Chapter 7
Facilitation and Antagonism in Mycorrhizal Networks

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Abstract Arbuscular mycorrhizal (AM) fungi are a group of soil and root inhabiting fungi that represent an ancient plant-fungi symbiosis. These fungi interconnect multiple plant individuals and species simultaneously generating a complex fungal network belowground that plays a significant role in shaping plant community composition and ecosystem productivity. However, the underlying mechanisms as to how AM fungal networks and their diversity influence plant performance and community structure are not always predictable and are frequently debated. Although all potential plant hosts may be able to associate with all AM fungi, plant-AM fungal associations can result in a range of AM fungal facilitative and antagonistic effects on plants. Although the facilitative effects of AM fungi have long been studied, the extent and mechanisms of AM fungal antagonistic effects are much less understood. Moreover, AM fungi are observed to vary in their functional properties and temporal patterns adding further complexity to the potential mechanisms by which AM fungi and the diversity of AM fungi determine plant community composition and productivity through their facilitative and antagonistic effects on plants. Here we review the potential mechanisms by which AM fungal communities facilitate greater diversity and productivity in plant communities, as well as the potential mechanisms by which AM fungi may be antagonistic to plant performance. Specifically we address how AM fungal communities might facilitate

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greater plant community performance through functional complementarity among AM fungi as a result of functional, spatial and temporal niche segregation. We also address facilitative and antagonistic aspects of AM fungi through their ability to allocate resources among plant community members that consequently facilitates plant recruitment and alters plant-plant competitive outcomes. By considering the multiple facets by which AM fungi may be facilitative or antagonistic to plants we identify potential knowledge gaps in mechanistically predicting how AM fungal communities shape plant community composition and maintain ecosystem productivity.

Keywords Facilitation · Antagonism · Mycorrhizal diversity · Functional complementarity · Community composition · Niche segregation · Phylogenetic dispersion · Competition · Biodiversity · Arbuscular mycorrhiza · Community ecology · Functional diversity

7.1 Introduction

It is thought that the first land plants formed arbuscular mycorrhizal (AM) fungal associations more than 400 million years ago and that this plant-fungal interaction played a significant role facilitating the establishment of the first terrestrial plants (Remy et al. 1994; Brundrett 2002). To date, the majority of land plants have maintained AM fungal associations (Harley and Harley 1987; Wang and Qui 2006; Smith and Read 2008). Only around 18–26 % of all vascular plants do not support symbiosis with AM fungi (Brundrett 2009). Some of these plants have developed alternative nutritional strategies (e.g. parasitism, carnivory, cluster roots), while others have lost the ability to become mycorrhizal by evolving under scenarios non-conducive for AM fungi and/or where AM fungal associations were no longer beneficial, but antagonistic (Brundrett 2009; Lambers et al. 2010; Lambers and Teste 2013). Several other mycorrhizal types developed over the past millennia, such as ericoid, ecto-, and orchid mycorrhizas (see Peterson et al. 2004 for an overview). Although these different types of mycorrhizal fungi hold key roles in ecosystems and perform specific functions, here we primarily focus on AM fungi.

AM fungi typically form direct symbiotic relationships with their host plants. This occurs via an intraradical nutrient exchange interface where photosynthetically derived carbons are allocated to the fungus, and in reciprocation, soil nutrients are provided to the plant (Smith and Read 2008). These soil nutrients are acquired by extensive AM fungal networks that interconnect roots of several different plants with potential impacts on the associating and non-associating plant communities (Reynolds et al. 2003; Leake et al. 2004; Selosse et al. 2006; van der Heijden and Horton 2009; Smith et al. 2009). The bidirectional relationship between AM fungi and plants is a key component of most terrestrial ecosystems as it shapes plant community composition, succession and productivity (Francis and Read 1994; Bever et al. 1997; van der Heijden et al. 1998; Bever et al. 2010).

However, the mechanisms by which AM fungal networks alter plant performance and plant community characteristics are more complex than a sole nutritional exchange between plants and fungi. It is now known that AM fungi can perform functions other than supplying limiting nutrients to plants (e.g. provide protection against pathogens, Newsham et al. 1995). A growing number of studies indicate that AM fungi can be associated with a decrease in plant productivity (Francis and Read 1995; Klironomos 2003; Rinaudo et al. 2010; Veiga et al. 2011, 2013). Such findings reveal the mycorrhizal symbiosis to be multi-functional and much more dynamic than previously thought. Consequently, a range of plant and fungal responses to the mycorrhizal association are potentially possible (Fig. 7.1; Francis and Read 1995; Johnson et al. 1997; Jakobsen and Hammer Chap. 4, this volume).

