



Review

Arbuscular mycorrhiza and soil nitrogen cycling

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ABSTRACT

Nitrogen is a major nutrient that frequently limits primary productivity in terrestrial ecosystems. Therefore, the physiological responses of plants to soil nitrogen (N) availability have been extensively investigated, and the study of the soil N-cycle has become an important component of ecosystem ecology and biogeochemistry. The bulk of the literature in these areas has, however, overlooked the fact that most plants form mycorrhizal associations, and that nutrient uptake is therefore mediated by mycorrhizal fungi. It is well established that ecto- and ericoid mycorrhizas influence N nutrition of plants, but roles of arbuscular mycorrhizas in N nutrition are less well established; perhaps even more importantly, current conceptual models ignore possible influences of arbuscular mycorrhizal (AM) fungi on N-cycling processes. We review evidence for the interaction between the AM symbiosis with microbes and processes involved in soil N-cycling. We show that to date investigations have rather poorly addressed such interactions and discuss possible reasons for this. We outline mechanisms that could potentially operate with regards to AM fungal – N-cycling interactions, discuss experimental designs aimed at studying these, and conclude by pointing out priorities for future research.

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1. Introduction

There are several reasons that justify the extensive attention of the scientific community on the nitrogen (N) cycle. N is one of the few nutrients in terrestrial ecosystems that may limit growth of both plants (Chapin et al., 2004) and microbial communities (e.g. Demoling et al., 2007) in ecosystems with high carbon availability. Thereby, plants and free-living microbes often compete for available N pools (e.g. Harrison et al., 2007). As microbes have a competitive advantage for resources, for example because of access to micropores, but on average have a shorter life span, these competitive interactions are complicated and involve both temporal and spatial elements (Bardgett et al., 2005). Additionally, the N-cycle is an almost entirely microbially-driven cycle and plant–microbe interactions may have a dramatic influence on the actual rates of N-cycling (e.g. Craine et al., 2007). Finally, N-limitation of the microbial and especially the plant community is characteristic of ecosystems developing on newly formed soil substrate (Vitousek, 2004; Lambers et al., 2008) and has strong implications to the establishment of vegetation in such areas.

Soil microbial ecology has long remained on the “dark side” of ecosystem ecology, due to a limited ability to study processes at a micro-scale (Tiedje et al., 1999; Wall et al., 2005). Development of

DNA-based methods provided tools that allowed the study of microbial communities, and represented a critical step in fostering integration of aboveground and belowground ecology (Wardle et al., 2004). The field of soil microbiology has largely focused on descriptive molecular characterization of microbial communities at the scale of single experimental sites (e.g. Mazzola, 2004). More recently, there have been pleas for a more systematic functional analysis of soil microbial processes with an ecosystem perspective (e.g. Rillig, 2004; van der Heijden et al., 2008), together with increasing recognition that ecosystem functioning could be regulated by groups of soil microbes with special functional importance (Harris, 2009), including mycorrhizal fungi (Jansa et al., 2008).

It is well recognized that different mycorrhizal types have varying capacities to access organic and inorganic forms of nutrients in soil (Smith and Read, 2008; Lambers et al., 2008; Read and Perez-Moreno, 2003). Ecto- and ericoid mycorrhizas are characteristic of plants that grow on organic soils, and it is now well established that the activities of the fungi mobilize N (and probably also P) from organic forms thus altering the source of N accessible to the plant symbionts (e.g. Read and Perez-Moreno, 2003). In contrast, arbuscular mycorrhizas are characteristic of plants growing on mineral soils, where inorganic N and P sources are prevalent. Arbuscular mycorrhizas are formed by members of the fungal phylum Glomeromycota (Schüßler et al., 2001). Although only a small fraction of plant species have actually been examined, it is believed that the majority of plant species are potentially capable of forming arbuscular mycorrhizas (e.g. Wang and

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Qui, 2006). This symbiosis is inarguably the most common and widespread root symbiosis, and we limit our discussion in this paper largely to this type of mycorrhiza. AM fungi are obligate symbionts and obtain all their organic carbon (C) requirements from their plant partners. In consequence their activities are not limited by organic C substrates in soil, as is the case for many free-living microbes including those involved in nutrient cycling. The symbiosis is often mutualistic based largely on exchange of C from the plant and P delivered by the fungi (Smith and Smith, 2011). Other benefits include tolerance of pathogens and improved water relations (Newsham et al., 1995; Sikes et al., 2010). AM fungi may therefore modulate ecosystem resilience to abiotic (e.g. nutrient deficiency, water stress, temperature stress – Garrido et al., 2010; Bunn et al., 2009) and biotic stresses (e.g. plant pathogens, herbivory - Koricheva et al., 2009; Shah et al., 2008) and could thus be important ecosystem drivers. AM associations are characteristic of plant species of an intermediate successional stage when the amount of N that has been immobilized in the organic litter layer is small (Smith and Read, 2008) and tropical biomes.

Within the manuscript our discussion addresses different hierarchical scales in the ecosystem but mainly focuses on the rhizosphere, the zone around the root that is directly influenced by rhizodeposition as well as by depletion or accumulation of nutrients (Uren, 2000). A hypothetical exclusion of AM fungi would cause massive changes to the rhizosphere; the term mycorrhizosphere may be more appropriate to describe the area that surrounds the root system in the mycorrhizal state (e.g. Andrade et al., 1998); to describe the analogous region surrounding individual AM fungal hyphae, the term hyphosphere has been used. Initially we discuss five potential pathways via which AM-induced effects on N-cycling may operate, arrayed from smallest spatio-temporal scale to largest (Fig. 1). We then analyze mechanisms relevant to main N-cycling processes. We conclude with potential solutions to experimental issues and make suggestions for prioritizing future research.

