed that interferes with the growth and development of neighboring plants. Its root leachates act by inducing chemical changes in soil, a process mediated by microorganisms (Inderjit and Foy 1999). Phytotoxicity in mugwort has also been attributed to compounds of the rhizome of this plant which significantly inhibit germination and seedling development of other plants (Onen and Ozer 2002). Incidentally, rhizome compounds also have nematotoxic, including nematocidal, effects (Costa et al. 2003).

RESOURCE UPTAKE AND PARTITIONING

Soil microbes might enhance plant coexistence by resource partitioning (Reynolds et al. 2003). In addition, mycorrhizal fungi increase plant availability of phosphorus and nitrogen from organic and inorganic pools mainly through enzymatic activities (Marschner 1995, Turnbull et al. 1996). The high multifunctional diversity observed for AMF and the specificity of ectomycorrhizal associations might also be related to nutrient partitioning among different plant species. This partitioning has been confirmed for different nitrogen sources in some Australian ectomycorrhizal isolates from *Eucalyptus maculate* (Turnbull et al. 1995) and in AMF isolates studied in vitro (Hawkins et al. 2000). Resource partitioning could also be related to the preferential association with rhizosphere bacteria. For instance, the ability of using molecular nitrogen as a source depends on the association with nitrogen-fixing bacteria. In the same way, the ability of some plants to selectively use ammonium, nitrate, or amino acids as source of nitrogen (McKane et al. 2002) could be related to the differential recruitment of microbial communities in their rhizosphere (Reynolds et al. 2003).

There is evidence that ectomycorrhizal fungi can mobilize complex and organic forms of nitrogen and phosphorus making them available to their plant partners. Ectomycorrhizal fungi can mobilize organic forms of nitrogen from litter and pollen grains transferring them to associated plants (Bending and Read 1995, Northup et al. 1995, Pérez-Moreno and Read 2000, 2001b). The species *Paxillus involutus* can transfer nitrogen and phosphorus from dead nematodes to symbiotic seedlings of *Betula pendula* (Pérez-Moreno and Read 2001a). Furthermore, the hyphae from *Laccaria bicolor* can even act as a predator of springtails, immobilizing the animals, colonizing their bodies, and subsequently transferring nitrogen to the symbiotic seedlings of *Pinus strobus* (Klironomos and Hart 2001).

INTERACTIONS BETWEEN MYCORRHIZAL FUNGI AND SOIL FAUNA

In spite of the great diversity of soil animals, we focused in the previous section on plant-feeding nematodes because they can have a strong impact on plant performance. The description of other soil invertebrates is not within the scope of this chapter but we refer here to some groups that are known to interact, directly or indirectly, with mycorrhizal fungi.

Some of these interactions are positive for the plant, for example, earthworms, isopods, diplopods, and insects can act as vectors of AMF by ingesting hyphal fragments or spores and transporting them in their movements (Gange and Brown 2002). Mycophagous mites, collembolan, and nematodes feed preferentially on nonmycorrhizal fungi, thereby releasing

mycorrhizal fungi from competition with other fungi (Gange and Brown 2002). Soil invertebrates can in theory have a negative impact on mycorrhizal fungi, by disrupting or feeding on the external mycelia, but these interactions have not been shown to have a major impact in natural systems.

It has been proposed that the main benefit that plants obtain from mycorrhizal fungi in natural systems is protection against pathogens and herbivores (Fitter and Garbaye 1994). Root-feeding insects and nematodes can have a serious negative impact on plant growth and performance, and, in general, AMF reduce plant damage by root herbivores, although this effect can be highly variable (Table 19.1). The outcome of the interaction seems to depend on several factors such as soil characteristics and the genotypes of plants, herbivores, and AMF.

