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Plant Coexistence and Diversity Mediated Below Ground

The Importance of Mycorrhizal Networks

Botanical Research and Practices

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PLANT COEXISTENCE AND DIVERSITY MEDIATED BELOW GROUND: THE IMPORTANCE OF MYCORRHIZAL NETWORKS

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CONTENTS

PREFACE

The acceleration of species' lost is such that understanding relationships between biodiversity and ecosystem function is a crucial aspect of ecology. Plant community composition and distribution has been thought, for a long time, to be a matter of aboveground interactions such as plant – plant feedbacks, plant – herbivores and/or parasites relationships, disturbance creating new patches for plant colonization, … Due to relevant advances in our understanding of plant and soil ecology, particularly in the investigation of rhizosphere (that is the soil biologically active compartment where root – root and root – microbes communications occurred), several findings provide evidence that plant – soil microbes feedbacks, particularly those with mycorrhizal fungi, are of great importance in determining plant species competitive performance and, could thus contribute to regulate plant community structure. Indeed, mycorrhizal symbioses are involved in plant nutrient mobilization and acquisition strategies, in plant health promotion, in interactions between plant and other biotic and/or abiotic factors, ... As plants differ in their specificity with mycorrhizal symbionts, plant host – mycorrhizal symbiont feedback would result in plant species' differential fitness and abilities when colonizing soil patches. Moreover, mycorrhizal hyphal network is known to interconnect conspecific as well as interspecific plants, and nutrient exchange may occur *via* this route to support subordinates. Consequently, mycorrhizal associations may be considered as an important biological mediator for plant coexistence and diversity.

This review presents some of the recent research work implemented on the involvement of soil microbial community in regulating plant community composition and distribution. We particularly focus on the implication of mycorrhizal symbioses in promoting multi-species assemblages in plant communities.

INTRODUCTION

An area of continued study in ecology is the investigation of mechanisms that allow for many species of plants to coexist in contravention of a simple interpretation of the principle of competitive exclusion. Ecologists have formerly emphasized physical heterogeneity that changes competitive hierarchies (Tilman, 1980), but theory does suggest that other above- and belowground biotic factors can also interfere and act as resources. Among belowground organisms that have been proposed to mediate coexistence of plant are mycorrhizal fungi (van der Heijden et al., 1998 a,b; Hart et al., 2003; Sanon et al., 2010). The influence of mycorrhiza in controlling plant diversity may be vitally important in ecosystems, where communities can be subjected to dramatic disturbances, and may rely on high diversity to maintain stability (Grime, 1997).

Mycorrhizas are symbiotic associations between fungi and the roots of numerous plant species in which soil resources accessed by fungi are exchanged for photosynthetic carbon produced by plants (Smith & Read, 2008). Associations with mycorrhizal fungi not only influence the performance of individual plants but also alter plant community structure, plant productivity, and nutrient cycling (van der Heijden et al., 1998a; Reynolds et al., 2003; Cardoso & Kuyper, 2006; Smith & Read, 2008) and, evidence suggests that mycorrhizal effect on the makeup of plant communities may derive directly or indirectly through multitrophic interactions (Figure1.; Janos, 1980; Eom et al., 2000; Bever, 2002b; Bidartondo et al., 2002; Duponnois et al., 2008; Gehring & Bennett, 2009).

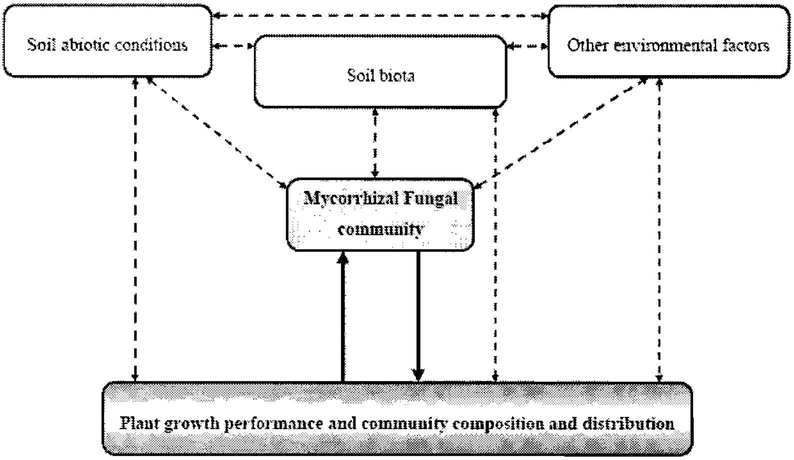

Figure 1. Conceptual diagram illustrating key interrelations susceptible to mediate plant competitive performance and community structure. Full arrows represent interrelations that are discussed in this chapter.

While mycorrhizal associations, particularly those with AM fungi, have been thought to be largely non-specific, there is growing evidence of host-specific differences in plant response to fungi and in fungal response to plants. The extent of plant growth promotion by mycorrhizal fungi depends upon the specific plant and fungal combinations (Streitwolf-Engel et al., 1997; van der Heijden et al., 1998 a,b; Hart et al., 2003). Conversely, the growth response and development of mycosymbionts also depends on the associated plant host species (Eom et al., 2000). Thus, host-specific changes in the mycorrhizal fungal community could lead to positive or negative feedbacks on the plant (Bever et al., 1997; Bever, 1999; Bever, 2002 a,b). These two dynamics lead to very different predictions for the community in terms of competing plant species' ability to coexist.