2. Potential pathways of AM-mediated effects on the N-cycle

2.1. Substrate availability

An obvious pathway via which the AM status of plants could exert an influence on N-cycling processes is via substrate availability in soil (Fig. 1). With the exception of nitrogen fixation, where high concentrations of N_2 are present in the soil air (Enoch and Dasberg, 1971), all other N-cycling transformation rates may be regulated by substrate availability. AM fungi may reduce availability of substrates for free-living N-cycling microbiota through immobilization of inorganic N into their mycelium or transfer of nutrients to their host. For example, they may reduce ammonium (NH_4^+) levels in the soil (e.g. Johansen et al., 1992), and thus introduce a potential limitation for nitrification, or mediate nitrate (NO_3^-) uptake (e.g. Govindarajulu et al., 2005; Fig. 1) and thus potentially limit denitrification and N leaching. Moreover, turnover of AM extraradical hyphae (Olsson and Johnson, 2005) and AM hyphal exudation (Hooker et al., 2007; Toljander et al., 2007) could enrich soil beyond the zone of direct root influence with carbon and lift carbon limitation for several groups of heterotrophic microbes involved in the N-cycle. Finally, mobility and availability of N-compounds is known to be regulated by several abiotic factors such as pH (Marschner, 1995), as discussed in the next section.

2.2. Modification of the abiotic soil environment

There have been a number of reviews on AM-mediated effects on soil aggregation showing improvement of soil aggregation in the mycorrhizosphere (e.g. Tisdall and Oades, 1982; Miller and Jastrow,

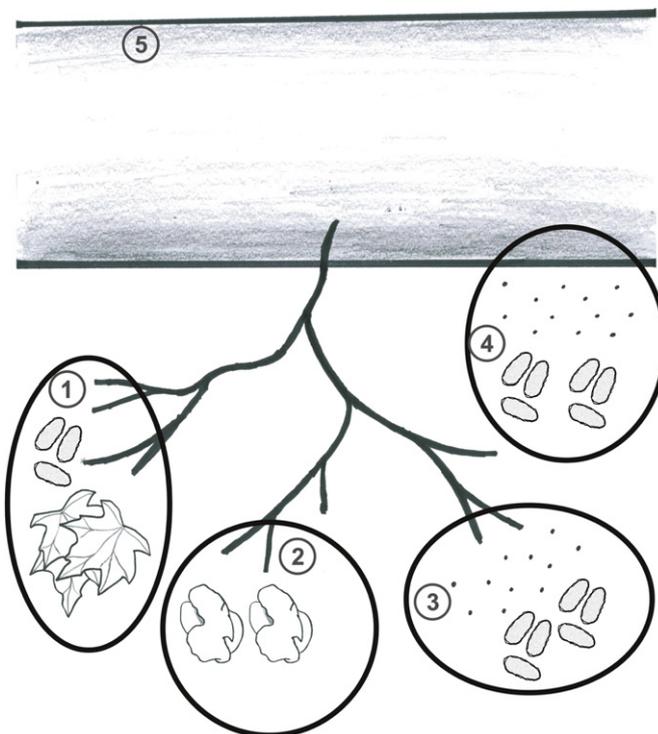


Fig. 1. Diagram of the five proposed general pathways via which arbuscular mycorrhizal fungi could cause changes in N-cycling processes. These include, as highlighted by the numbered bullet points, (1) substrate availability; (2) modification of the abiotic soil environment; (3) microbial community shifts; (4) individual host plant level effects; and (5) plant community shifts. For more information on the proposed pathways the reader is directed to text Sections 2.1–2.5, respectively. For the example of denitrification –for more details please consult Section 3.4, (1) could correspond to NO_3^- availability; (2) could be the influence of improved aeration through macroaggregate formation; (3) could be hyphal exudation and the resulting shifts in hyphosphere microbial communities; (4) would refer to proximity of denitrifiers to plant roots as more denitrifiers may benefit from exudation of a larger host plant; and (5) signifies the effects of plant identity and/or plant community composition.

2002; Rillig and Mummey, 2006). Modification of soil aggregation (Fig. 1) affects aeration of soil, and this could have an impact on nitrification and denitrification, the two N-cycling processes that are affected by oxygen concentration in the soil air. Moreover, AM presence could affect soil pH, as suggested by a limited number of studies (e.g. Li et al., 1991; Bago et al., 1996; Marschner and Baumann, 2003), and consequently modify availability of N-compounds (for example pH below 5.5 is detrimental for nitrification (e.g. De Boer and Kowalchuk, 2001) and this may reduce availability of NO_3^-). Modification of carbon content of the soil could mediate changes in soil properties such as water holding capacity (e.g. Bouyoucos, 1939) and thus influence moisture-sensitive N-cycling processes such as nitrification (e.g. Avrahami and Bohannan, 2007), denitrification (e.g. Davidson et al., 1993) and leaching (e.g. Currie and Aber, 1997).

2.3. Microbial community shifts

Changes in resources (substrates) and abiotic conditions as well as generation of specialized niches in the hyphosphere and potential allelopathic interactions (i.e. interference competition) could result in AM-mediated shifts in microbial communities (e.g. Marschner et al., 2001). Increasing evidence over the last few years reveals that AM fungi have the ability to modify the microbial community in the rhizosphere (e.g. Marschner et al., 2001; Rillig

et al., 2006a; Singh et al., 2008) and hyphosphere (e.g. Toljander et al., 2006). Specific groups of microbes such as bacteria of the genus *Azospirillum* and some species of *Pseudomonas* (e.g. Walley and Germida, 1997; Vázquez et al., 2000; Fig. 1) have been reported to be favored whereas others decline (e.g. *Burkholderia capacia* – Albertsen et al., 2006). N-cycling processes could be affected directly, through modification of densities of microbes directly related to N-cycling processes such as *Azospirillum* spp. (e.g. Vázquez et al., 2000) or indirectly through shifts in the intensity of competition for exudates (e.g. Christensen and Jakobsen, 1993) and rhizoplane colonization (Fitter, 2005) with non-N-cycling heterotrophic microbes. Direct allelochemical suppression of microbes by AM fungal hyphae is also a theoretical possibility, although no evidence for this exists.