Plant—AM fungal associations are typically considered a mutualistic relationship implying both plant and fungal partners benefit from the association (Fig. 7.1). However, it is difficult to quantify the benefits and costs to AM fungi since these fungi are solely dependent on a plant host for carbon (Pfeffer et al. 1999). Thus, AM fungal responses to a plant host may be generally considered as positive (Smith and Read 2008; Whitfield 2007). For this reason we discuss facilitation and antagonism from a phytocentric viewpoint. We refer to facilitation as a positive plant response and antagonism as a negative response by a plant to interactions with AM fungi (Fig. 7.1). Plant responses to AM fungi are not easy to predict since the forces that govern facilitative and antagonistic effects of AM fungi are understood to be fairly complex and dynamic. For instance, the outcome of interactions between AM fungi and their host plants depend on a multitude of factors like plant species identity, the stage of development, the identity and diversity of the fungal partners, and the surrounding abiotic environment. In addition, both facilitative and antagonistic interactions between AM fungi and their plant hosts can occur via direct mechanisms, such as through an imbalance in the resource exchange between fungi and associated plants (Kiers et al. 2011; Walder et al. 2012; Merrild et al. 2013), as well as indirect mechanisms such as AM fungal mediated plant-plant competition (Fitter 1977; Zobel and Moora 1995; Wagg et al. 2011a; Merrild et al. 2013). Here we

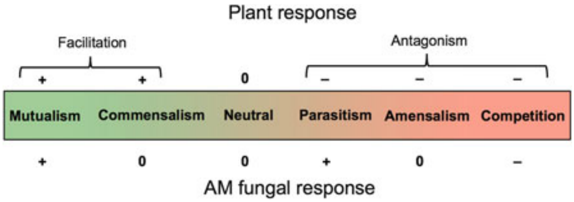

Fig. 7.1 The range of possible plant and fungal responses to mycorrhizal associations (modified from Francis and Read 1995). We refer to facilitation as a positive plant response and antagonism as a negative response by a plant to interactions with AM fungi. This effect can be mediated by many factors, such as the presence of neighboring plants or abiotic conditions

review the current knowledge and concepts regarding the mechanisms responsible for facilitative and antagonistic effects of AM fungi on associating plant communities. Finally we summarise the importance of furthering the current knowledge based on this dynamic plant-fungal relationship for the maintenance and productivity of both natural and managed ecosystems.

7.2 Facilitation

The facilitation of plant establishment and performance by AM fungi in ecosystems can occur through various mechanisms (see Table 2 in van der Heijden and Horton 2009 for an overview). Typically, plants associating with AM fungal partners benefit from a direct relationship where the fungus improves the ability of the host plant to acquire soil resources. Plant productivity may also be facilitated by the extensive hyphal networks in the soil that connects multiple plants; frequently referred to as a 'mycorrhizal network' (MN) in that a continuous fungal mycelium can connect to multiple plants of various species (e.g. Fig. 7.2; Selosse et al. 2006; Kiers et al. 2011; Walder et al. 2012). This MN can mediate the performance among plants (e.g. van der Heijden and Horton 2009). For instance, the support for AM hyphal proliferation and maintenance of the fungus by plants can increase the inoculation potential in the soil such that seedlings become more rapidly colonized, which can improve seedling establishment and may reduce the cost the establishing

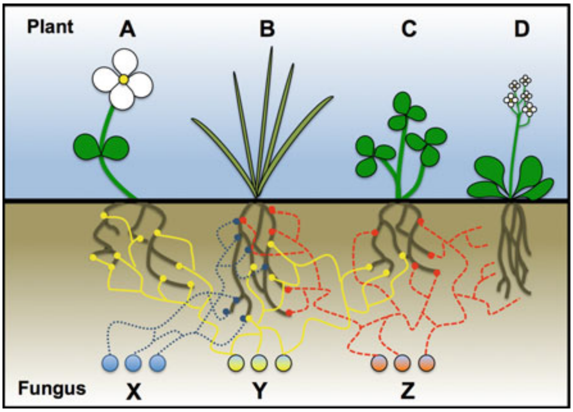

Fig. 7.2 An Illustration of associations between a plant community (species *A*, *B*, *C*, and *D*) and a fungal community (species *X*, *Y*, and *Z*). Hyphal networks are illustrated as different line types with colors corresponding to the originating fungus. *Points* where lines meet plant roots indicate the strength in association between the plant and fungus (i.e. fungus *Y* has 9 connections with plant *A*, while only 3 with plant *C*. Plant *D* does not associate with any AM fungus and is defined here as a non-host). *Note* the number of associations could represent abundance within the plant roots or a relative number of plant *A* individuals associating with fungus *Y*