The effects of mycorrhizal fungi diversity and species composition are thought to arise through differential effects of different mycorrhizal fungi taxa, i.e. different mycorrhizal fungi-plant host combinations that may evolved, on the growth of individual plant species (van der Heijden et al., 1998 a,b; Eom, 2000; Vandenkoornhuyse et al., 2002, 2003). Such varying effects on the growth performance of plant species, in an environment characterized by high heterogeneity in resource availabilities (Tilman, 1980; Ryel et al., 1996), may constitute a strong driving force for the regulation of plant species coexistence and community composition and distribution.

Also, in plant communities, the influence of mycorrhizae on individual plant growth is affected by interactions between the individual plants. An established mycorrhizal mycelium is a potential resource and co-occurring plant species may differ in their ability to compete for this resource despite showing individual responsiveness to mycorrhizal association when grown separately in pots (Newman et al., 1992).

This manuscript aims to review some of the recent advances in the understanding of the implication of mycorrhizal symbioses in the maintenance of multi-species assemblages in plant communities. We will specifically focus on the two most widespread types of mycorrhizal fungal associations: the Arbuscular Mycorrhizal (AM) fungi and the Ectomycorrhizal (EM) fungi (Smith & Read, 2008). We highlight whether mycorrhizal community diversity and abundance could evolve and whether the symbiotic associates community influences plant growth and competitive performance. Finally, we address the consequence of the 'multi-facets' plant host – fungal symbiont feedbacks on plant community composition and distribution.

Chapter 1

REGULATION FORCES SELECTING FOR MYCORRHIZAL FUNGAL COMMUNITY COMPOSITION AND DISTRIBUTION

Whether high diversity of mycorrhizal fungi is maintained in a single community is steadily debated by specialists in mycorrhizae studies (Eom et al., 2000; Bever et al., 2001; Richard et al., 2005; Tedersoo et al., 2010). When trying to address this question, Bever et al. (2001) documented two hypotheses to support high diversity within their study site. The first hypothesis related to ecological equivalence of all fungal species; that means they are competitively equivalent within the cortical cells of plant roots and in this case, diversity is sustained by random drift processes. This hypothesis of functional redundancy suggested that the fungi are in some ways equivalent or redundant, given that a wide range of fungal species can colonize a particular plant species. Nevertheless, fungi have been clearly reported to differ in their effects on plant hosts (Bever et al., 1996; Hart et al., 2003). In addition, the distribution of fungal species within the study area strongly suggested that the local isolates of the species might differ in ecologically traits (Bever et al., 2001). These inconsistencies thus encourage the authors to formulate a second hypothesis postulating that fungal species are ecologically distinct and occupy different niches. That is, individual fungi would therefore be competitively superior in their specific niche, and the presence of multiple niches in a habitat results in the active maintenance of a speciose fungal community (Bever et al., 2001; Hart et al., 2003). The fungal diversity pattern discovered in the study of Bever et al. (2001), displaying different fungi predominating in various trap cultures under different environmental conditions, thus supports the second hypothesis described above. More specifically, this second hypothesis could be investigated by addressing the importance of individual environmental variables on which mycorrhizal symbionts differentiate, namely plant hosts, seasonality, and edaphic factors.

1.1. HOST SPECIFICITY

Mycorrhizal fungi are thought to have evolved at the same time as land plants, allowing the latter to colonize and radiate on land (Brundrett, 2002). Identifying the fungi that form mycorrhizas with a plant species and the specificity of these relationships are important for understanding how plants interact with their environment. Knowledge of fungal identity and specificity can be used to determine how susceptible plants are to habitat alterations and to assess how the conservation of threatened plant species should be approached. Knowing the identity of the mycorrhizal fungi provides insight into nutritional pathways of the host plant while the specificity of the relationship often elucidates plant species distribution patterns, rarity and growth requirements (Bougoure et al., 2009). For instance, a 'successful' plant species, that is, one that is widely distributed amongst a variety of habitat types, will associate with one or more fungal species with collectively high tolerances to a broader range of particular environmental variables, such as nutrients availability, temperature, aridity etc. In contrast, 'susceptible' plant species, that is, those with limited distribution in specific habitat types, will form mycorrhizae with only one or few fungal species that have specific growth requirements and limited distribution (Selosse et al., 2002; Bidartondo et al., 2004).

AM fungi are documented to display low specificities of association with their plant host species, but these findings almost exclusively followed from experiments carried out separately with individual isolates of species, apart from competitive interactions. When fungi are examined as a community, evidence suggests that host plant species composition strongly influences AM fungal species composition, underlying that '*plant host preferences*' (Bever, 1996; Eom, 2000; Vandenkoornhuyse et al., 2002, 2003) or '*alteration inmycorrhizal fungal community*' (e.g. by phytotoxic mechanisms; Mummey et al., 2005; Mummey & Rillig, 2006) may exist. For instance, in an experiment in which AM fungi were trapped on different plant hosts, isolates of different fungal species sporulated differentially, with the relative dominance of fungal species being reversed, depending on the plant species with which they were associated (Bever et al., 1996). Similarly, Eom et al. (2000) conducted a greenhouse study in which different host plant species were grown in similar tallgrass prairie soil. After 4 months of growth, AM fungal species composition was significantly different beneath each host species and, the authors concluded that AM fungi show degree of host-specificity and are not randomly distributed in tallgrass prairies. Importantly, Mummey et al. (2005) and Mummey & Rillig (2006) documented that the presence of the exotic plant species, *Centaurea maculosa*, may alter AM fungi communities indirectly *via* phytotoxic mechanisms as *C. maculosa* is known to secrete catechin, which exhibits antimicrobial properties (Bais et al., 2002, 2003).