TABLE 19.1
Summary of Available Data on the Effect of Mycorrhizal Colonization for Plant Feeding Nematodes and Host Plants in Natural Systems

Nematode Species	Plant Species	Mycorrhizal Fungi Species	Effect on Plant	Effect on Nematodes	Reference
<i>Pratylenchus</i> spp.	<i>A. brevigulata</i>	<i>Glomus etunicatum</i> , <i>Glomus aggregatum</i> , <i>Glomus geosporum</i> , <i>Gigaspora albida</i> , <i>Acaulospora scrobiculata</i> , <i>Acaulospora spinosa</i> , <i>Scutellospora calospora</i>	Positive	Not described	Little and Maun 1996
<i>Heterodera</i> spp. <i>M. incognita</i>	<i>Trifolium repens</i>	<i>Glomus mosseae</i>	Positive	<i>G. intraradices</i> reduced number of nematodes and galls	Habte et al. 1999
<i>Pratylenchoides magnicauda</i>	<i>L. arenarius</i>	<i>Glomus intraradices</i> <i>G. aggregatum</i> <i>Glomus fasciculatum</i>	Positive	Not described	Greipsson and El-Mayas 2002
<i>Paratylenchus microdorus</i> <i>Rotylenchus goodeyi</i> <i>Merlinius joctus</i>		<i>Glomus caledonium</i> <i>G. mosseae</i>			
<i>Tylenchorhynchus gladiolatus</i> <i>Pratylenchus pseudopratensis</i>	<i>Afzelia africana</i>	Six strains of <i>Scleroderma</i> and other native EM	None (Nematodes did not affect plant growth)	None	Villenave and Cadet 1998
<i>Pratylenchus penetrans</i>	<i>A. arenaria</i>	Mixed native inocula of AMF	None (Nematodes did not affect plant growth)	Suppression	de la Peña et al. 2006

Most of the research in this field, especially for natural systems, has been done on root-feeding nematodes.

The presence of AMF can offer plant protection through increased host resistance (Azcón-Aguilar and Barea 1996). Many of the chemicals present in mycorrhizal roots—phenolics, isoflavonoids, terpenoids—can negatively affect root-feeding insects and suppress sedentary nematode parasite reproduction and feeding (Gange and Brown 2002).

Root colonization by AMF also changes the quality of root exudates, an effect that depends on the identity of the fungi. Since root exudates are the main source for microbial activity, these changes would also affect the rhizosphere communities. In some cases, the presence of AMF is correlated with a reduction in the number of pathogens in the rhizosphere and an increase in the number of beneficial organisms (Azcón-Aguilar and Barea 1996). In addition, shifts in root exudates can affect chemotactic attraction of nematodes and egg hatching (Smith and Kaplan 1988).

Mycorrhizal protection against nematodes might occur also through increased host tolerance, because of the improvement in plant health due to an increased uptake of P, Ca, Cu, Mn, S, and Zn (Smith and Kaplan 1988). This protection is only effective if roots are mycorrhizal before they are attacked by the nematodes. In this case, AMF might be considered an extension of the plant that can compensate for plant damage. In agriculture, plants can be preinoculated with mycorrhizal fungi before planting, but in natural communities the outcome of the interaction depends on which organism colonizes the root first (Gange and Brown 2002). AMF might compete with endoparasitic nematodes for space and photosynthates inside plant roots. Competition for photosynthates, especially affecting sedentary nematodes, has received little support from experimental data. Competition for space is well documented, and several studies have shown that both groups of organisms can negatively affect each other, that is, the presence of one reduces infection by the other (Roncadori 1997). Finally, some studies have suggested that *Glomus* can be a weak parasite of the sedentary endoparasite *Heterodera glycines* (Francl and Dropkin 1985).