plant needs to invest into the fungal association to improve its performance (e.g. Newman 1988; van der Heijden 2004; van der Heijden and Horton 2009). The production and maintenance of an extensive mycorrhizal network by plants can also have indirect effects on soil environmental characteristics that may be favourable to the establishment and performance of some plants, such as reduced nutrient leaching (van der Heijden and Horton 2009), improved stability in the soil structure (Rillig and Mummey 2006) and the liberation of nutrients from senescing roots and plant litter (Lindahl et al. 2007; Mikkelsen et al. 2008). It is important to note, however, that not all fungi function similarly or benefit plant hosts equally (Nara 2006). AM fungi can vary in their functional niche, from resource acquisition strategies to pathogen protection, and vary in their interaction with plants depending on the species identity of both the fungus and host plant (Klironomos 2003; Powell et al. 2009; Sikes et al. 2009; Hoeksema et al. 2010). As a result there has been a growing interest in whether the differing functions performed by various AM fungi complement each other such that a greater diversity of AM fungi might facilitate greater plant community performance as it is often observed that greater AM fungal richness can be associated with greater plant performance (van der Heijden et al. 1998; Maherali and Klironomos 2007; Jansa et al. 2008; Wagg et al. 2011b).

This positive AM fungal biodiversity effect on plant performance could occur by three mutually non-exclusive mechanisms; functional complementarity, spatial niche segregation and temporal niche segregation. These differences among AM fungi are the foundation by which they can facilitate plant performance and plant community composition. In this chapter we review (1) how the varying functions performed by different AM fungal taxa might be combined to improve the plant facilitative effects of an AM fungal community, (2) the potential for spatial and temporal niche segregation as mechanisms of complementarity among AM fungi, (3) how AM fungi relax plant-plant competitive interactions to promote plant species coexistence, and (4) how AM fungi facilitate plant communities through a common mycorrhizal network.

7.2.1 Functional Complementarity in AM Fungal Communities

The AM fungal association may benefit plants through the various different functions and characteristics associated with different AM fungal taxa (Powell et al. 2009). For example, plants have been shown to benefit from various AM fungal taxa that increase plant community biomass (van der Heijden et al. 1998), increase uptake of phosphorus and other soil resources (Joner and Jackobsen 1994; Smith et al. 2009; Marschner and Dell 1994; Hodge et al. 2001), and improve plant pathogen and pest protection (Gange and West 1994; Newsham et al. 1995; Azcón-Aguilar and Barea 1996). Additionally, AM fungi can vary in the strategies by which they acquire soil resources (Smith et al. 2000; Jansa et al. 2005; Thonar et al. 2010). These functional differences among AM fungal taxa could potentially complement each other to improve the overall facilitative effects of an AM fungal community on plant performance (Koide 2000; Fig. 7.3). For example, fungi co-colonising roots of the same host have been demonstrated to differ in phosphorus acquisition strategies, where one fungus acquires phosphorus within close proximity to the roots, while another acquires phosphorus from colonizing soil patches at greater distances from the root (Smith et al. 2000; Jansa et al. 2005; Thonar et al. 2010; see Wallander and Ekblad Chap. 3, this volume). Therefore increasing the number of AM fungi within the soil that interact with the plant community could theoretically increase the facilitative effects of the AM fungal community.

Indeed it has been shown that increasing AM fungal richness can be related to improved plant productivity in a number of studies suggesting that, in some cases, plants may gain greater benefits from multiple AM fungal associations (van der Heijden et al. 1998; Vogelsang et al. 2006; Maherali and Klironomos 2007; Wagg et al. 2011b). However, it is also often unclear if the functioning of the AM fungal community as a whole is truly greater than the sum it its parts. For example, some studies illustrate that a richer community of AM fungi provides similar benefits as the single most beneficial AM fungus in the more species rich community (Jansa et al. 2008; Wagg et al. 2011a, b). Subsequently, this has been associated with the