2.4. Individual host plant level effects

The outcome of colonization of plants with AM fungi is commonly an increase in their size (Lekberg and Koide, 2005; Hoeksema et al., 2010). Although some experimental procedures such as sterilization may have contributed to these observed effects on plant growth (e.g. Brinkman et al., 2010; Hoeksema et al., 2010), we have no reason to believe that AM fungi do not induce an increase in plant size that could include also a bigger root system (for a quantitative analysis of root/shoot ratio responses see Veresoglou et al., 2011a). Spatial extension of the rhizosphere, a well known “hot spot” of microbial activity (Nannipieri et al., 2003), means that N-cycling processes may thus occur in a larger soil volume (Fig. 1). Despite the high overlap of plant roots in the surface soil, root exploitation of soils becomes less intense deeper in the soil profile (e.g. Jackson et al., 1996), and an AM-induced increase in root size at these depths could stimulate N-cycling processes.

2.5. Plant community level shifts

The AM fungal community can induce plant community shifts (e.g. van der Heijden et al., 1998; Landis et al., 2005; Wolfe et al., 2006). This raises the question whether these shifts could lead to changes in N-cycling processes (Fig. 1). Plant species identity is a well known regulator of N-cycling rates in the rhizosphere (e.g. Olsson and Falgengren-Grerup, 2000; Van der Krift and Berendse, 2001; Veresoglou et al., 2011b) and thus AM fungus-induced changes in plant community composition should impact the N-cycle.

An example of a case of AM-induced plant community shifts is the shift from C₃ grass dominance to C₄ grasses. Studies on AM species dependency, the weighted difference in dry weight biomass of a plant in the presence and absence of mycorrhizas, have revealed that C₄ grasses are considerably more responsive to AM fungi than C₃ grasses (Wilson and Harnett, 1997, 1998). Additionally, Collins and Foster (2009) were able to establish AM-free and AM-inoculated mesocosms of adequate size to address community shifts in abundance of grasses. Their targeted experimentation revealed a decline in abundance of C₄ grasses in the AM-free mesocosms with a concomitant increase of C₃ grasses (Collins and Foster, 2009). This shift may be one example of a more generalized change toward plants that respond positively in terms of growth. Interestingly, plant litter from C₄ grasses typically is of inferior quality (less decomposable) of that from C₃ grasses (e.g. Dijkstra et al., 2006). Litter quality is known to be a key trait that affects N-mineralization (Van der Krift and Berendse, 2001) and consequently other N-cycling processes such as nitrification (Booth et al., 2005).

3. AM-mediated effects on individual N-cycling processes

3.1. N-uptake and N-mineralization

3.1.1. Available evidence for AM fungal involvement

AM fungi assimilate N either exclusively (Tanaka and Yano, 2006) or predominantly (Govindarajulu et al., 2005) in the form of NH₄⁺. Moreover, evidence accumulates that AM fungi may possess the ability to mobilize N from organic sources (Hodge et al., 2001, 2010; Atul-Nayyar et al., 2009; Leigh et al., 2009; Hodge and Fitter, 2010; Barrett et al., 2011). Abovementioned studies have revealed that the N mobilized from patches can account for up to 32% of the total N present in the patch (Leigh et al., 2009), that N mobilization is possible at temperatures close to 10 °C (Barrett et al., 2011) and that N mobilization may take place even when an AM fungus fails to stimulate plant growth (Hodge and Fitter, 2010). It is striking, however, that the vast majority of studies that addressed the ability of AM fungi to facilitate N acquisition have targeted AM fungal isolates in the Glomeraceae. By contrast two studies that included isolates from the Gigasporaceae detected an inferior ability of these isolates to contribute to plant N nutrition (Reynolds et al., 2005; Veresoglou et al., 2011c). The N requirements of the AM fungus are known to be high (Hodge and Fitter, 2010) and this may complicate the interpretation of pot experiments.

Notwithstanding the consensus that AM fungi are able to transfer N to the host plant, the ecological importance of such N transfer via the AM pathway remains controversial, for several reasons. Experiments often reveal little or no increase in plant N content (reviewed by Leigh et al., 2011; but see Atul-Nayyar et al., 2009; Veresoglou et al., 2011c; Smith and Smith, 2011). Smith and Smith (2011) have criticized the large size of the hyphosphere compartments in microcosm experiments commonly used to assess N transport, which would lead to biased estimates of amounts transferred. Additionally, experimental designs to date also did not adequately control for mass flow and diffusion. Another criticism of experimental work has been that many studies neglected to introduce a bacterial/microbial community (Frank and Groffman, 2009). This could have either led to an overestimation of the ability of AM fungi to translocate labeled N from hyphosphere compartments (Leigh et al., 2011) but, also, may have allowed non-mycorrhizal plants in non-compartmented microcosms to more efficiently assimilate exchangeable N since competition with the microbial community was suppressed. Thus, the quantitative contribution of the AM pathway remains unclear as far as physiological data are concerned. Reynolds et al. (2005) suggested that the ecological significance of N transfer might be greatest when N availability is low, but as argued by Fitter et al. (2011) not much data are available in support of this notion. We suggest that the ecological significance of AM fungi may also be in the exploitation of pulses in NH₄⁺ availability in the soil environment. The idea is in agreement with Fitter et al. (2011) that proposed that AM fungi might be able to contribute to plant N nutrition under conditions of high N availability. Root proliferation in NH₄⁺-rich, ephemeral patches may be costly for the host plant but much more cost-effective for the high-turnover fraction of the AM fungal mycelium (Staddon et al., 2003). Improved ability of the AM fungi – compared to plant roots – to assimilate NH₄⁺ (as revealed from their ability to more effectively deplete NH₄⁺ in the soil environment e.g. Johansen et al., 1992) might allow them to better compete with soil microbes and assimilate adequate N first for their needs, but also in the case of N pulses, for transferring N to their plant hosts.