Most of our understanding about the interaction between mycorrhiza and root herbivores comes from studies with agronomic species. Research on natural systems has mainly focused in coastal dune systems. Greipsson and El-Mayas (2002) found that a commercial AMF inoculum protected the dune grass *L. arenarius* against migratory endoparasitic nematodes. In addition, Little and Maun (1996) showed that mycorrhizal protection of *Ammophila brevigulata* against *Pratylenchus* and *Heterodera* spp. was effective if sand burial occurred simultaneously. De la Peña et al. (2006) demonstrated that AMF can also protect *A. arenaria* through the suppression of *Pratylenchus penetrans* colonization and reproduction. The data suggest that AMF can indeed directly outcompete migratory endoparasitic nematodes in the roots of the plant host. Root colonization by *P. penetrans* and nematode multiplication were drastically reduced by AMF through local mechanisms that were more efficient in premycorrhizal plants. The authors could not detect mutual inhibition between AMF and nematodes, and further conclude that root colonization by AMF was not inhibited by the nematodes.

INTERACTIONS BETWEEN PLANT-FEEDING NEMATODES, LEGUMES, AND BACTERIAL SYMBIONTS

Plant-parasitic nematodes and rhizobia can interact in the rhizosphere and inside the roots of host legumes, although the outcome of these interactions for legumes is not clear. Some studies suggest that plant-feeding nematodes may reduce nodule formation (Villénave and Cadet 1998, Duponnois et al. 1999). But rhizobial strains have also been shown to elicit plant-induced resistance against plant-feeding nematodes (Reitz et al. 2000, Mitra et al. 2004). In addition, ectomycorrhizal fungi can increase plant tolerance to sedentary endoparasitic nematodes like *Meloidogyne javanica* (Duponnois et al. 2000b). There is also evidence of

horizontal gene transfer from rhizobia to plant-feeding nematodes, which might have conferred parasitic nematodes the ability to successfully invade the roots of some plant species (Scholl et al. 2003).

AMF and rhizobial symbionts also interact in the roots of legumes and this can affect plant growth and nutrient content and nodulation. Flavonoids exuded by the legume roots play a key role in the establishment of both rhizobial and mycorrhizal associations. In fact, the establishment of one of the symbiotic partners in the root can change root flavonoid concentrations and stimulate root colonization by the other (Antunes et al. 2006). In general, colonization by AMF enhances nodulation and nitrogen fixation. But the outcome of the interaction varies with the identity of the host plant and the symbiotic partners (Xavier and Germida 2003). Compatible species or strains of AMF and rhizobia interact synergistically to improve N and P content and plant growth, but incompatible strains can also lead to a reduction of the efficacy of nitrogen fixation (Xavier and Germida 2003).

INTERACTIONS BETWEEN NEMATODES AND THEIR MICROBIAL ENEMIES

Research on nematode interactions with other soil microorganisms has increased dramatically in an attempt to develop biologically based control systems in agriculture (Whipps and Davies 2000). Nematode natural enemies include fungi and bacteria, and with a smaller effect, predatory nematodes, protozoans, and soil microarthropods (Rodriguez-Kabana 1991). There are complex communities of fungal and bacterial natural enemies with high intraspecific variability, and the role of this biodiversity is poorly understood (Kerry and Hominick 2002).

The nematode-destroying fungi are notoriously diverse, occurring throughout all fungal groups with the possible exception of ascomycetes (Barron 1977) and can be divided in three main groups (Siddiqui and Mahmood 1996): endoparasites, predatory (or trapping) fungi, and opportunists (or facultative parasites). The majority of endoparasitic fungi are obligate parasites (e.g., *Nematophthora gynophila*, *Hirsutella rhosiliensis*). They spend most of their life cycles inside the body of their host and do not produce extensive hyphae in the rhizosphere. Frequently, these fungi are only detected in soil in the form of spores (Barron 1977, Siddiqui and Mahmood 1996).

Although the primary ecological role of predatory fungi appears to be that of wood decay (Barron 2003), their ability to capture nematodes using trapping devices has led to further specification and diversification (Ahren and Tunlid 2003). The traps formed by these fungi can consist of adhesive branches, hyphal networks or knobs, and constricting and nonconstricting rings. Although they can colonize the rhizosphere, their sensitivity to environmental changes makes them poor competitors in soil (Siddiqui and Mahmood 1996).

