

Biotic interactions in the rhizosphere in relation to plant and soil nutrient dynamics

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Abstract

The rhizosphere is the interface between roots and the soil where nutrient absorption for plant growth in agroecosystems is facilitated. An abundant and diverse rhizosphere biome is involved in biogeochemical processes, including bacteria, fungi and soil fauna, driving soil C, N and P dynamics. Plant carbon photosynthates allocated to the root and rhizosphere are priming microbial activities important for plant nutrition such as organic matter decomposition, P solubilization, N fixation, mycorrhizal nutrient transport and biocontrol of root pests. While substantial information is available on the role of individual groups of the rhizosphere microbiome in biogeochemical processes, less attention has been given to the interactions between different beneficial rhizosphere microorganisms. Also, interactions between soil fauna and rhizosphere microorganisms still remain relatively unexplored. In order to improve our knowledge on the role of the rhizosphere in C, N and P biogeochemical processes a more holistic and functional approach is required. In this review, state of the art information on the role of biotic interactions in the rhizosphere on C, N and P biogeochemical processes relevant for plant nutrition in agroecosystems is presented.

Keywords: Biogeochemistry, rhizosphere microbiome, mycorrhizosphere, root health, soil fauna

1. Introduction

Plant production relies on biogeochemical processes, which are mainly driven by biotic factors. However, abiotic processes such as weathering to some extent, also contribute with the release of essential nutrients for plant growth. This

is especially true for C, N and P biogeochemical processes, which are pivotal for plant production in agroecosystems (Drinkwater and Snapp, 2007). The rhizosphere, which is defined as “the field of action or influence of a root” (Lynch and Leij, 2012), is

the interface between the plant and the soil, where plants acquire nutrients facilitated by biogeochemical processes. Carbon flows from the plant to the soil ecosystem as simple organic compounds providing the necessary food basis for the corresponding microbiological processes that are vital for soil ecosystem functioning (Jones *et al.*, 2009). In this way, photosynthates flow rapidly from the plant to the soil feeding the rhizosphere microbiome, which in turn provides food for microbial grazers and their predators (Fitter *et al.*, 2005). The rhizosphere microbiome is abundant and diverse with bacteria and fungi being the key players in relation to plant and soil C, N and P dynamics (Lynch, 1987; Philippot *et al.*, 2013). However, bacterial and fungal grazers (protozoa, nematodes, mites and collembolans) and grazer predators (predator mites and nematodes) are also important regulators of biogeochemical processes (Bonkowski, 2004; Coleman, 2008). Both plant beneficial microorganisms (plant growth promoters and biocontrol agents) and pests (root pathogens and root feeding insects) are common inhabitants of the rhizosphere (Whipps, 2001; Morgan *et al.*, 2005; Raaijmakers *et al.*, 2009), all affecting C, N and P biogeochemical processes in the soil. Functional traits of the beneficial rhizosphere microbiome in relation to plant nutrition and health include organic matter decomposition, P solubilization and transport, N fixation and biocontrol of root pests (Philippot *et al.*, 2013).

Plant-microbe-soil interactions strongly modulate C, N and P dynamics in the soil. However, the conventional rhizosphere concept focuses mainly on root-microbe interactions in relation to plant nutrition (mycorrhiza and rhizobium) and microbe-microbe interactions in relation to plant health (biocontrol of root pathogens). Less information is available on the interactions between beneficial rhizosphere microorganisms from different functional groups and interactions between soil fauna and rhizosphere microorganisms still remains relatively unexplored.

In order to improve our knowledge on the role of the rhizosphere in C, N and P biogeochemical processes a more holistic and functional approach is required.

Hence, the main objective of this review is to provide state of the art information on the role of biotic interactions in the rhizosphere on C, N and P biogeochemical processes relevant for plant nutrition in agroecosystems.