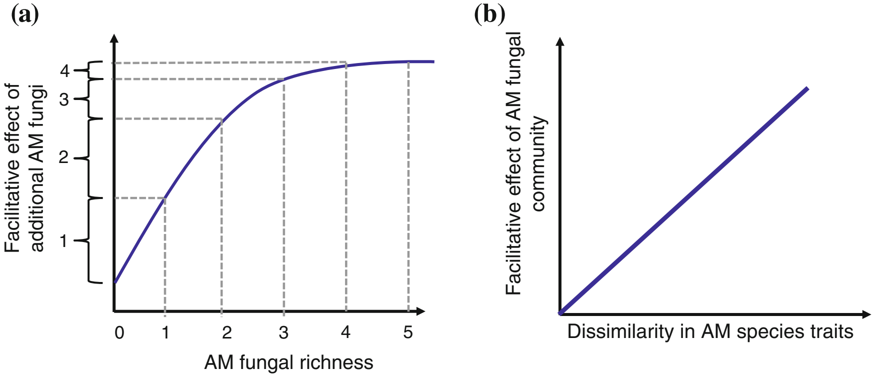

Fig. 7.3 The facilitative effects of additional AM fungi as AM fungal taxa richness increases are shown in panel (**a**). Each additional fungus is able to provide an additional service to plants and it thus, provides an additional improvement to plant performance (functional complementarity). Plant productivity and AM functions are not infinite. Therefore, facilitative effects plateau where all services AM fungi can provide to the plant host are saturated and additional fungi do not improve plant productivity (additional fungal taxa are functionally redundant in improving plant productivity). The facilitative effect of increasing AM fungal dissimilarity among traits (e.g. functional, spatial, or temporal variation among AM fungi) is shown in panel (**b**). Dissimilarity among AM fungi (i.e. plant host or soil substrate patch preference-specificity, as well as seasonal differences) could be represented within the dissimilarity along the *x*-axis. The facultative effect of the overall AM fungal community on the overall plant community is indicated on the *y*-axis

occurrence of a sampling probability or selection effect (e.g. Vogelsang et al. 2006). In general, this implies that a particularly effective fungus is supporting the overall facilitative effects of the AM fungal community, as opposed to a communal contribution of AM fungi to plant facilitation. Therefore additional AM fungal species increases the probability of including such a particularly effective fungus (Wardle 1999). Caution should hence be warranted when interpreting biodiversity effects of increasing AM fungal richness based on plant performance alone and the effect of each individual AM fungus should be considered to elucidate whether the greater facilitative effect of a more rich AM fungal community is driven by all or only a few of the fungal taxa present (see Wagg et al. 2011b).

Whether the facilitative effects of a more diverse AM fungal community are driven by the communal contribution of the fungi, or the probability of a particularly effective AM fungus, is likely context dependant. For instance, both scenarios have been shown to occur depending on the fertility and structure of the soil substrate (Wagg et al. 2011b). By assessing the community composition of AM fungi colonizing plants and the facilitative effects of all AM fungi independently in monoculture, Wagg et al. (2011b) were able to illustrate the mechanisms behind the facilitative effects of a more diverse AM fungal community. In a relatively nutrient poor sandy soil the fungus best fit for the environment was able to dominate the facilitative effects of more diverse AM fungal community—referred to as a “selection effect” (Loreau and Hector 2001). Conversely, in a relatively more fertile environment, the same fungal communities provided similar facilitative effects but were driven by a more even contribution of AM fungi—referred to as a “complementarity effect” (Loreau and Hector 2001). This indicates that the resources available in the environment can mediate AM fungal coexistence and their communal functioning.

It is also important to consider that the differences in services AM fungi provide for plants can be associated with phylogeny (Maherali and Klironomos 2007; Powell et al. 2009). In a keystone paper on the function of AM fungal diversity Maherali and Klironomos (2007) demonstrate the potential for using phylogenetic dispersion in AM fungal communities as a predictor of facilitative effects. They show that AM fungal communities consisting of a mixture of AM fungal taxa from the Gigasoporaceae, Acaulosporaceae, and Glomeraceae families could improve plant productivity more than an AM fungal community comprised of taxa from a single family. Perhaps even more intriguing in the study by Maherali and Klironomos (2007) is that the realized richness in the AM fungal community was greatest when the AM fungal community, initially consisting of 8 taxa, consisted of fungi from all three AM fungal families. This indicates greater phylogenetic dispersion as a mediator of greater coexistence among AM fungal taxa and their facilitative effects.

7.2.2 *Spatial and Temporal Niche Segregation as a Mode of Complementarity*

Results, such as those previously discussed by Maherali and Klironomos (2007) and Wagg et al. (2011b) provide evidence for a link between AM fungal coexistence and facilitation in AM fungal communities. Trade-offs between competition and performance are fairly common and an important aspect in understanding the functioning of communities (Herms and Mattson 1992; Mouquet et al. 2002). Bennett and Bever (2009) illustrate that the ability of an AM fungus to compete with another AM fungus has a trade-off with the ability to facilitate the performance of the host plant. Considering this, facilitation by an AM fungal community can be maintained at a higher level if competition among AM fungi is avoided by not only functional differences, but also by spatial segregation among AM fungi (Bever et al. 2009). This could arise from the colonization of different soil resource patches, such as mentioned previously concerning phosphorus acquisition strategies (e.g. Jansa et al. 2005), but also through host preference and functional compatibility between specific plant and fungal taxa (Ravnskov and Jakobsen 1995; see Molina and Horton Chap. 1, this volume). Although no true host specificity is known to commonly occur between AM fungi and plant taxa, certain plant-fungal species combinations have been known to be more effective than others (Klironomos 2003). Additionally, preferences toward particular host plants have been shown to occur in natural environments (Sanders 2003; Vandenkoornhuyse et al. 2003; Croll et al. 2008). This avoidance of competition among AM fungi through differences in plant host preferences may allow for the potential that different fungi differentially benefit the various potential host plants such that increasing AM fungal richness increases the potential of the AM fungal community to improve the overall plant community productivity.