With regards to claims on accelerated decomposition in the AM mycorrhizosphere (e.g. Hodge et al., 2001) we note that superior ability to mobilize organic N from patches does not necessarily imply accelerated mineralization of the patch because in non-mycorrhizal

systems much of the net mineralized N might have been immobilized by the surrounding microbial community. The literature, so far with the sole exception of the work of Hodge et al. (2001) where decomposition was assessed indirectly through isotope labeling, has addressed plant nutritional aspects of N-decomposition and this is reflected in the absence of a single study that actually assesses N-mineralization or ammonification in the presence/absence of AM fungi. Hodge et al. (2001) have been able to demonstrate that AM colonized labeled carbon patches were more depleted in ^{13}C but this could as well be attributed to factors not related with decomposition. Such factors include hyphal exudation of unlabeled C (Hooker et al., 2007) that was then incorporated in microbial biomass or higher microbial activity in the presence of the AM fungus that would have modified the amount of labeled ^{13}C that was respired. Thereby, we believe that more targeted experimentation is required with regards to the fate of the patch following AM colonization, as well as the ability of the surrounding community to assimilate the label in the presence and absence of AM fungal extraradical hyphae.

3.1.2. Mechanisms of AM fungal involvement

Identification of AM fungal genes related to primary N nutrition such as glutamine synthetases and some nitrate reductases (Govindarajulu et al., 2005; Tian et al., 2010) suggested that extraradical hyphae of AM fungi have the ability to assimilate N in the forms of NH_4^+ and, possibly NO_3^- . The ability of AM colonized plants to more effectively deplete inorganic N from soil (e.g. Johansen et al., 1992) could be attributed either to their more thorough colonization of the soil environment or to an improved ability to assimilate inorganic N through efficient high-affinity NH_4^+ and NO_3^- transporters. Alternatively, exudation of sugars from the AM fungal hyphae could intensify microbial competition in the hyphosphere and consequently immobilization. An improved ability of AM fungi to explore the soil environment could explain why AM fungi preferentially assimilate immobile NH_4^+ and not the highly diffusible NO_3^- . Other reasons that may be used to explain this observation include the absence of benefits for the plant from acquiring NO_3^- via the mycorrhizal pathway (Fitter et al., 2011) or the higher assimilation cost of NO_3^- compared to NH_4^+ (e.g. Raven et al., 1992) that could render the supply of the host plant with NO_3^- derived N inexpedient. However, much of the evidence on AM-mediated N uptake has been obtained in controlled experiments where the soil environment of the microcosms is extensively colonized by plant roots and AM fungal hyphae (e.g. Johansen et al., 1992 – as reviewed by Smith and Read, 2008) and in the absence of a representative soil bacterial community (Frank and Groffman, 2009); under these conditions an improved physiological capacity of AM fungi to lower inorganic N levels is more plausible.

Less is known about the pathway through which AM-assimilated N could be transferred to the host plant and the extent of such a transfer (Jin et al., 2005; Tian et al., 2010; Smith and Smith, 2011). High concentrations of NH_4^+ may become toxic to living organisms (Temple et al., 1998) and transformation of N to a less toxic form is required. There is evidence that this organic compound may be arginine (Arg) (Jin et al., 2005; Tian et al., 2010). The fate of the organic skeleton of Arg following N transfer, whether the AM fungus is able to recapture the carbon and how, remains an issue (reviewed in Smith and Smith, 2011). Also, it is not known, as noted by Fitter et al. (2011), if mycorrhizal plants (compared to non-mycorrhizal plants) are able to down-regulate plant N-transporters in a way similar to P transporters (Bucher, 2007; Javot et al., 2007). Moreover, it is not yet clear why AM fungi should engage in the costly process of transferring N to their host plants, unless direct benefits exist. Helgason and Fitter (2009) proposed a model according to which AM fungal supplied phosphate through an increase of background levels of hexoses in the apoplast allows the AM fungus to better

scavenge for carbohydrates – a model that has been supported by the experimental results of Kiers et al. (2011); this mechanism, that assimilated nutrients may be “exchanged” by the AM fungi for carbohydrates in the apoplast, could be generalized for the case of NH_4^+ .

There appears to be no evidence that AM fungi contribute to N-mineralization directly through secretion of N-mineralization enzymes. However, they may exert indirect effects through modifying the microbial community so that the degradation ability of organic matter is enhanced (e.g. Griffiths et al., 2001; Liebich et al., 2007). Evidence is accumulating that AM fungi initiate a modification of the microbial community in the hyphosphere/(mycor)rhizosphere (e.g. Rillig et al., 2006a; Toljander et al., 2006) and there could potentially be indirect ways through which N-mineralization and uptake is affected. A typical example with regards to P nutrition is growth of phosphate solubilizing bacteria that appears to be promoted in the presence of AM fungi (Toro et al., 1997), which should in turn lead to improved P economy of the host plant. According to the N-mining hypothesis (Moorhead and Sinsabaugh, 2006; Craine et al., 2007) accelerated decomposition is predicted when availability of N declines; AM fungi are believed to intensify bacterial competition for inorganic N sources (e.g. Johansen et al., 1992) and this could facilitate decomposition. However, the contribution of bacteria to the decomposition of complex substrates is believed to be more limited than that of fungi (e.g. de Boer et al., 2005) and possibly any modification of the bacterial community following AM colonization would be of minor importance.