2. Biogeochemical processes in the mycorrhizosphere

Most plants naturally form mycorrhizae with fungi from the phylum Glomeromycota (Smith and Read, 2008). This common mycorrhizal association is characterized by the bidirectional nutrient exchange, where the fungus receives sugar from its host plant and in return provides important ecosystem services for plant production, which improve both plant nutrition and health (Gianinazzi *et al.*, 2010). Arbuscular mycorrhizae (AM) are known to strongly affect rhizosphere microbial communities, as presented in several reviews (Linderman, 1988; Barea *et al.*, 2002; Johansson *et al.*, 2004; Artursson *et al.*, 2006; Bending *et al.*, 2006), which is why the term mycorrhizosphere was employed to emphasize the vital importance of mycorrhizal associations in root function (Linderman, 1988).

2.1. The role of AM fungi in the C cycle

Despite the biotrophic nature of AM fungi, acceleration of organic matter decomposition has been linked to these microorganisms (Hodge *et al.*, 2001). Improved growth of AM fungi in patches that are rich in organic matter has been reported (Albertsen *et al.* 2006; Ravnskov *et al.*, 1999, Gavito and Olsson, 2003) and growth of AM fungi has been shown to be stimulated by the decomposition of organic compounds (Gryndler *et al.*, 2008). Acceleration of organic matter decomposition by AM fungi could lead to an increased release of CO₂ from the soil through microbial respiration (Cheng *et al.*, 2012), but this may

be counteracted by the increased photosynthetic activity and therefore CO₂ uptake by plants (Hughes *et al.*, 2008). Furthermore, since a substantial part of the photosynthates from the host plant are invested in the formation of AM fungal biomass, both in terms of root colonization and mycelial network in the soil, AM fungi have been suggested to be important in carbon sequestration in the soil, hence mitigating CO₂ emissions from agricultural soils (Solaiman, 2014). Though information on the importance of AM fungi in the C cycle is being generated in various areas of interest, especially regarding climate change (Fitter *et al.*, 2000) a more thorough analyses of the role of AM fungi in the C cycle could provide missing information required to develop a more solid model on this matter.

2.2. The role of AM fungi in the N cycle

Regarding the importance of AM fungi on the N cycle in agroecosystems, recently more focus has been directed to this issue providing new information especially in relation to N mineralization and N denitrification (Hodge and Storer, 2015). In general, it is well established that AM fungi can transport N as NH₄⁺ to the host plant (Johansen *et al.*, 1992; Hawkins *et al.*, 2000; Hodge *et al.*, 2001; Atul-Nayyar *et al.*, 2009). Only recently a more complete model of the importance of AM fungi in N biogeochemical processes has been addressed (Veresoglou *et al.*, 2012; Hodge and Storer, 2015), which suggests that arbuscular mycorrhizae reduce N loss from the soil in terms of leaching and denitrification (Cavagnaro *et al.*, 2012).

2.3. The role of AM fungi in the P cycle

The importance of AM fungi in biogeochemical processes has focused mainly on P since these fungi are known to transport immobile P from the soil to the

host plant (Jeffries and Barea, 1994). However, it is still unclear whether AM fungi can solubilize organic (Joner *et al.*, 2000) and mineral forms of P (Bagyaraj *et al.*, 2015), but P solubilization is a well-known trait of some bacteria associated with AM fungi (Cruz and Ishii, 2012; Wang *et al.*, 2012). Thus it is logical to assume that at least some of the P transported by the AM fungi to the host plant may be derived from P, which is solubilized by associated microorganisms (Azcon *et al.*, 1976; Souchie *et al.*, 2006; Osorio and Habte, 2013; Zhang *et al.*, 2014). Though synergistic interactions between AM fungi and other soil microorganisms in relation to P uptake from organic and mineral P sources has now been studied for decades, more detailed information needs to be obtained in order to reveal the role of AM fungi and other soil microorganisms in this matter.