The competition among AM fungi may also be avoided by their temporal life strategies. Different taxa of AM fungi are known to be active during different seasons (Gemma et al. 1989; Merryweather and Fitter 1998; Dumbrell et al. 2011) and show successional patterns across years (Oehl et al. 2009). Such functional, spatial, and temporal segregation could aid in the avoidance of competition among AM fungi and result in greater facilitative effects on host plants. This may be an explanation why certain combinations of AM fungi have been shown to be more beneficial than others (e.g. Wagg et al. 2011b). It is thought that temporal variation among plant species life strategies and performance is an underlying mechanism by which a greater diversity of plant species can coexist and contribute to the performance of the community (Loreau and de Mazancourt 2013). In a similar manner, the temporal variation among AM fungal taxa in their life strategies (e.g. Gemma et al. 1989; Merryweather and Fitter 1998; Oehl et al. 2009) may also reduce AM fungus-fungus competition and, as a result, consistently maintain the benefits the plant community gains from the AM fungal community over seasonal changes. However, it is not fully known whether such temporal asynchrony in the activity among AM fungi is a mechanism for reducing niche overlap and competition among AM fungi. Moreover, it has yet to be tested whether temporal variation among AM taxa is a potential mechanism by which an AM fungal community can function complementarily to help maintain ecosystem productivity.

Much research is still required to fully unravel the mechanisms by which the facilitative effects of AM fungal communities can be improved. However, current knowledge suggests that community dissimilarities—spatially, temporally and functionally—among individuals has much to offer to the understanding the mechanisms behind the performance of diverse AM fungal communities (see Fig. 7.3b). Specifically, (a) improving dissimilarity through reducing niche overlap spatially, temporally and functionally (b) improving the phylogenetic dispersion within an AM fungal community and (c) improving the resource heterogeneity available for AM fungi, may be particularly promising avenues for the future.

7.2.3 Facilitation Through Mediating Plant—Plant Interactions

An increase in the number of plant species in grasslands has been shown to result in increasing net plant productivity (e.g. Tilman 1996; Hector et al. 1999; Tilman et al. 2001). If this species richness productivity relationship is driven by the contribution of each additional plant species present, it requires that the additional plant species is able to capture the resource margin, such that it is able to improve the productivity of the community (Loreau and Hector 2001, also see Fig. 7.3a for an example). Differences among plant species in their ability to utilize different resource pools has previously been observed to be one mechanism by which sympatric species coexist and contribute to the overyielding in plant species mixtures (McKane et al. 2002; Harrison et al. 2007; Ashton et al. 2010). Considering AM fungal associations play a pivotal role in the ability of plants to acquire soil resources, there is a large potential for mycorrhizal fungal associations to alter plant coexistence, promote productivity in plant communities, and drive aboveground biodiversity ecosystem functioning relationships.

Indeed past studies have shown AM fungal associations are able to improve coexistence, productivity, and overyielding in plant communities (van der Heijden et al. 1998; Maherali and Klironomos 2007; Wagg et al. 2011a, b). Often the increased access to phosphorus and other soil resources through the direct association is attributed to the beneficial effects of AM fungal associations in plant communities, particularly when these resources are limiting for plant growth (Hoeksema et al. 2010; Johnson 2010). This ability of AM fungi to acquire and mobilize soil recourses otherwise unavailable to plants can therefore ease competitive interactions between plants by increasing the overall resource pool available to the plant community. Klironomos et al. (2000) nicely illustrate how the addition of AM fungi alters the resource space utilized by plant communities. They found the presence of AM fungi resulted in productivity reaching saturated levels at lower plant species richness. This demonstrates that fewer plant species were required to utilize the resources available and achieve maximum productivity when AM fungi were present. In comparison, the absence of AM fungi resulted in a linear relationship between plant richness and productivity showing that additional plant species were needed to capture marginal soil resources to improve the productivity of the community. One outcome of this may result from plants dependent on AM fungal associations performing poorly in plant mixtures in the absence of AM fungi as they are unable to access soil nutrients efficiently and are outcompeted by neighboring plants. It is generally established that in the presence of AM fungi, the fungi mediate the access to resources between competing plants by sequestering soil resources for the less competitive AM dependent plant (Fitter 1977; Hartnett et al. 1993; Zobel and Moora 1995; Urcelay and Diaz 2003; Scheublin et al. 2007; Collins and Foster 2009; Wagg et al. 2011a; Veiga et al. 2011). However, this can depend on the AM fungal dependency of the dominant species within a plant community (Urcelay and Diaz 2003). For instance, in a tall grass prairie Hartnett and Wilson (1999) found the suppression of AM fungi by the use of fungicide reduced the performance of the dominant C4 grasses resulting in a greater performance of the subdominant C3 grasses. This overall competitive shift resulting from reduced AM fungal abundance improved the overall diversity of the plant community.