Opportunistic fungi can use both living and nonliving matter as sources of nutrients (Jaffee 1992). These fungi can infect sedentary stages of endoparasitic nematodes within the roots or when exposed on the root surface or in soil. Their saprophytic ability makes them good colonizers of the rhizosphere, even in the absence of their nematode hosts. The opportunistic fungi *Pochonia chlamydosporia* (formerly known as *Verticillium chlamydosporium*) and *Paecilomyces lilacinus* have been studied extensively and are being developed as biological control agents of sedentary nematode parasites (Jatala 1985, Stirling 1991).

Nematophagous fungi can also produce nematode-antagonistic compounds. A crude extract of the nematode parasitic fungus *Myrothecium* sp. has nematicidal activity against a wide range of plant parasitic nematodes, and is now under development as a bionematicide (DiTera TM) (Warrior et al. 1999, Twomey et al. 2000).

Perhaps one of the best studied bacterial enemies of nematodes is the endospore-forming *Pasteuria penetrans*, a potential biocontrol agent of sedentary endoparasitic nematodes (Stirling 1991). As an example, infection of root-knot nematodes by an isolate of *P. penetrans* allowed a better development of *Acacia holosericea* seedlings (Duponnois et al. 2000a).

The genus *Pasteuria* includes four species that have been found parasitizing several different genera of nematodes (Sturhan 1988). However, most nematode antagonistic bacteria are not natural enemies, but act by producing metabolic by-products with nematode toxicity (Siddiqui and Mahmood 1996). A surprising example comes from an apparently obscure interaction between two nematodes that are obligate parasites: the root-feeding nematode *Meloidogyne incognita* and the insect parasite *Steinernema glaseri*. Bird and Bird (1986) demonstrated that *M. incognita* feeding on the roots of tomato plants was suppressed by the addition of the insect parasite. Further research demonstrated that *S. glaseri* has a symbiotic relation with the bacterium *Xenorhabdus* sp., which produces a nematotoxic allelochemical that induces mortality in the root-knot nematode and also inhibits egg hatching (Grewal et al. 1999).

Although several fungal and bacterial natural enemies of nematodes have been described, knowledge is lacking on their population biology and dynamics. Community diversity and population dynamics can be influenced not only by nematode identity, but also indirectly by the nematode host plant, in a tritrophic interaction (Kerry and Hominick 2002).

Field studies on the population dynamics of *Hirsutella rhossiliensis* have concluded that high levels of parasitism can occur in soil, but build up very slowly, resulting in a time-lagged density-dependent effect (Jaffee 1992). A similar conclusion was reached for *P. chlamydosporia* and *N. gynophila* after a 10-year monitoring study of their populations and that of their sedentary endoparasitic nematode host, *Heterodera avenae*, in four field sites. After 3–4 years of the establishment of fungal enemies in the soil, the nematode populations dropped to almost nondetectable levels, even under monoculture of their cereal host (Kerry and Crump 1998). On the other hand, the population dynamics of the interaction between *P. penetrans* and *Xiphinema diversicaudatum* has been described as a typical predator–prey system, in which the number of *Pasteuria* endospores in soil is dependent on the number and activity of available hosts (Ciancio 1995).

In summary, by reducing plant-feeding nematode populations, these microbial enemies contribute to improved plant growth, and could further influence their distribution.

ECOLOGICAL IMPLICATIONS

The importance of soil biodiversity for ecosystem processes is an ongoing debate, but unraveling the impact of soil diversity on ecosystems is extremely difficult. Soils are highly heterogeneous and complex, which makes it complicated to reproduce in laboratory or greenhouse experiments. Experimental studies have failed to show a uniform pattern of the effect of removing groups or species of soil organisms. For example, the removal of soil fauna affects plant community composition through its effects on the rhizosphere microbial biomass that alters decomposition rates and nutrient cycling, but major ecosystem functions such as net ecosystem productivity were reportedly unchanged (Bardgett et al. 1999a,b). As a result, different theories based on the concept of key species, functional traits, or functional dissimilarity have been proposed. These theories are not discussed further here (for more information on the topic see Bradford et al. (2002), Bardgett (2004), and Heemsbergen et al. (2004)). Instead, we move a step further to link the described interactions between rhizosphere organisms and single plant species with the dynamics of plant communities and terrestrial ecosystems.