Host specificity in ectomycorrhizal communities may also be a rule (Bruns et al., 2002; Richard et al., 2005; Morris et al., 2009; Tedersoo et al., 2010). In their study, Richard et al. (2005) analyzed the ectomycorrhizal (EM) fungal diversity in a Mediterranean old-growth *Quercus ilex* forest stand from Corsica (France) where *Arbutus unedo* was the only other EM host. Regarding the distribution of the EM fungi community among the two host species, 46 RFLP (Restriction Fragment Length Polymorphism) were found on *A. unedo* and 112 on *Q. ilex* with some taxa (12.9% of the taxa recorded) infected both plant hosts (Richard et al., 2005). The authors also reported that senescent (170-yr-old) plants of *Q. ilex* harbored more rare species than seedlings (1-yr-old) and saplings (10-yr-old) of the same plant species. These findings thus strongly confirm the hypothesis that the hosts contribute to mycorhizal fungal diversity and also support the conclusion that established conspecific seedlings recruit EM symbionts in an opportunistic way among mycobionts colonizing the old surrounding trees (Jonsson et al., 1999; Kranabetter & Friensen, 2002).

Also, Diédhiou et al. (2010) investigated the diversity of EM fungi on root system of adult trees and seedlings of five plant species in a tropical rain forest of Guinea by sequencing the rDNA Internal Transcribed Spacer (ITS) region. Thirty-nine EM fungal taxa were recorded of which 19 were multi-hosts, 9 single-hosts and 11 singletons (Diédhiou et al., 2010). The same authors found that the multi-host fungi represented 92% of the total abundance. In addition, except for one plant species, namely *Anthonotha fragrans*, the adults of the host species displayed significant differentiation for their fungal communities whereas their seedlings harbored a similar fungal community. Their results thus indicated variation in EM fungal diversity with respect to the seedling *vs* adult development stage of trees. However, Diédhiou et al. (2010) documented low specificity of EM associates, owing to the dominance of multi-host fungi over single-host in their studied area and, similar observation has also been recorded in other area (Cullings et al., 2000). Importantly, difference could exist in the colonization pattern of multi-host fungal associates when taking into account the distribution of the fungal species on the host root system (Morris et al., 2009; Tedersoo et al., 2010), and such differential colonization pattern might reveal potential specificity between a host and its fungal associates.

1.2. SEASONALITY

Evidence exists in the literature highlighting seasonality in the occurrence and abundance of mycorrhizal fungal propagules in the rhizosphere. Schultz et al. (1999) found that AM fungi differ in their seasonality, with some fungi sporulating in late spring and others doing so at the end of summer. Likely, Pringle & Bever (2002) found that AM fungi maintained different and contrasting seasonalities and they concluded that contrasting seasonal and spatial niches may facilitate the maintenance of a diverse community of AM fungi.

It has been stated that if mycorrhizal infection is high in a large number of individual plants in a community, then potentially, a significant part of the photosynthate produced by those individuals could be directed to the fungal symbionts, i.e. the carbon cost to the hosts would be high. Nevertheless, in a situation of high cost to the plant host, selection pressure should act to reduce infection, unless there are corresponding benefits, thus decreasing the level of infection within the community (Fitter, 1991). Also, in a survey of AM fungi in temperate deciduous woodland, Brundrett & Kendrick (1990) attributed variation in infection levels to periods of root growth and senescence. Sanders & Fitter (1992) documented variation in AM fungi infection between plant species and seasonal changes in infection under field conditions. Interspecific differences in mycorrhizal structures colonizing the root might indicate that aspects of the fungus/plant relationship are different in different plant species (Sanders & Fitter, 1992). More recently, DNA-based methods have been used to accurately explore the dynamic of AM fungi colonizing the root systems of different species (Husband et al., 2002; Vandenkoornhuyse et al., 2002; Rosendahl & Stukenbrock, 2004; Santos et al., 2006; Santos-González et al. (2007). All together, those studies did suggest seasonal variations in the composition of AM fungi communities across the growing season. For instance, in the experimental work implemented by Santos-González et al. (2007), though results indicated no significant seasonal changes in the species compositions of the AM fungi communities as a whole, the two studied plant species hosted significantly different AM fungi communities. In addition, *Prunella vulgaris* hosted a rich AM fungi community throughout the entire growing season and the presence of AM fungi in *Antennaria dioica* decreased dramatically in autumn, while an increased presence of *Ascomycetes* species was recorded.

Similar pattern in seasonal dynamics was also documented for the occurrence of ectomycorrhizal fungus assemblages. In this respect, the abundance and diversity of ectomycorrhizal fungi have been assessed based on the collection of basidiocarps during 12 months in southern Brazil. The results indicated that fruiting patterns of EM fungi differed with host and season, and host specificity was apparent in some (Giachini et al., 2004). Consistently, Walker et al. (2008) compared EM fungus distributions on root systems of out-planted oak seedlings at two sites in mixed southeastern Appalachian Mountain forests in North Carolina (USA) from samples taken in mid-July and early September. Seventy-four EM fungal ITS were recorded, most of which occurred only in the midsummer or early-fall samples. Abundance and relative frequency of EM fungal types, except *Cenococcum geophilum*, were significantly higher in the July samples, while *C. geophilum* was significantly more frequent and abundant in September (Walker et al., 2008). Globally, though their study is based on a single growing season, it did suggest that changes in abundance and frequency, detection of significant indicator species, and the apparent systematic affinities of shifting EM types support the potential for seasonal variability in EM associations in their system