It is important to also consider that not all coexisting plant species benefit equally from AM fungal associations and some plants depend more upon AM fungal associations for maintaining productivity than others (van der Heijden 2002; Klironomos 2003). For example, some plant species show little response to AM fungal associations, such as C3 grasses (Hetrick et al. 1990). Plants appearing not to benefit directly from a mycorrhizal association may indirectly benefit from AM fungal associations. For instance, plants supporting an AM fungal network may indirectly benefit by facilitating neighboring plants that improve the environment, such as by improving defense against a common predator or N fixation by legumes (see Fig. 7.4 for an example). Many studies have illustrated that plants can facilitate the establishment and performance of other plant species through supporting a mycorrhizal network demonstrating that plant-plant facilitation through a common mycorrhizal network to be an important ecological determinant of plant communities (van der Heijden and Horton 2009).

7.2.4 AM Fungi as a Support Network for Plants?

An AM hyphal network can co-colonize numerous intra- and interspecific plants through a common mycorrhizal network (Fig. 7.2). A number of studies have illustrated that seedlings benefit through establishing an association with an AM fungal network supported by a pre-established plant (see van der Heijden and Horton 2009 and citations therein; Nara Chap. 6, this volume). This may be a

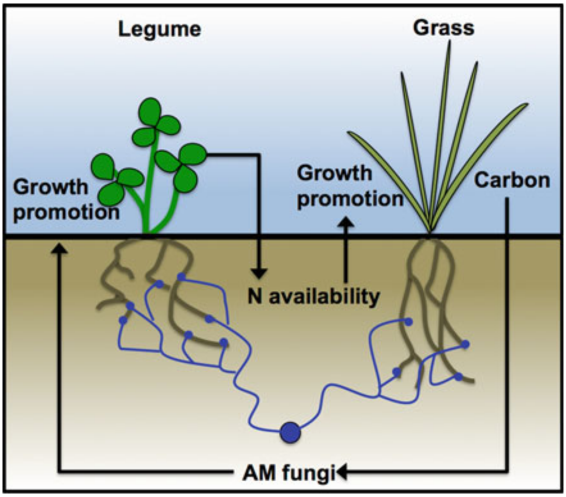

Fig. 7.4 An example of a hypothetical indirect mechanism by which AM fungi facilitate plant community productivity. For instance, facultative mycorrhizal plants, such as C3 grasses, do not typically seem to benefit directly from supporting an AM fungal association. However, considering grass-legume plant mixtures exhibit overyielding effects in agricultural and natural environments, the nitrogen demands of the grass are subsidized by a neighbouring nitrogen fixing legume that depend heavily on AM fungal associations for productivity and to support their nitrogen fixing bacteria. Therefore by supporting the development of an AM fungal community the grass may indirectly benefit from increased nitrogen availability through the improved growth of its neighbouring legume

consequence of pre-established plants investing carbon into the development and proliferation of a mycorrhizal network that other plants may benefit from (Newman 1988). This facilitative influence of an AM fungal network shared between plants can occur through an imbalance in investment to support AM fungi that co-connects plants. For instance, one plant may invest more carbon into the AM fungal association and receive little nutrients in exchange, while another plant invests little carbon while receiving greater amounts of resources (Walder et al. 2012). This is thought to be one of the potential mechanisms behind the facilitation in establishment of seedlings unable to invest large amounts of carbon to an AM fungal association (van der Heijden 2004). This facilitative effect may be of particular importance for seedling recruitment in environments where fungal networks are limiting to plant establishment, such as during succession and post disturbance (Gange et al. 1990, 1993; Korb et al. 2004; Simard and Durall 2004; Selosse et al. 2006; Nara 2006).

It has been proposed that plants associating through a MN are able to translocate carbon and nutrients along fungal networks such that the fungus is able to redistribute resources throughout the plant community, from nutrient sufficient to nutrient deficient plants (Newman 1988; Simard et al. Chap. 5, this volume). This has inspired studies in the past to explore whether plants can aid neighbouring plants co-colonized by a shared AM fungal network. It has been proposed that the previously established larger "nurse plant" could provide resources, such as nitrogen, phosphorus and carbon, to neighbouring plants via the shared mycorrhizal network (Chiarello et al. 1982; Francis and Read 1984; Francis et al. 1986). For instance, there is some evidence that the transfer of phosphorus and nitrogen between plants through a shared mycorrhizal network can occur (He et al. 2003; Wilson et al. 2006). However, although resources may be transferred between plants via an AM fungal network, there is little supporting evidence that these resources are actually transferred directly from the AM fungi to the host and incorporated into plant organs aboveground.