3.2. N_2 -fixation

3.2.1. Evidence for AM fungal involvement

N_2 -fixation represents the single most studied N-cycling process with respect to the impact of AM colonization. Puppi et al. (1994) hypothesized that AM colonization could alleviate the high P requirements of the nitrogenase enzymes and, thus, result in an increase of plant-host growth. Indeed, co-inoculation of legumes with AM fungi results in increases in their N-fixing ability (e.g. Smith and Daft, 1977; Abbott and Robson, 1978; Abbott et al., 1979; Ibijbjen et al., 1996; Toro et al., 1998). Moreover positive effects on *Frankia* (Jha et al., 1993; Yamanaka et al., 2005; Oliveira et al., 2005), *Azotobacter* (Sharma et al., 2002) and *Azospirillum* (Vázquez et al., 2000; Volpin and Kapulnik, 1994) N_2 -fixing ability or abundance have been recorded in several studies. However the interactive effects of AM fungi and N_2 -fixing organisms are not necessarily positive for plant-host growth. Larimer et al. (2010) and Kaschuk et al. (2010) conducted meta-analyses on the available literature and noted an absence of further plant-host responses when plants were simultaneously colonized with AM fungi and either rhizobia or free-living N_2 -fixers, despite the fact that responses to separate inoculation with either AM fungi or N_2 -fixers were positive. With regards to qualitative shifts in the nitrogen fixers-community, Welsch et al. (2010) manipulated the AM community through the addition of benomyl in the rhizosphere of *Spartina patens* and recorded *nifH* gene community differences that were maximized at the vegetative point of *S. patens* growth. In the absence of sequencing, though, it could not be evaluated which specific nitrogen fixers were favored through the suppression of mycorrhizas.

AM fungi have been found to colonize non- N_2 -fixing legume nodules only rarely (Scheublin and van der Heijden, 2006). A potential reason of inhibition of N_2 -fixation in the nodules in the study of Scheublin and van der Heijden could have been AM colonization (Scheublin and van der Heijden, 2006). Garg and Manchanda (2008), however, were able to demonstrate that *Glomus mosseae* possesses the ability to moderate premature nodule senescence. Analysis of the fungal communities of the AM colonized nodules

revealed differences from those that supported an active rhizobial community (Scheublin et al., 2004). Additional N₂-fixation may occur in the AM extraradical hyphae as AM extraradical hyphae appear to possess the potential ability to fix atmospheric N₂ through harboring intracellular bacteria of the genus *Burkholderia* (Bianciotto et al., 1996; Minerdi et al., 2001). However, the ecological significance of this N₂-fixing mechanism needs to be determined (Kneip et al., 2007), and the existence of a gene or even the expression of it does not necessarily imply a physiological effect.

3.2.2. Mechanisms of AM fungal involvement

Nitrogen fixers represent a heterogeneous group of organisms with large ecological niche differentiation among species. Some occur at comparable densities in rhizosphere and “bulk” soil such as the genera *Azotobacter* and *Azoarcus*; others, such as the genera *Herbaspirillum* and *Azospirillum* represent typical rhizosphere colonizers (Mrkovački and Milić, 2001; Bashan et al., 2004), whereas rhizobia possess the ability to infect roots and elicit formation of root nodules (Stacey, 2007). Much of the available literature on nitrogen fixation focuses on the rhizobium-legume symbiosis because of its high impact on ecosystem primary productivity (Rengel, 2002). The ability of legumes to partition root carbon amongst the two groups of symbionts, rhizobium and AM fungi, has been insufficiently addressed (a single study is available by Paul and Kucey, 1981), and the two groups of microorganisms may represent competing carbon sinks. The high P requirements of nitrogenase (Puppi et al., 1994), however, could mask any competitive interactions and allow an increase in the N-fixing ability of *Rhizobia* following association with AM fungi as a result of improved P nutrition.

On the other hand, extension of P depletion zones in the mycorrhizosphere could be detrimental to the N-fixing ability of associative N-fixers. Interactions of AM fungi with non-symbiotic N-fixers would be based on different mechanisms, and these are likely weaker. A potential relationship may be stronger for typical rhizosphere colonizers such as *Herbaspirillum* and *Azospirillum* as they are more dependent on plant derived carbon. Qualitative modification of exudates following AM colonization is believed to involve a decline in total sugars and an increase in release of N-rich compounds (Jones et al., 2004). Both changes could intensify carbon limitation of rhizosphere microbes and diminish the potential advantage of N-fixers over other microbes. Thus, a decline in the performance of N-fixers could be expected. However, many of the rhizosphere colonizers are versatile organisms. *Azospirillum* spp., the most studied non-symbiotic N-fixers, exhibit extensive phenotypic adaptation to conditions of carbon and N-limitation (Blaha and Schrank, 2003). As a result, the non-symbiotic N-fixing microbial community may not be very responsive to AM-induced changes.