1.3. ABIOTIC FACTORS

Mycorrhizal symbioses are also known to respond to a set of abiotic factors, which can strongly affect mycorrhizal fungi community abundance and composition. The mineral status of the soil, by influencing plant nutrients budget and availability, may affect the need for the plant to associate with mycorrhizal symbionts for nutrients mobilization and acquisition. Indeed, it is well established that mycorrhizal symbioses are more efficient and beneficial in nutrient-deficient soil and that plants may control their infection by mycorrhizal fungi when the cost mycosymbionts impose to the plant extends the benefit they provide (Fitter, 1991; Smith & Read, 2008).It is generally assumed that large amount of nutrients, especially phosphorus, negatively affects plants infection by mycosymbionts as well as the development of mycorrhizal propagules in soil (Cardoso & Kuyper, 2006; Smith & Read, 2008). Nevertheless, individual fungi could show opposite associations with certain soil parameters. In some instances, the distribution and abundance of *Acaulospora colossica* was negatively associated with soil phosphorus concentration, while the reverse was true for *Gigaspora gigantea* (Schultz, 1996). Several other parameters, including soil pH, drought, soil temperature, soil degradation status, soil compaction, tillage, pesticides, salinity, pollution, … are also documented to have ramifications on mycorrhizal fungi development (Furlan & Fortin, 1973; Daniels & Trappe, 1986; Cairney & Meharg, 1999; Cardoso & Kuyper, 2006; Smith & Read, 2008).

1.4. ADDITIONAL FACTORS

Other factors, such as difference in life history characters, including duration of dormancy, germination and sporulation requirements are documented to affect mycorrhizal fungi community (Bever et al., 2001). Additionally, these fungi may also differ in their palatability and resistance to grazing by belowground herbivores. Consistently, species-specific differences in palatability have been explicitly reported for ectomycorrhizal hyphae (Schultz, 1991), and similar patterns might likely occur among the arbuscular mycorrhizal fungi as well (Moore, 1985; Klironomos & Ursic, 1998; Bever et al., 2001).

Chapter 2

MYCORRHIZAL SYMBIOSIS EFFECTS ON PLANT GROWTH AND COMPETITIVE PERFORMANCE

Though parasitic interactions have, sometimes, been documented regarding mycorrhizal partners (see Johnson et al., 1997; Purin & Rillig, 2008), mycorrhizal fungi have generally been found as essential components of sustainable soil – plant systems and consistently, the successful establishment of certain plant species has been conditioned by the presence of a suitable mycorrhizal symbiont (Janos, 1980; Richardson et al., 1994). In this respect, major benefits of mycorrhizae include an improved mobilization and acquisition of nutrients by their hosts and, this has been documented for a large range of macro- and micronutrients (Caris et al., 1998; Pare, 2000; He & Nara, 2007; Lambers et al., 2008; Smith & Read, 2008). Increased access to nutrients by plant hosts may result from a greater soil volume, more efficiently, explored by external hyphal network (Sylvia, 1988; Smith & Read, 2008) but also, from active release of nutrients from mineral particles and rock surfaces through weathering (Landeweert et al., 2001; Finlay, 2004, 2008) and from breaking down complex organic matter by the production of extracellular hydrolytic enzymes (Hodge et al., 2001; Cappellazzo et al., 2008; Lambers et al., 2008; Smith & Read, 2008). Additional benefits of mycorrhizae are related to an enhanced plant resistance to pathogens and others environmental stresses (i.e. metal and organic pollution, salinity, acidity, soil compaction, …), an improved water relations and, an improved formation and stability of soil aggregates that could significantly impact on plant growth and sustain productivity(St-Arnaud et al., 1997; Auge, 2001; Joner & Leyval, 2003; Cardoso & Kuyper, 2006;Rillig & Mummey, 2006; Smith & Read, 2008; Miransari, 2010).

Furthermore, interactions of mycorrhizal fungi with other soil microorganisms are diverse and, stimulatory, inhibitory or no effect on either partner could be reported (Founoune et al., 2002; André et al., 2005; Frey-Klett et al., 2005; Smith & Read, 2008).Mycorrhizal fungi and rhizosphere microorganisms like the plant growth promoting fungi (PGPF) or rhizobacteria (PGPR) have equally good potential in both plant growth promotion and plant disease control and, since both are beneficial microorganisms, their synergistic or additive effects could be more valuable than their individual effects (Hyakumachi & Kubota, 2004; Lesueur & Sarr, 2008; Siddiqui & Pichtel, 2008; Bonfante et al., 2009). Also, certain microorganisms have been found to stimulate the development of mycorrhizae in the root system of the plant hosts, which resultantly affects mycorrhizal efficiency on the growth of the hosts (Founoune et al., 2002; Duponnois & Plenchette, 2003).