3. Microbial interactions in the mycorrhizosphere

Microbial interactions in the rhizosphere have been extensively examined especially in terms of plant health and nutrition (Whipps, 2001; Morgan *et al.*, 2005; Lambers *et al.*, 2009; Ryan *et al.*, 2009; Larsen *et al.*, 2015; Phillipot *et al.*, 2015). However, knowledge on how biotic interactions in the rhizosphere affect C, N and P plant-soil dynamics is still limited. Moreover, information on functional aspects of microbial interactions has been largely ignored. In most cases, biotic interactions in the rhizosphere have been examined in terms of biomass quantification of the biota in question and to a lesser extent in functional terms.

In this regard, arbuscular mycorrhizae play a key role in bridging the gap in the plant-soil interface with an extensive external mycelial network (Jakobsen *et al.*, 1994).

3.1. The mycorrhizosphere microbiome

AM fungi not only associate with plant roots, but also establish close associations with bacteria in the AM

fungus-mycosphere and may include spores (Xavier and Germida, 2003b; Bharadwaj *et al.*, 2008; Cruz and Ishii, 2012) and external mycelia (Mansfeld-Giese *et al.*, 2002). Mycorrhiza-associated bacteria seem to be thriving from AM fungal exudates (Toljander *et al.*, 2007). Even more intimate associations between endosymbiotic bacteria and the AM fungus *Gigaspora margarita* (Bianciotto *et al.*, 1996) demonstrate the very complex tripartite symbiosis between plants, AM fungi and associated bacteria. Known functional traits of AM fungus associated bacteria include N fixation, P solubilization and root pathogen biocotrol (Bonfante and Anca, 2005). Hence mycorrhiza-associated bacteria may facilitate N and P nutrition for both plant and fungal partners in mycorrhizal associations as well as protecting arbuscular mycorrhizae against root pests.

AM fungi have been reported to shape the rhizosphere microbiome both in qualitative and quantitative terms (Linderman, 1988; Barea *et al.*, 2002; Bending *et al.*, 2006). This is most likely achieved through quantitative and qualitative changes in root exudates (Jones *et al.*, 2004). AM fungi differentially affect microbial communities both in the mycorrhizosphere and in the AM fungal hyphosphere (Welc *et al.*, 2010), which could be closely related to changes in exudates (Toljander *et al.*, 2007). In most cases, reduced microbial biomass and activity in the mycorrhizosphere compared to that of the non-mycorrhizal rhizosphere have been reported (Ravnskov *et al.*, 2006; Larsen *et al.*, 2009) and different AM fungal species differentially affect rhizosphere microbial communities. In this way the nutrient resources for the mycorrhizal symbiosis are maintained in a tight connection minimizing microbial N and P immobilization.

3.2. Organic matter decomposition

Though mycorrhizal associations may suppress other microbiota, this does not seem to affect their activity in terms of organic matter decomposition, which

on the contrary, has been shown to be accelerated by arbuscular mycorrhizae (Hodge *et al.*, 2001; Ravnskov *et al.*, 2006; Cheng *et al.*, 2012). Dual inoculation with the AM fungus *Glomus intraradices* and the saprotrophic fungus *Clonostachys rosea* counteracted growth depressions in tomato plants grown in soil amended with organic matter despite of mutual inhibition between these fungi (Ravnskov *et al.*, 2006). Interestingly, both fungi reduced the microbial biomass in the rhizosphere and changed the microbial community perhaps improving the energy and nutrient use efficiency in question. Despite of the biotrophic nature of AM fungi, they seem to thrive well in organic matter patches (Ravnskov *et al.*, 1999; Gavito and Olsson, 2003), which may be facilitated by their saprotrophic microbial associations, but this remains to be demonstrated. In general, more attention should be given to better address the underlying mechanisms for these microbial interactions in relation to organic matter decomposition.