It has been known that atmospheric carbon captured by a plant is allocated to the AM fungal partner and transferred into the roots of a neighbouring plant through its incorporation in the AM fungal tissue colonizing the roots (Graves et al. 1997; Fitter et al. 1998; Zabinski et al. 2002). However, these studies conclude that the carbon is retained in the fungal tissue and not transferred to the host plant, therefore providing no direct facilitative benefit to the plant. Overall, however, it is unclear whether shared AM fungal mycorrhizal networks provide means for a direct reallocation of resources between plants (Robinson and Fitter 1999; Selosse et al. 2006). The translocation of resources between plants by AM fungi may result indirectly through hyphal turnover and microbial mediated diffusion through the soil (Robinson and Fitter 1999). In general the consensus regarding the direct translocation of carbon among plants via AM fungal networks for the benefit of a neighbouring connected plant does not seem to hold up as an ecologically meaningful mechanism by which AM fungi facilitate plant community composition and productivity (Robinson and Fitter 1999; Bever et al. 2010; van der Heijden and Horton 2009). However, the translocation of nitrogen and phosphorus between plants via AM fungal networks and the ecological consequences of resource redistribution throughout the soil via the extensive AM hyphal networks remain largely unresolved (but see Lekberg et al. 2010 and Weremijewicz and Janos 2013).

It is important to consider that carbon allocation to the fungus does not necessarily reflect a cost to the plant. In many ecosystems nutrients are limiting plant growth and genes responsible for photosynthesis are down-regulated as carbon (e.g. as starch) accumulates in the plant. Hence, if this is the case, carbon can be considered a luxury good for the plant and investment into mycorrhizal networks may not produce a cost for the plant (e.g. Kiers and van der Heijden 2006). As such fungi merely stimulate the sink strength and do not reduce the amount of carbon available for growth. This scenario is most likely to be relevant for strongly nutrient limited ecosystems where photosynthesis does not run at full capacity (e.g. Qui and Israel 1992, Poorter and de Jong 1999). Thus, the facilitative effects of mycorrhizal networks are likely to be related to soil nutrient availability.

7.3 Antagonism

Although facilitative effects of AM fungi are commonly observed, AM fungi have also been known to be associated with growth depressions and other negative effects on affiliated plants (Jakobsen and Hammer Chap. 4, this volume). The fact that such effects have not only been reported in pot experiments, but also in field conditions, suggests that AM fungal antagonism is not a mere artifact (Smith and Smith 2011). Nonetheless, as in AM fungal facilitation, AM fungal antagonism is very context dependent and may change through time (Johnson 2010). Moreover, most studies usually focus on one or few indicators of plant performance, usually growth responses or nutrient uptake (typically phosphorus; Johnson and Graham 2013). Hence, an apparently plant growth antagonistic AM fungal association might may be regarded as beneficial if other AM fungal functions are considered throughout the life cycle of the plant (e.g. seedling establishment, protection against pathogens, drought tolerance, fecundity, etc.).

Recently, there has been growing interest in the antagonistic effects of AM fungi on host plants and on the drivers that may cause this typically beneficial association to become antagonistic. Therefore, several mechanisms by which AM fungal associations incur growth depressions in plants have been proposed. Many of these are similar to those by which AM fungi facilitate plant productivity, but with the opposite effect. However, generally, very little is known about the mechanisms responsible for antagonistic effects of AM fungal associations relative to facilitative effects. In this section we review mechanisms by which AM fungi may function as plant antagonists: (1) nutrient exchange imbalance between plants and fungi, (2) AM fungal mediated enhanced performance of competitors, (3) AM fungal allelopathy and activation of defence responses.

7.3.1 Plants at the Losing End of Resource Exchange

Perhaps the most well known driver of AM fungal antagonism is a consequence of the resources available to the plant for direct uptake from the soil (Johnson 2010). For instance, soils with high levels of plant available nutrients, particularly nitrogen and phosphorus, can result in a negative effect of AM fungi on plant productivity (Hoeksema et al. 2010; Johnson 2010). This effect may be particularly evident if plants do not require an AM fungal partner for acquiring resources to achieve optimal growth. Thus, AM fungal associations may provide no benefit, or incur a cost, to the plant for it to maintain the fungal association under certain abiotic conditions that limit the mycorrhizal association (Johnson et al. 1997; Graham and Eissenstat 1998; Johnson 2010). However, when conditions are not optimal for the host plant to maintain the AM fungal association, such as under high phosphorus relative to nitrogen nutrient conditions, a reduced AM fungal colonization of roots is commonly observed (Jasper et al. 1979; Thomas et al. 1986; Johnson 2010).

This would reflect a more complex resource supply and demand scenario between plants and fungi based on the plant available soil resources (Johnson 2010; Kiers et al. 2011).