Importantly, individual mycorrhizal fungal species are thought to have a multiplicity of effects on different hosts, promoting growth in one host while showing neutral effect or, in extreme case, inhibiting growth in other hosts (Streitwolf-Engel et al., 1997; van der Heijden et al., 1998a; Klironomos, 2003). Moreover, when fungi are examined as a community, they are expected to differentially impact on plant species with respect to plant host-fungal species preference and the generated feedback on plant host (Bever, 1996; Eom, 2000; Hart et al., 2003; Vandenkoornhuyse et al., 2002, 2003). Thereby, differential plant host-fungal species feedbacks may strongly alter and direct competitive relationships between plants (Hart et al., 2001). Importantly, van der Heijden et al. (1998b) and Stampe & Daehler (2003) demonstrated that the identity of AM fungi present could influence the outcome of plant competitive relationships as much as whether AM fungi are present or absent. In addition, evidence did suggest that mycorrhizae presence can significantly mediate resource acquisition by plants or alter resource distribution between competing plant species, thus affecting the growth performance of co-occurring plant species (Zabinski et al., 2002; Reynolds et al., 2003; Simard & Durall, 2004; Selosse et al., 2006; Sanon et al., 2010).

Table 1. Potential mechanisms mediated by mycorrhizae and though to affect coexistence and diversity within plant communities

Potential mechanism of action responsible for the promotion of plant coexistence	Type of mycorrhiza	Reference
Specificity/Preference in the plant host-fungal symbiont relation	AMF; EMF	van der Heijden *et al.* (1998a,b); Eom *et al.* (2000); Klironomos, 2000; Vandenkoornhuyse *et al.* (2002,2003); Richard *et al.* (2005).
Resource niches specialization	AMF; EMF	Bever *et al.*, 2001; Facelli & Facelli (2002); Hartnett & Wilson (2002); Reynolds *et al.* (2003).
Inter-canopy resource exchanges through mycorrhizal networks	AMF; EMF	Grime *et al.* (1987); Newman (1988); Bidartondo *et al.* (2002); Leake (2004); Simard & Durall (2004).
Alleviation of dominant canopy allelopathic/inhibitory effect	AMF	Sanon *et al.* (2006); Kisa *et al.* (2007); Sanon *et al.* (2009); Barto *et al.* (2010).
Multitrophic interactions with other organisms	AMF; EMF	Gange (2001); Gehring & Bennett (2009).
Successional dynamics within mycorrhizal communities	Non-mycorrhizal *vs* mycorrhizal plants; AMF *vs* EMF plants	Gorham *et al.* (1979); Janos (1980); Boerner *etal.* (1996); Smith & Read (2008).
Negative feedback within the mutualism	AMF	Bever. (2002b).

AMF, Arbuscular Mycorrhizal Fungi; EMF, Ectomycorrhizal Fungi.

Chapter 3

IMPLICATIONS OF MYCORRHIZAL SYMBIOSIS FEEDBACKS FOR PLANT DIVERSITY AND COMMUNITY DISTRIBUTION

Mycorrhizal symbioses and their feedbacks on plant growth performance might have strong ramifications on the relative abundance of plant species and their distribution within a community and these interrelations would be translated both in terms of promotion of multi-species assemblages and in terms of species replacement as succession proceeds (Table 1).

3.1. MAINTENANCE OF MULTI-SPECIES ASSEMBLAGES IN PLANT COMMUNITY

With most plants possessing similar nutritional requirements, competition is a key factor in their interactions and only best competitors are expected to establish successfully thereby reducing diversity in communities. Nevertheless, multi-species assemblages are common within plant communities indicating that driving forces, counterbalancing species exclusion and encouraging diversity in plant communities, may exist. '*Agent-mediated coexistence*' is a non-interaction theory that has been proposed as a mechanism for maintaining multi-species assemblages in plant communities (Pacala & Crawley, 1992). Among the agents able to promote plant coexistence, mycorrhizal fungi have been proposed as efficient drivers for the maintenance of biodiversity within plant communities (Janos, 1980; Allen & Allen, 1990; Zobel & Moora, 1995; van der Heijden et al., 1998a,b; Renker et al., 2004; Simard & Durall, 2004; Kisa et al., 2007; Smith & Read, 2008). It is clearly demonstrated from various studies that mycorrhizae have large influences on plant community structure and are an important factor for the stability of plant species composition, as evidenced by the large magnitude of changes in plant communities reported in response to the presence *vs* absence of mycorrhizal symbionts or to the particular species of mycorrhizal fungi present (Grime et al., 1987; van der Heijden et al., 1998 a,b; Hart et al., 2003).

Spatial heterogeneity of mycorrhizal fungal infectivity may increase plant species diversity, allowing non-mycotrophic and mycotrophic species to coexist in patches of low and high mycorrhizal soil potential, respectively (Allen, 1991). Hartnett & Wilson (2002) further extend Allen's hypothesis and suggest that, in habitats with significant spatial heterogeneity in mycorrhizal soil infectivity, there will be a positive relationship between interspecific variability in host plant mycotrophy and plant species diversity. A related hypothesis is that spatial heterogeneity in mycorrhizal soil infectivity, coupled with variation in host species mycorrhizal dependency for colonization and establishment (e.g., regeneration niche differences) may enhance species diversity in plant communities (Hartnett et al., 1994).