The first point to be mentioned is that the impact of rhizosphere organisms on plant community processes is a function of environmental factors (Reynolds et al. 2003). For example, the availability of phosphorus and nitrogen determines plant dependence on mycorrhizal fungi and symbiotic nitrogen-fixers. In addition, the deleterious effect of pathogens can be reduced under optimal nutrient and light conditions; conversely, such conditions can

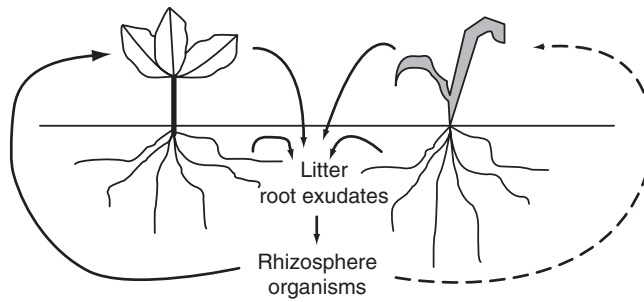


FIGURE 19.2 Representation of feedbacks between plants and soil organisms. Plants change the composition of rhizosphere communities through the quantity and the quality of litter and root exudates. In turn, the rhizosphere communities affect different plant species in different ways.

switch mycorrhizal outcomes for the plant from beneficial to detrimental. In addition, most studies have been done with a fairly limited set of AMF species from culture banks. This raises the question of the relevance of the results obtained in greenhouse or laboratory experiments for ecosystems functioning. Undoubtedly, valid data have been obtained from those experiments that help the understanding of the different mechanisms involved in the plant–rhizosphere interactions. The challenge now is to obtain a broader knowledge from field experiments or mathematical models that integrate that information with the naturally changing environment.

The existence of feedbacks between plants and soil communities that affect above- and belowground processes is now widely accepted (Ehrenfeld et al. 2005) (Figure 19.2). Plants modify the composition of the rhizosphere mainly through the quality and the quantity of exudates and litter that they produce (Bardgett 2004) (and references therein). Therefore, the existence of different plant functional types is more important for the rhizosphere biota than plant diversity per se. Rhizosphere organisms can in turn affect plant community composition and dynamics because they change the outcome of competition between plants. In this way, specific feedbacks between plants and soil organisms are established and can determine the functioning of many terrestrial ecosystems (Van der Putten 2003). Soil feedbacks are considered positive if beneficial organisms for the plant accumulate in the rhizosphere over time. Soil feedbacks are negative when plant growth is hampered by its own soil community, either due to the increase of detrimental organisms or because other plant species have a higher benefit from that soil community.

Positive feedbacks lead to the dominance of the associated plant, and therefore, to the reduction of plant diversity (Bever 2003). This mechanism is evident for plant species with a high dependency on mycorrhizal or rhizobial symbiosis. Plant establishment depends on the initial abundance of the symbiotic partners and fails without these organisms in the rhizosphere. As an example, the introduction of pine trees in the tropics was only successful when the trees were inoculated with the compatible ectomycorrhizal fungi (Reynolds et al. 2003). There is also evidence that plants select for AMF that benefit them most, creating patches of positive feedbacks between them and those AMF species (Hart and Klironomos 2002, Klironomos 2002). Thus, positive feedbacks lead to a reduction of plant diversity in local patches but to an increase of landscape heterogeneity.