3.3. AM hyphal P transport

Since AM fungi promote host plant P nutrition via AM hyphal P transport from the soil to the plant it is important to know how other soil biota affect this key function of AM fungi. P isotope tracer technology combined with the use of compartmented growth systems with root-free compartments (Jakobsen, 1994) has improved the knowledge on the interactions between AM fungi and other soil biota. Employing the isotope method platform developed by Jakobsen (1994), effects of microbial the biocontrol agents (*Trichoderma harzianum*, Green *et al.*, 1999; *Burkholderia cepacia*, Ravnskov *et al.*, 2002; *Pseudomonas fluorescens*, Ravnskov *et al.*, 1999), plant growth promoters (*Aspergillus niger*, Medina *et al.*, 2006), root pathogens (*Fusarium culmorum*, Larsen *et al.*, 1998) and soil animals (Collembola, *Folsomia candida*, Larsen and Jakobsen, 1996) on AM hyphal P transport have been

examined. Surprisingly, the general conclusions from these experiments suggest that AM hyphal P transport is relatively unaffected by other soil microorganisms. Most likely the ecological advantage of AM fungi receiving energy directly from its host plant makes these fungi superior soil competitors in comparison to saprotrophic rhizosphere inhabiting microorganisms. In addition, most studies on interactions between AM fungi and mycophagous soil animals suggest that AM fungi are less palatable as a food source than other filamentous fungi (Larsen *et al.*, 2008), which explains why limited effects of soil fauna on AM hyphal P transport have been reported (Larsen and Jakobsen, 1996a,b). On the other hand, information on the interactions between soil fauna and other functional groups of microorganisms such as P solubilizing, N fixing and biocontrol microorganisms is limited and could be relevant to determine the interactions between soil fauna and microorganisms in terms of biogeochemical processes.

3.4. Microbial P solubilization

In relation to plant and soil P dynamics it is also important to consider microbial P solubilization and how other rhizosphere microorganisms affect this process. A broad range of bacteria, actinomycetes, filamentous fungi and yeasts have been shown to solubilize different types of minerals as well as organic P (Sharma *et al.*, 2013). On the other hand, the solubilized P can be immobilized by the same microorganisms that solubilized the P and/or by other microorganisms while the microbially solubilized P at first may not be available for plant roots. Again, here the mycorrhizal association most likely plays a crucial role in sequestering the phosphorous from the soil solution and subsequently storing P as polyphosphate granules in the fungal structures in soil and roots providing the basis for P and C interchange between fungal and plant partners in the

mycorrhizal association. However, at this point the abovementioned theory is merely a hypothesis that needs to be further addressed. Interestingly, AM fungi have been shown to increase alkaline phosphatase activity in the rhizosphere (Bagyaraj *et al.*, 2015), but little is known about the influence of AM fungi on mineral P solubilization by other soil organisms.

3.5. Microbial N fixation

Biological nitrogen fixation carried out by both symbiotic and free-living rhizospheric bacteria provide substantial amounts of N to both crops and soil biota in agroecosystems (Franché *et al.*, 2009; Xu *et al.*, 2012). However, limited information is available on how other soil biota affect this important biogeochemical process. Regarding rhizobial associations between symbiotic nodule-forming bacteria and leguminous crops in general, mycorrhizal plants seem to improve rhizobial N fixation though the two symbionts are competing for allocation of plant sugar (Javaid, 2010).

Free-living diazotrophic bacteria such as *Azospirillum*, *Burkholderia* and *Bacillus* are known to promote plant growth not only through N fixation but also by inducing root branching, P solubilization and biocontrol of root pathogens (Dobbelaere *et al.*, 2003; Vessey, 2003; Lugtenberg and Kamilova, 2009). Information on how other rhizosphere microorganisms affect free-living diazotrophic bacteria is limited and to the best of our knowledge information on the impacts of other soil biota on N fixation from this group of rhizosphere bacteria is missing.

4. Root health

Main root pests include plant pathogens (fungi, oomycetes, protozoa and nematodes) and root-feeding insects, which all obtain their basal energy from the

root system though in different forms depending on the life strategy of the individual pest. Knowledge of the role of root pests in biogeochemical cycles and C, N and P dynamics in soil is limited. In some cases, root disease symptoms especially from oomycete and nematode pathogens can be confused with nutrient and water deficiency because the root system fails to support the plant with sufficient nutrients and water. Root feeding insects cause similar nutrient and water deficiency symptoms since root herbivory damages the root system and thereby its absorptive capacity (Johnson *et al.*, 2013). Another important aspect to consider is that the nutrient absorptive capacity of the plant also depends on the external mycelium of root-inhabiting AM fungi. Root damage will eventually lead to reduced production of external mycelium by AM fungi and thereby reduce the capacity of AM hyphal P transport to the plant. On the other hand, AM fungi have been shown to alleviate plant stress from root pests, which may be related to induction of tolerance related to compensation by improving host plant nutrient and water dynamics (Whipps, 2004; St. Arnaud and Vujanovic, 2007).