Importantly, plant host specificity, in combination with mycorrhizal fungal diversity, is tightly involved in the maintenance of diversity in plant communities. Indeed, because different species of mycorrhizal fungi have different effects on the growth of particular plant species, variation in mycorrhizal fungus species composition could cause changes in the strength of plant-plant interactions. For instance, in settings by van der Heijden et al. (1998a), increasing fungal diversity resulted in greater plant species diversity and higher productivity, suggesting that changes in belowground diversity of mycorrhizal symbionts can drive changes in aboveground diversity and productivity. The mechanism behind these effects is likely to be differential effects of specific plant-fungus combinations on the growth of different plant species. With respect to this, some authors argued that higher AM fungi diversity could lead to higher plant coexistence simply by increasing the probability of individual plant species to associate with a compatible and effective AM fungi partner (Hart et al., 2003). Therefore, if the addition of new fungal species leads to increases in the survival and vigor of more plant species that are responsive to mycorrhizal colonization, there may be a positive feedback of the mycorrhizal fungi, leading to more efficient resource utilization and increases in overall productivity (Finlay, 2004, 2008). Nevertheless, these effects may be context dependent as Vogelsang et al. (2006) suggested that plant diversity and productivity are more responsive to AM fungi identity than to AM fungi diversity *per se*, and that AM fungal identity and P environment can interact in complex ways to alter community-level properties. Whatever, increased AM fungi species richness is argued to be beneficial both in terms of host compatibility (Sanders & Fitter, 1992; Bever et al., 1996; van der Heijden et al., 1998b; Eom et al., 2000; Klironomos, 2000; Klironomos et al., 2000) and in terms of multifunctionality of AM fungi (Newsham et al., 1995; Klironomos, 2000). However, as previously underlined by van der Heijden & Scheublin (2007), defining functionally distinct AM fungal groups is essential to fully understand the interactions between plant and AM fungal communities in agricultural and natural ecosystems.

Also, if mycorrhizal fungi are capable of direct access to pools of soil nutrients (e.g. N and P) not necessarily or really inaccessible to non-mycorrhizal plants (Lambers et al., 2008; Smith & Read, 2008), two hypotheses could emerged: the first assumes that mycorrhized plants could colonize certain soil patches that could be unsuitable for non-mycorrhized plants and secondly, it may be possible to predict for mycorrhized plants that different fungal species might facilitate differential access of plant species to these pools. The evolvement of these two hypotheses might thus promote plant species coexistence through nutritional niche partitioning (Reynolds et al., 2003). Later, Reynolds et al. (2006) reported that nutrient partitioning might be a less advantageous strategy than an ability to take advantage of multiple forms of nitrogen or phosphorus, especially for sessile organisms in a temporally and spatially heterogeneous world. Thereby, partitioning along any number of other niche dimensions (Tilman & Pacala, 1993) or competitive equivalence (Hubbell, 2001; Silvertown, 2004; Tilman, 2004) must account for the coexistence of largely co-dominant plant species, reflecting the ‘fundamental’ but not the ‘realized’ niches of these species (Reynolds et al., 2006). Additionally, plant mycorrhizal dependence and their position in the local dominance hierarchy (Urcelay & Diaz, 2003) in combination with AM fungal presence and abundance in soil may strongly influence plant community dynamics. In this context, it has been suggested that if an otherwise less competitive plant species is infected by more AM fungi than is a highly competitive plant species, then AM fungi should promote coexistence by increasing the ability of less competitive species to access nutrients (Zobel & Moora, 1995; Moora & Zobel, 1996). Consistent with this, Facelli & Facelli (2002) documented that mycorrhizal symbiosis has the potential to strongly influence plant community structure by favoring coexistence of mycorrhizal plants when soil nutrient distribution is heterogeneous because it promotes pre-emption of limiting resources. Contrastingly, one may note that if a highly competitive plant species is also more infected by mycorrhizal fungi, then mycosymbionts could simply reinforce competitive dominance by that species (West, 1996). Accordingly, Hartnett & Wilson (1999) have shown that suppression of mycorrhizal fungi, through a mycorrhizal fungal-specific fungicide, resulted in an increase in floristic diversity in a tallgrass prairie, likely because the dominant C4 grasses in that system are more strongly responsive to mycorrhizal colonization than the other species present. Therein, the competitive dominance of a mycorrhized plant may be related to his mycorrhizal dependence and his position in the local dominance hierarchy (Urcelay & Diaz, 2003).

Different plant species can be compatible with the same species of mycorrhizal fungi and be connected to one another by a common mycelium and to a large extent, plants within communities can be interconnected and form a common mycorrhizal network based on their shared mycorrhizal associates (Francis & Read, 1984; Simard et al., 1997; Selosse et al., 2006; Richard et al., 2009; Diédhiou et al., 2010). Common mycorrhizal networks either could originate from fungal genets colonizing neighboring roots during their growth, but also from hyphal fusions uniting previously separated mycelia (Selosse et al., 2006). Transfer of carbon, nitrogen, and phosphorus (Finlay & Read, 1986; Newman & Eason, 1993; Simard & Durall, 2004; Selosse et al., 2006) are well documented between interconnected plants and, exchanges may occur either with conspecific and interspecific plants. One important ecological consequence of nutrient transfer through common mycorrhizal networks is that adult plants could favor early establishment of conspecific or interspecific seedlings (Newman, 1988; Simard & Durall, 2004) but also, subordinate species could be maintained in plant community due to nutrients uptake from mycorrhizal mycelia guilds (Hoeksema & Kummel, 2003; Smith & Read, 2008). Over 400 non-photosynthetic species from 10 families of vascular plants obtain their carbon from fungi and are thus defined as myco-heterotrophs (Leake, 1994). Many of these plants are epiparasitic on green plants from which they obtain carbon by likely '*cheating*' shared mycorrhizal fungi (Selosse et al., 2002; Leake, 2004). Most epiparasitic plants examined have been shown to depend on ectomycorrhizal fungi networks for carbon transfer and exhibit exceptional specificity for these fungi. Recently, Bidartondo et al. (2002) show that non-photosynthetic plants associate with AM fungi and can display the characteristic specificity of epiparasites.