3.3. Nitrification

3.3.1. Evidence for AM fungal involvement

Available literature for impacts of AM on nitrification is limited to three studies. Amora-Lazcano et al. (1998) observed that inoculation of maize with *G. mosseae* and *Glomus fasciculatum* facilitated establishment of culturable ammonia oxidizing bacteria in the soil. However, in this study, sequential harvesting of the microcosms revealed that the AO community had not reached equilibrium till the final harvest. By contrast, Cavagnaro et al. (2007) failed to detect differences between mycorrhiza defective mutant tomatoes and their wild-type progenitors in either the composition (assessed through denaturing gradient gel electrophoresis –DGGE– fingerprinting) or the density (assessed through real-time polymerase chain reaction –PCR) of ammonia oxidizing bacteria. The authors noted that this could have been due to the short (2 months) duration of the experiment (Cavagnaro et al., 2007). By contrast, Veresoglou

et al. (2011b) were able to demonstrate in a series of four experiments that nitrification potential rates (an indirect measure of the size of the AO community) of mycotrophic plants were consistently lower than those of non-mycorrhizal representatives. Thus, in three different studies the full range of potential results of AM on nitrification or nitrifying organisms has been obtained: increase, no change, and decrease. While the studies are not directly comparable, there is a clear need for systematic study of this N transformation process.

3.3.2. Mechanisms of AM fungal involvement

As autotrophic organisms, ammonia oxidizers (AO) are not directly affected by AM-colonization related changes in rhizodeposition or carbon-substrate related hyphosphere effects, at least compared to the direct effects on heterotrophic soil microbiota. Nevertheless, there could still be indirect effects, via physio-chemical changes mediated by AM fungi. With regards to interspecific competition for nutrients other than C and N, dependence of the competing microbial community on plant derived C could generate favorable conditions for ammonia oxidizer proliferation in the mycorrhizosphere through the decline in sugar exudation that follows AM colonization (Jones et al., 2004). However, a suppression of the competing microbial community could, also, be detrimental if N-mineralization rates are affected and NH₄⁺-substrate availability declines. The “priming effect” describes the disproportionate increase in N-mineralization that may be induced following the addition of very small amounts of carbon (de Nobili et al., 2001; Ma et al., 1999). In a similar way, the decline of carbon availability that occurs in the mycorrhizosphere could possibly result in a decline in ammonification that would induce substrate limitation in ammonia oxidizers.

Ammonia oxidizers are weak competitors for soil exchangeable NH₄⁺ (Bollmann et al., 2002) and, thus, under N limiting conditions, sensitive to the presence of other NH₄⁺-depleting organisms such as AM fungi. A potential explanation of decreased nitrification rates in the mycorrhizosphere (e.g. Veresoglou et al., 2011b) could thus be competition for NH₄⁺. If it is a selective advantage for AM fungi to deliver NH₄⁺ (rather than NO₃⁻) to their hosts to receive carbon in exchange, AM fungi may also possess the ability to suppress ammonia oxidizers via interference competition, i.e. with allelochemicals.

A final mechanism could be an indirect AM-mediated effect on nitrification through altered root structure. AM fungi can cause increases in lateral root length, branching and fine root length (Hooker et al., 1992; Yao et al., 2009). Since fine roots decompose much faster (e.g. Gill and Jackson, 2000), a more elaborate system may permit accelerated root N-mineralization and, thereby, favor nitrification rates (Booth et al., 2005). Simultaneously, a more elaborate root system may allow the plant to more effectively compete for nutrients (e.g. Fitter et al., 1991). In both scenarios the outcome of the altered root structure is an acceleration of N-cycling.

3.4. Denitrification

3.4.1. Evidence for AM fungal involvement

There has been one study of the interactive effect of AM fungi on the denitrifying community. Amora-Lazcano et al. (1998) were able to demonstrate a decrease in counts of denitrifying bacteria in the presence of AM fungi. However, their harvesting technique (coring) could have affected carbon availability in the microcosms through severing roots, thus impacting denitrification rates. Some additional evidence is available on the interactive effect of AM fungi and some verified denitrifying strains of *Pseudomonas* such as *Pseudomonas putida* (evidence from Kim et al., 2008) and *Pseudomonas fluorescens* (evidence from Samuelsson et al., 1998), even though it is unclear to what degree these results can be generalized to

denitrifying microbes at large. In most instances, results on modified bacterial abundance may provide little information of changes in the rates of the respective N-cycling processes as bacteria are well known to possess a remarkable physiological flexibility, here defined as their ability to respond to micro-environmental changes and modify their metabolic activity (Prosser et al., 2007). Thus, bacterial data, unless related to autotrophic organisms such as ammonia oxidizers, should be interpreted with caution. In general, the literature reports that co-inoculation of plants with AM fungi and *Pseudomonas* strains results in a growth stimulation for both groups of microbes. In brief, Walley and Germida (1997) demonstrated that the plant growth promoting (PGP) ability of *P. fluorescens* R92 and *P. putida* R104 on wheat was unaffected by inoculation with *Glomus clarum* NT4. Edwards et al. (1998) reported an increase in rhizosphere abundance of *P. fluorescens* following inoculation of a range of plants with *G. mosseae* (Nico. and Gerd.). Ravnskov and Jakobsen (1999) grew cucumber in association with *P. fluorescens* DF 57 and one of the AM fungi *Glomus intraradices* and *Glomus caledonium*. Along with an interactive increase in P content following co-inoculation with *G. intraradices* and *P. fluorescens* they reported an increase in hyphal length density of *G. caledonium* following co-inoculation with *P. fluorescens* (Ravnskov and Jakobsen, 1999). Finally, Gamalero et al. (2004) report that co-inoculation with *G. mosseae* BEG 12 and *P. fluorescens* 92rk resulted in an interactive increase in growth of tomato.