Negative feedbacks can increase plant coexistence and, therefore, diversity. Negative feedbacks that happen due to the accumulation of deleterious organisms are very obvious in agricultural soils, and can be alleviated by crop rotation. There are more examples of negative feedbacks shaping natural plant communities than positive feedbacks. Sometimes these feedbacks are caused by a single group of organisms like those described for

pathogenic fungi or plant-feeding nematodes. In addition, complexes of pathogenic fungi and plant-feeding nematodes can drive the decline of the pioneer dune species *A. arenaria* and plant succession in general (Van der Putten et al. 1993, Van der Putten and Peters 1997, Greipsson and El-Mayas 2002). Negative feedbacks can also occur if the mutualistic fungi that accumulate in the rhizosphere of one species translocate nutrients to a competing neighboring species. This mechanism occurs in the invasion of North-American grasslands by invasive *Centaurea* species, where the growth of some native species decreases in the presence of the invader only when growing with the native soil community (Callaway et al. 2004).

Soil feedbacks contribute to both plant rarity and invasiveness (Klironomos 2002). In an experiment conducted to compare soil feedbacks between coexisting rare and abundant plants, Klironomos (2002) demonstrated how rare plants have strong negative soil feedbacks as a consequence of the accumulation of fungal pathogens in the rhizosphere. In addition, positive feedbacks between plants and mutualistic rhizosphere organisms can increase the ability of the plant species to colonize and invade new areas (Richardson et al. 2000). The importance of positive and negative feedbacks in large-scale vegetation patterns might also shift over temporal and spatial gradients (Reynolds et al. 2003). In the early stages of plant succession, mutualists play an important role in the establishment of their host plants and facilitate the establishment of new plant species (Figure 19.3). Since nitrogen is more limiting in the early stages of succession, the positive rhizobia–legume interaction plays a key role at that stage. With the progression in succession and the accumulation of organic matter, ecto- and ericoid mycorrhizas are favored due to their ability to break down complex organic compounds. Negative feedbacks should be more important at those later stages of succession, when there is also an accumulation of soil pathogens. Some authors postulate that early successional species are quick-growers and, therefore, poorly defended against pathogens. Over time, the accumulation of soil pathogens leads to a replacement of those by other slow-growing, better-defended species. Progression in succession also leads to more specific interactions since better-defended species are usually less susceptible to the attack of generalist pathogens and herbivores.

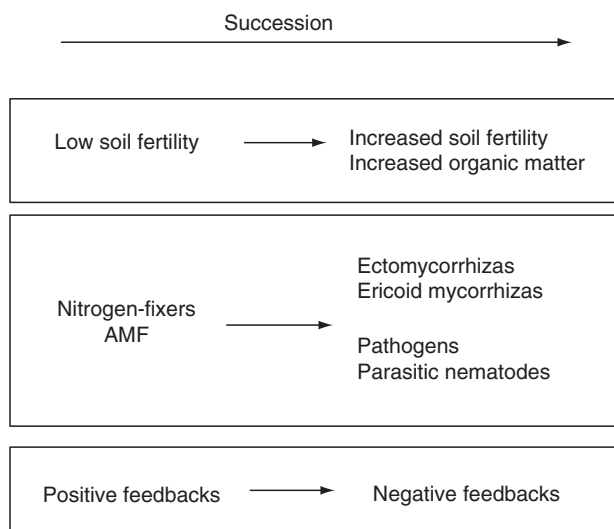


FIGURE 19.3 Changes in soil fertility, relative abundance of rhizosphere organisms, and feedbacks between plants and the rhizosphere communities that occur with succession.

CONCLUSION

The organisms associated with the rhizosphere can greatly influence plant performance. They establish close associations that have a positive or negative effect on plant establishment, growth, and fecundity, but the net effect for a plant species also depends on the interactions that occur between those organisms in the rhizosphere. The implications of belowground interactions for ecosystem functioning are widely documented. They affect plant richness and abundance, landscape heterogeneity, and plant succession. In turn, the rhizosphere is also a dynamic part of the ecosystem that changes with plant diversity and identity and with successional processes. Therefore, the interactions between plants and their rhizosphere should not be ignored in ecological studies.

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