Also, Grime et al. (1987) hypothesized that their detected increase in plant species diversity in turfgrass microcosms in response to the presence of mycorrhizae was due to extensive mycelial networks facilitating interplant resource transfer *via* hyphal connections. They postulated that, allowed small, suppressed plants to obtain carbohydrates from the larger, dominant species *via* shared mycorrhizal hyphae, ultimately increased the equitability of species abundances. These same authors then suggested that the "export of assimilate from 'source' (canopy dominants) to 'sink' (understory components) through a common mycelial network may be an important mechanism for the maintenance of multi-species assemblages in infertile soils". Nevertheless, Pfeffer et al. (2004) found no evidence to support the movement of carbon between interconnected roots of AM plants.

Contradictorily, it is crucial to consider that mycorrhizal networks may, in certain situations, lead to lower diversity if one species in the network is the dominant sink for nutrients (Connell & Lowman, 1989; Allen & Allen, 1990). This case is well illustrated by the ability of some nonnative invasive plant species to divert to their advantage carbon and nutrients (P) transfers through the common mycelial network, thus severely reducing the growth performance of native plants (Zabinski et al., 2002; Carey et al., 2004). In the same line of ideas, some findings did document that the common mycorrhizal networks may maintain tropical monodominance. Tropical rainforest is known to harbor a hotspot of tree diversity; however, tree diversity is not uniformly diverse, and the existence of tropical monodominance, i.e. where a single tree species dominates the canopy, is one example of the extreme variation found in rainforests (Torti et al., 2001; Leigh et al., 2004). Indeed, McGuire (2007) reported a positive distance-dependant distribution and survival with respect to conspecific adults, suggesting that the negative distance-dependant mechanisms at the seedling stage thought to maintain tropical rain forest diversity (Janzen, 1970; Condit et al., 1994; Harms et al., 2000) are reversed for ectomycorrhized seedlings, which experience positive feedbacks from the EM network. The incorporation of seedling roots to the common EM network served as an effective mechanism for higher seedling survival in the monodominant forest, potentially providing seedlings with photosynthate from overstory individuals of the same species (McGuire, 2007).

The results of these various experiments indicate the potential that the movement of plant resources through hyphal interconnections may be an important mechanism influencing plant species interactions and community structure in grasslands and other plant communities. However, results are equivocal and much further studies are needed to determine whether this mechanism plays a significant role in patterns of species abundances and diversity in natural communities. In addition, the methodological limitations and difficulties in measuring the patterns and consequences of this phenomenon in the field will be the greatest challenge (Hartnett & Wilson, 2002).

Mycorrhizal associations have recently been reported to counterbalance the allelopathic effects of exotic fast growing trees against native herbaceous plant species community adjacent to stands of exotic plants. In experiments carried out in greenhouse in Sahelian conditions, Sanon et al. (2006) and Kisa et al. (2007) observed that previous inoculation of exotic trees, *Gmelina arborea* or *Eucalyptus camaldulensis*, with the AM fungus *Glomus intraradices* significantly increased the growth of native herb species in the mesocosms where the trees were cultivated; thus favoring coexistence of exotic trees and native understory herbaceous plants. In the same lines of ideas, from experiments carried out in greenhouse conditions, we observed that the growth of native *Acacia* species was severely reduced in the soil invaded by *Amaranthus viridis*, an annual weed native from Central America (Sanon et al., 2009). Interestingly, the inoculation of *G. intraradices* was highly beneficial to the growth and nodulation of *Acacia* species. From both studies (inoculation of exotic fast growing trees to alleviate their allelopathic effect against endogenous communities and inoculation of native *Acacia* species to favor their reestablishment in soils displaying severe alteration of chemical and microbial characteristics due to invasion of *A. viridis*), the authors postulated that the beneficial effect of AM fungus inoculation may result from either the well-developed mycelial network owing equalization of distribution of soil resources among competitively dominant and subdominant plant species (Grime et al., 1987; Wirsel, 2004) or allelochemical-mediating effects from AM fungi which altogether with their mycorrhizosphere microbial communities are known to inactivate or catabolize toxic compounds (Pellissier & Souto, 1999; Blum et al., 2000). Similar results regarding restoration of native plant diversity by utilizing AM fungi have also been reported in southern California by Vogelsang et al. (2004). In these ecosystems, most native weed plant species were dependent on AM symbioses for optimal growth. Conversely, growth of many of the pernicious exotic weedy species was not improved, and could be reduced by these fungi. Then, inoculation of AM fungi enabled speeded establishment of vigorous locally adapted vegetation in these areas, which will ultimately reduced exposure of natural communities to the forces of erosion.

In combination to their direct effects on their host plants, mycorrhizal fungi may influence plant communities indirectly through their effects on interactions between plants and their herbivores, pathogens, pollinators, and other microbial patners (Finlay &Soderstrom, 1989; Wurst et al., 2004 ; Cahill et al., 2008 ; Gehring & Bennett, 2009). In turn, these interactions can indirectly and, occasionally directly influence mycorrhizal fungal communities and their functions (Eom et al., 2001; Gehring & Bennett, 2009). Accumulating evidence suggests that indirect effects of mycorrhizae may be of great relevance in plant communities' composition and dynamics and should not be ignored (Hartnett & Wilson, 2002). Such complex, multitrophic interactions still remain not enough documented and may strongly vary in time and space. In addition to plant P and N content, other plant compounds, such as secondary metabolites (Gange & West, 1994; Koide, 2000), are affected by AM fungi root colonization. Changes in foliar chemistry may influence plant herbivore interactions and, herbivore performance has been reported to be positively affected (Gange & West, 1994; Gange et al., 1999) or negatively (Gange & West, 1994; Gange, 2001) by AM fungus colonization, depending on plant, herbivore and fungal species present. Ecosystem multitrophic interactions may result ultimately in subsequent effects on plant fitness, community composition and distribution. These ecological data underscore the importance of above-and belowground linkages and indicate that alterations in mycorrhizal and rhizosphere processes can have large indirect effects on plant communities through their effects on plant responses to above- and belowground consumers.