4.1. Nematodes

Plant parasitic nematodes cause substantial crop losses in most agricultural crops worldwide (Zasada *et al.*, 2008). Root feeding by ectoparasitic nematodes and formation of numerous root galls by endoparasitic nematodes, reduces plant nutrient absorption causing the plant to become stunted or chlorotic (Ellis *et al.*, 2008). Often, this is misdiagnosed as nutrient deficiency by the farmer rather than nematode infestation.

Non-parasitic nematodes are also common in the rhizosphere and an increase in the populations of free-living species of nematodes can be an indicator of soil health, reflecting improvements on the availability of

nutrients, water-holding capacity, soil structure, pH, and buffering capacity (Magdoff, 2001; Widmer *et al.*, 2002). The ubiquitous distribution of nematodes is due to the fact that they have very diverse and specialized feeding habits contributing to soil processes related to nutrient cycling. There is an estimated half a million species of nematodes that feed on a wide range of organisms, including bacteria, fungi, and other nematodes (Strange, 2003). Due to the interactions among nematodes and so many different organisms, they are key players in various food webs at several trophic levels (Ingham *et al.*, 1985). As a result of these interactions, many elements are released in the soil matrix, serving as plant nutrients (Neher, 2001). An estimated 8 - 19% of N mineralization in soils is attributed to the activity of predatory and bacterial feeding nematodes (Beare, 1997).

Addition of soil organic amendments has been shown to enhance the activity of “grazer” nematodes that feed on soil bacteria and fungi (Freckman, 1988; Ferris and Fu *et al.*, 2000; Matute, 2003; Oka, 2010). This frenzy of microbial activity creates ideal conditions for improved nutrient cycling, which in turn benefit root development and plant growth (Hamilton III and Frank, 2001). Akhtar and Malik (2000) reviewed the various roles of organic amendments and how they favor the proliferation of predatory nematodes, sporozoan parasites, and other natural enemies of phytoparasitic nematodes. The application of organic matter to agricultural soils may also have an effect on various components of the soil food web, increasing the propagule density of nematophagous fungi (Venette *et al.*, 1997) and the adhesive network of traps and knobs that allow nematophagous fungi to reduce plant-parasitic nematode populations (Jaffee, 2004). Akhtar and Alam (1993) reviewed the direct or indirect stimulation of biocontrol agents that reduce plant-parasitic nematodes. Furthermore, the application of organic amendments that are high in N may have a

negative effect on plant-parasitic nematodes because they produce compounds such as ammonia and nitrous acid that have nematicidal properties (Oka, 2010). These properties are enhanced by certain physical and chemical changes such as soil buffering capacity, pH, and organic matter content resulting from the application of organic amendments (Lazarovits, 2001). Amendments such as meat and bone meal have shown promising results in reducing some soilborne diseases, but their efficacy depends on the characteristics of the soil to which the amendments are applied (Tenuta and Lazarovits, 2004). Soils with low organic carbon and to some extent the amount of sand present were very important in ammonia accumulation which in turn resulted in effective control for some of these soilborne diseases (Tenuta and Lazarovits, 2002). Several studies have shown the potential of parasitic and non-parasitic bacteria to control plant-parasitic nematodes (Trudgill *et al.*, 2000; Meyer *et al.*, 2000). Chen *et al.* (1994) documented that *Pasteuria penetrans* can act as a biocontrol agent for the suppression of plant-parasitic nematodes. Non-parasitic rhizobacteria have the potential of reducing plant-parasitic nematode populations by means of colonizing the roots of the host plant and producing certain compounds that have nematicidal properties (Siddiqui and Mahmood, 1999).