3.4.2. Mechanisms of AM fungal involvement

Denitrification is a dissimilatory process in which, due to limiting levels of O_2 , NO_3^- is used as an alternative terminal electron acceptor (Heylen et al., 2006). The factors other than soil aeration that could affect denitrification in soils include nitrate availability, carbon availability and quality, temperature, pH and soil heterogeneity (reviewed by Myrold (2005)). Proximity of denitrifiers to plant roots and plant identity could be additional factors. A multi-fold increase in denitrification rates has been reported in several instances in proximity to the root (e.g. Smith and Tiedje, 1979; Hojberg et al., 1996; Mahmood et al., 1997). Moreover, there is evidence of qualitative differences between denitrifying communities of the rhizosphere and the “bulk soil” (Chêneby et al., 2004). A decline of exuded carbon following AM colonization that is redirected to the AM mycelium may reduce the differences in denitrification rates between the rhizosphere and the “bulk” soil.

An obvious way through which AM fungi could influence denitrification rates is through modification of substrate availability (here: the terminal electron acceptor, NO_3^-). AM fungi are believed to predominantly assimilate N in the form of NH_4^+ (e.g. Tanaka and Yano, 2006) and so they may not have a direct effect on NO_3^- availability. However, as reviewed above, there is a high likelihood that they interact with nitrification, which represents a source of soil exchangeable NO_3^- . While AM fungi require good aeration of soil to proliferate, denitrification is an anaerobic process, characterized by high spatial variability under typical soil conditions (Parkin, 1987). AM fungi are known to form macroaggregates through a variety of mechanisms (Rillig and Mummey, 2006); thus it is likely that inside these aggregate interiors conditions conducive to denitrification prevail through the generation of anaerobic zones. Modification of carbon availability away from the root, in the hyphosphere, through hyphal exudation (Toljander et al., 2007) and the resulting shifts in the microbial community in this zone (Toljander et al., 2006) could be factors that might promote denitrification. However, it is not possible to predict the exact effect of AM colonization on the denitrifying community, primarily because of the remarkable physiological flexibility of denitrifiers, mentioned above.

3.5. N-Leaching

3.5.1. Evidence for AM fungal involvement

The role of AM fungi in leaching has not been extensively studied. van der Heijden (2010) used three plant species tested at two nutrient supply rates. He was able to demonstrate significant differences in the composition of the leachate with respect to phosphate concentration for all three plants at the low nutrient supply; also with respect to NH_4^+ for *Festuca ovina* at the low nutrient supply and for *Poa pratensis* at the high nutrient supply. Given the absence of differences in the size of the plants in the experiment of van der Heijden (2010), these results signify that AM fungi may represent an effective way to limit N-losses from an ecosystem. Asghari and Cavagnaro (2011) were, also, able to detect a decline in NO_3^- , NH_4^+ , and phosphate concentrations in the leachate, which, however, could partly be attributed to the bigger size of the mycorrhizal plants. By contrast, Rillig et al. (2006b) studied leaching of DOC/DON components that may be related to AMF, but detected no measurable amounts of a putatively AMF-derived protein; this study only targeted glomalin-related soil protein, and thus it cannot be used as exhaustive evidence against the occurrence of AM fungal derived N-compounds in leachate.

3.5.2. Mechanisms of AM fungal involvement

Leaching is an important pathway of N-loss especially in intensively managed ecosystems (e.g. Zhang et al., 2004). An obvious way to reduce N-leaching would be to reduce the amount of leachate. This could occur in AM-colonized plants as a result of the improved water relations following AM colonization that include higher stomatal conductance and faster soil-drying (Augé, 2001). Moreover, improvement of soil structure in the AM mycorrhizosphere (Rillig and Mummey, 2006) and possibly water held in the hyphae could result in an increase of the water holding capacity of soil. In support of these ideas, van der Heijden (2010) detected a trend toward lower leachate volumes, in the presence of the AM community, for all six AM vs non-mycorrhizal contrasts he established. Asghari et al. (2005) also demonstrated lower leachate volumes of AM colonized plants but did not control for the bigger size of the AM treatments.

A second mechanism through which AM fungi could impact N-leaching could be by affecting NO_3^- concentration in the soil solution, as hypothesized in Rillig (2004). As reviewed earlier (see Sections 3.1 and 3.3), it is quite likely that AM fungi facilitate uptake of inorganic N and may simultaneously interact with nitrification rates. We may not know the exact effect of AM fungi on nitrification rates, however, the more efficient uptake of inorganic N recorded for AM plants should result in a decline in the levels of inorganic N in the soil solution, including NO_3^- . We thus predict a decline in N-losses through leaching in the AM mycorrhizosphere.

4. Difficulties associated with experimentation with AM fungi – optimal experimentation procedures

Given the ubiquity of AM associations in nature and their importance in plant nutrition it is striking how little we know of the way AM fungi could impact N-cycling processes. There may be several reasons that can explain this gap in our knowledge. An important one is likely the historical focus of AM researchers on P nutrition, which is partially well justified owing to the higher intensity of AM interactions with P cycling processes. It can be safely stated, however, that our limited knowledge on AM interactions with N-cycling organisms largely reflects the well known difficulties inherent to experimentation with AM fungi; these are compounded with specific issues regarding the N-cycle, as discussed in the following.