3.2. SPECIES REPLACEMENT IN PLANT COMMUNITY

Species replacement could be considered as a mechanism to ensure plant diversity mainly in the situation where some individuals of a dominant species are progressively replaced by individuals of a single one or several other species. We explicitly avoid extreme situations such as those in which for instance, a species B completely displaces a species A as in this case we assist to species replacement during succession rather than long-term coexistence (Van der Putten et al., 1993).

Plant species ability to specifically associate with particular symbionts could be of crucial importance in mediating species replacement during succession. Mycorrhizal associations are relatively ubiquitous and act to increase access to soil nutrients. The availability of P and other nutrients often decrease in late succession (Walker & Syers, 1976; Lambers et al., 2008). In this concern, Reeves et al., (1979) and Janos (1980) envisioned a shift from nonmycorrhizal to obligately mycorrhizal plants from early to late secondary succession, with low levels of facultatively mycorrhizal associations throughout. Contrarily to these previous observations, more recent studies rather suggest that very mycotrophic plants species would be pioneers in early successions in certain environmental conditions, acting as '*nurse plants*' as termed by Carrillo-García et al. (1999) to promote '*fertility islands*' (Garner & Steinberger, 1989) or '*resource islands*' (Reynolds et al., 1990; Schlesinger et al., 1996) where facilitation and replacement among plants species may be highly fostered (Callaway, 1995, 1997). Again, Smith & Read (2008) also reported in sand dune and many other successional communities a shift later in succession from herbaceous plant species involved in obligate symbioses with AM fungi to woody species involved in obligate symbioses with ecto- or ericoid mycorrhizae, coincident with a shift in predominance of inorganic *vs* organic N (Read, 1993). Consistently, some authors postulated that higher host specificity of ecto- compared to endomycorrhizae leads to dominance by ectomycorrhizal species (Connell & Lowman, 1989). Nevertheless, positive feedback, operating alone, would be expected to lead to monocultures, or even, in the absence of soil building or temporal shifts in forms of nutrients (e.g., inorganic to organic N), arrested successions (Reynolds et al., 2003).

Resource partitioning mediated by soil microbes might play a role in species replacements if the forms of available nutrients (N or P) change through succession. Gorham et al. (1979) implicated fungal symbionts in such sequential partitioning. Indeed, the example of a shift from arbuscular to ecto- or ericoid mycorrhizal plant species with change in inorganic to organic forms of N, previously reported in our discussion, well illustrated this process. Others shifts in forms of nutrients over succession (e.g., nitrate to ammonium, or protein to chitin) would also provide opportunity for additional species replacements on the basis of soil resource specialization (Reynolds et al., 2003).Again, Reynolds et al. (2003) also document that as the diversity of microbes and nutrient inputs increase over succession, the opportunity for microbially mediated differentiation in resource use would increase, promoting increase plant community diversity over succession. Supporting this idea, ectomycorrhizal infectiveness and diversity has been found to increase over a successional gradient (Boerner et al., 1996). In addition, mycorrhizal fungi associations typically exhibit higher levels of specificity as successions proceeds and, some authors envisioned the same pattern for the majority of microorganisms involved in mediating resources differentiation, thus predicting that greater opportunities for species coexistence (i.e., greater specialization of resource niches) may arise as succession proceeds (Reynolds et al., 2003, Smith & Read, 2008).

Negative feedback dynamics have been reported on plant growth through changes in the composition of their mutualistic fungal symbionts, AM fungi, deriving from plant host-mycorrhizal symbiont specificity (Bever, 2002b). Negative feedback results from asymmetries in the delivery of benefit between plant and AM fungal species in which the AM fungus that grows best with the plant *Plantago lanceolata* is a poor growth promoter for *Plantago*. Growth of *Plantago* is, instead, best promoted by the AM fungal species that accumulate with a second plant species, *Panicum sphaerocarpon*, which is not inhibited in its soil of culture. The resulting community dynamic leads to a decline in mutualistic benefit received by *Plantago* and that effect contributes to the coexistence of these two competing plant species (Bever, 2002b).

CONCLUSION

Overall, evidence suggests that the presence or absence of mycorrhizal fungi, the growth responses (nutrient uptake improvement but certainly mycorrhizal mediation of other biotic interactions such as plant-herbivore or plant-pathogen interactions also) or mycorrhizal dependency of host plant species, differential plant species responses to particular species of mycorrhizal fungi may be potentially important factors shaping the performance and relative abundance of plant species within local communities.

Nevertheless, complementary experimental works remain needed for a better understanding of whether mycorrhizal community density may impact on plant community composition and dynamic. For instance, at a high concentration of mycorrhizal inoculum, infection by the symbiotic fungi is thought to become detrimental rather than beneficial because heavily infected plants might experience a large carbon removal that outweighs any benefit (Gange & Ayres, 1999; Hart et al., 2003). Experimental works must then be undertaken to fully address the outcome of plant – plant relationships in a context of high mycorrhizal soil infectivity.

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