4.2. Root feeding insects

Ecology of root herbivores has received little attention, among other reasons because of the inherent difficulty of working with soil dwelling insects. Due to the diversity of taxonomic groups of insects affecting cultivated plants there is little or no information available about underground behaviour of some immature stages of certain insects that have been identified as pests (Morón, 2004). Root feeding insects not only cause damage to underground parts of plants, but their activity may also include positive effects on the ecosystem because they stimulate renewal

of root systems. This happens because these insects feed on old roots and this promotes the development of secondary root meristem. Additionally, they consume fungal mycelia regulating its growth and taking part in the dispersion and conservation of mycorrhizae (Rabatin and Stinner, 1988). Some root feeding insects not only feed on roots, but also on organic matter, favoring mineralization and recycling of plant nutrients, particularly N, S, and P, through immobilization, which prevents nutrient losses from leaching (Villalobos, 1994; 1994a). In an experiment to assess the role of soil nutrients as mediators of the interactions between root feeding and leaf insects, Johnson *et al.* (2009) determined that foliar and root herbivory caused by aphids (*Rhopalosiphum padi*) and wireworms (*Agriotes* spp.) respectively, had several interactive effects; generally reversible on plant nutrients. Wireworms caused little impact on the nutritional chemistry when compared to aphids, which were negatively related to the P content in both leaves and roots. In the short term, wireworms favored aphid population density to increase due to an increase of S in the soil. However, contrary to previous explanations, root herbivory had little impact on the concentration of foliar amino acids. In contrast, aphids caused a significant increase in the concentration of minerals present in the root, especially S, which could potentially promote the activity of wireworms. Recently, there has been increased interest to investigate the role of root herbivores and how they interact in natural ecosystems and agroecosystems (Johnson and Murray, 2008).

5. Microbial biocontrol in the rhizosphere

A broad range of microorganisms including bacteria and fungi carry out biocontrol activities in the rhizosphere. Multiple biocontrol modes of action include: parasitism, antagonism, competition for nutrients and space and induction of plant defense (Whipps, 2001). Possible non-target effects of biocontrol agents on other soil

microorganisms and their functions are largely ignored (Brimner and Boland, 2003), which is hampering a successful integration of these plant beneficial microorganisms in agroecosystems. Several of the microbial biocontrol agents against root pathogens and root feeding insects have also been shown to promote plant growth independently from their biocontrol features. The plant growth promoting effect of the biocontrol agent *Trichoderma harzianum* (Harman *et al.*, 2004) has been suggested to be based on the production of antagonistic compounds against root pathogens, which also serve as plant hormones, which can increase root growth (Vinale *et al.*, 2008).

The soil is a natural reservoir of insect pathogens. Diverse taxonomic groups of pathogenic microorganisms isolated from a number of soil dwelling pests include: viruses, bacteria, fungi, protozoa and nematodes (Jackson and Glare, 1992). These pathogens are able to infect and cause epidemics at immature and adult insect stages with agricultural significance.

In the soil environment, abiotic factors play a role in the incidence, persistence and spread of entomopathogenic microorganisms and nematodes (Studdert and Kaya, 1990, Ignoffo, 1992). Many of the interactions between pathogenic microorganisms in the rhizosphere and their potential hosts are yet to be determined because the aspects related to their ecology and performance in complex multi-trophic food webs in soils are still unknown. Such is the case of entomopathogenic fungi including *Metharizium anisopliidae* and *Beauveria bassiana*, which in addition to infecting insects, may act as plant growth promoters or antagonists of plant diseases (Goettel, 2008; Vega *et al.*, 2008).

6. Conclusions

Biotic interactions in the rhizosphere drive biogeochemical processes and modulate plant nutrient

availability in agroecosystems. However, in order to improve our knowledge on the role of the rhizosphere in C, N and P biogeochemical processes a more holistic and functional approach is required.

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