Ubiquitous occurrence of AM fungi makes it difficult to either reduce or retrieve soil without AM fungal propagules. Systemic fungicides often fail to effectively reduce AM root colonization (e.g. Pedersen and Sylvia, 1997), suppress a large segment of the soil fungal community (non-target effects), or result in indirect effects such as an increase in nutrient availability due to mineralization of fungal biomass (Milenkovski et al., 2010). Most importantly there is evidence that they may interfere with nitrification and N-cycling processes (Martens and Bremner, 1997). The only available process to effectively remove AM fungal propagules from soil is a sterilization procedure. Sterilization and reinoculation with an extracted microbial community and/or AM fungi is a common way to overcome some of the problems introduced by soil sterilization. However, the logistics of conducting large scale ecological experimentation using that technique are daunting. On the other hand, the microbial community of the mesocosms, even following an equilibration period as suggested in some studies (e.g. Shaw et al., 1999), may not be representative of the indigenous microbial community of the original soil. While working with such re-established microbial communities (for the purposes of equilibrating microbial 'background' among treatments) may be sufficient for general experimentation, when the focus is the microbially regulated N-cycle, it becomes absolutely critical to achieve conditions that resemble the non-sterilized soil as much as possible. A good example of a microbial group that may be difficult to work with is ammonia oxidizers. Their low duplication rates, exceeding several days under laboratory conditions (Prosser, 1989), mean that the actual equilibration time required for them to reach pre-sterilization densities may involve a waiting stage of several months. As a result, long preparatory phases may be required to allow for optimal conditions of experimentation.

A parallel major problem lies in the difficulty of segregating the root/rhizodeposition effect from the AM-mediated impact in the hyphosphere. AM fungi are obligate symbionts; this means that in experiments the combined effect of roots and hyphae are commonly measured, with the root influence likely of much greater importance. To study the AM-associated changes the most common approach is to use compartmented systems with the incorporation of fine meshes that permit access only to hyphae, excluding roots. Following such a procedure, it is often speculated that soil that has not been in the reach of the roots represents the hyphosphere. However, visualization of the hyphosphere is not possible prior to destructive harvest of the microcosms; this is in contrast to ectomycorrhizal systems where it is possible to work with non-sterilized material and to sample hyphosphere soil in the proximity of rhizomorphs (e.g. Bomberg et al., 2003). In some instances microcosms have been harvested without checking the successful establishment of the AM fungi in the hyphosphere compartment, and interpretation of results from those studies may be difficult. Even in the instances of verified presence of a dense hyphosphere, AM colonization of soil could be biased toward "runner hyphae", long, thin exploratory hyphae that form few to no branches (Friese and Allen, 1991; Smith et al., 2000). Though there have been no studies to specifically target the microbial communities supported in the different types of AM hyphae, given the potential inability of runner hyphae to absorb nutrients it is quite likely that their potential overrepresentation at sampling represents an additional source of bias.

Using soil that has a short history of colonization from terrestrial plants such as the glacial forefront plant communities may be an interesting alternative to the use of sterilized/reinoculated soil (Cázares et al., 2005). The specific ecosystems lack or contain only few AM propagules, and thus soil can be used without pre-treatment to establish AM-inoculated and AM-free treatments that may be directly compared, but at the cost of potential lack of external validity beyond these soils. Another caveat may be that

these areas may be colonized by plants that are not responsive to AM fungi, or by plants which do not form this association.

An exciting opportunity is working with AM-deficient mutants/wild-type pairs (e.g. Cavagnaro et al., 2004; Facelli et al., 2010). Although a wide range of AM-deficient plant mutants is available, preliminary experimentation for indirect effects of mutants is important and simultaneous experimentation with more than one mutant desirable because the identity of plant mutant could interact with the results (e.g. Rillig et al., 2008). The clear advantage of pursuing this approach, when properly validated, is that the microbial community does not need to be modified, as the non-mycorrhizal status is created experimentally by a non-host; this represents a near-ideal condition for mechanistic studies.

While not typically permitting detailed mechanistic understanding, observational/correlational approaches represent a choice for obtaining results with a high level of ecological realism. It may be possible to use dissimilarities based analysis of interactions of microbial communities or path analysis to tease apart factors related to AM fungal abundance and its relationship with different N-cycling process rates; this approach has already been used for the study of general microbial community relationships (Singh et al., 2008) and other AMF functions, such as soil aggregation (Barto et al., 2010). Through the use of these techniques, it is also possible to simultaneously and explicitly examine direct and indirect effects (paths).

5. Conclusions

We have shown that the amount of available evidence on the potential effects of AM fungi on individual N-cycling processes varies considerably. The majority of studies on the interactive effect of AM and the N-cycle unsurprisingly focuses on economically/agriculturally important aspects of the N-cycle such as the ability of plants to assimilate N and symbiotic N₂-fixation. Yet despite the wealth of studies that have addressed the interactive effect of AM fungi on N-assimilation the ecological significance of the process (Smith and Smith, 2011) as well as the conditions under which the role of AM fungi may be important (Fitter et al., 2011) are still not well understood. There appears to be solid evidence that AM fungi do contribute to an increased ability of legumes to fix N₂ and also to a decline in the amount of inorganic N that leaches. By contrast, literature available to date does not allow us to reach a definitive conclusion whether there is also an AM effect on associative nitrogen fixation, nitrification and denitrification, despite the fact that plausible mechanisms exist for these effects. Taken together, there is a high likelihood that AM fungi play a role as drivers of N-cycling, which has not been appreciated hitherto.

Much of our knowledge on soil microbial communities associated with plants results from experimentation in the absence of mycorrhizal fungi or in systems where the plant's mycorrhizal status was not characterized. As a result, our understanding of microbial communities in the rhizosphere of plants still remains biased to the non-mycorrhizal condition (Hartmann et al., 2009). Many open questions that could guide future research remain: (i) what is the relative importance of the AM fungal influence, i.e. when should mycorrhiza be considered and when is it safe to ignore them; (ii) what is the role of diversity of AM fungi, given that there are tendencies within the phylum *Glomeromycota* for diverging functions (Powell et al., 2011); (iii) how can the study of AM impact be focused on isolated N-cycling processes given the high interdependence of N-cycling processes; (iv) what is the relative importance of direct AM-induced effects compared to more general AM-mediated plant and microbial community effects on N-cycling processes. We hope to have stimulated soil microbial ecologists and mycorrhizal biologists to tackle some of these important issues.

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