Negative AM fungal effects on plant growth are hence often explained by carbon demands of the fungus that exceed any reciprocal benefit, primarily through enhanced phosphorus uptake by the plant (Tinker 1975; Graham and Abbott 2000; Smith et al. 2009). Consequently, AM fungi that induce growth depressions are usually regarded as “cheaters” or “parasites” (e.g. Johnson et al. 1997). In fact, fungal carbon demands on a plant host have been estimated to be as high as 15–20 % of its total carbon budget (Jakobsen and Rosendahl 1990; Wright et al. 1998). Additionally, some studies suggest that mycorrhizal C costs are linked to lower plant allocation to growth and defense (Buwalda and Goh 1982; Peng et al. 1993; Graham and Abbott 2000; Jifon et al. 2002; Vannette and Hunter 2011).

Recent experiments using radioactive phosphorus (^{32}P or ^{33}P) have shown that in some unresponsive or negatively-responsive plants, a great percentage of plant phosphorus is derived from the AM fungal partner (Smith et al. 2003; Li et al. 2006; Grace et al. 2009). In such situations, it seems that the AM fungus is not acting like a “parasite” by delivering little or no phosphorus to the host. It may be that the growth of such plants is nitrogen limited and additional phosphorus supply by the fungus does not lead to enhanced plant growth. Alternatively, it has been proposed that growth depressions may arise from phosphorus deficiency as a result of a decrease in direct phosphorus uptake (via plant roots) in mycorrhizal plants, that is not compensated for by the phosphorus delivered via the AM fungus (Grace et al. 2009; Smith et al. 2009; Smith and Smith 2011, 2012). Furthermore, it has been observed that, in some plants, photosynthetic rates can be stimulated by the carbon sink exerted by AM fungal colonization, counteracting mycorrhizal carbon costs (Kaschuk et al. 2009; Lendenmann et al. 2012). Together, these observations have led to an ongoing debate on how imbalanced carbon-for-phosphorus trade might be an over simplified model that cannot universally explain negative effects of AM fungi on plants and on whether the fungus is truly antagonistic (Smith and Smith 2012; Johnson and Graham 2013; Smith and Smith 2013). Regardless, nutritional exchanges between a plant and its fungal partner(s) are still a key factor determining plant responses (Johnson 2010), and might be especially important in mycorrhizal plant communities where plants are linked by a mycorrhizal network (MN).

Previously we discussed how a MN could have facilitative effects through the translocation of resources among plants. However, the MN interconnecting two (or more) plants may also have antagonistic effects. A number of studies have shown that competition between plants for soil resources can be altered due to the presence of a MN, where two neighboring plants unequally invest and benefit from a MN (Janouskova et al. 2011; Walder et al. 2012; Weremijewicz and Janos 2013; Merrild et al. 2013). Typically, a plant host will invest carbon into the AM fungal association, but the nutrient rewards from the AM fungus may be preferentially allocated to a neighbouring plant connected to the AM fungal network (Lekberg et al. 2010; Kiers et al. 2011). This could have potential negative effects to the carbon-investing plant. In these cases, the plants receiving the unwarranted benefits are referred to as "cheaters". Walder et al. (2012) nicely illustrate how carbon and phosphorus exchange rates between plant and fungus can be altered by the presence of other plants tapping into the mycorrhizal fungal network. They found that when sorghum (*Sorghum bicolor*) and flax (*Linum usitatissimum*) were interconnected by a MN, sorghum provided large amounts of carbon to the fungus and received little nutrients in return, performing marginally poorer as a result. Conversely, flax invested little carbon but gained much more in nutritional benefits from the fungus and its performance was enhanced.

Interestingly, negative effects of AM fungi on plant growth have also been observed in non-mycorrhizal plants (Allen et al. 1989; Sanders and Koide 1994; Francis and Read 1995; Rinaudo et al. 2010; Veiga et al. 2012, 2013) and in mycorrhiza-defective mutants (Neumann and George 2005; Facelli et al. 2010). These and other studies usually report AM fungal structures colonizing roots of typically non-AM fungal host plants (Ocampo et al. 1980; Horton et al. 1998; Smith et al. 1998; Wagg et al. 2008, 2011c). In nearly all cases arbuscules, the primary site for nutrient exchange between plant and fungus (Parniske 2008; Bonfante and Genre 2010), are reported as being absent. Although it is generally unknown what functional role this atypical colonization has on the plant, the absence of arbuscules suggests the lack of a trophic interaction and root infection may be more associated with the life strategy of the fungus (Wagg et al. 2011c). Therefore, imbalanced nutrient exchanges between the plant and AM fungus likely do not explain antagonistic effects of AM fungi on non-mycorrhizal plants and it is plausible that other mechanisms are involved.

7.3.2 AM Mediated Plant—Plant and Plant—AM Fungal Competition

Competition for soil resources between plants and between plants and AM fungi can result in indirect antagonistic effects of AM fungi. As discussed earlier some plants depend more upon AM fungal associations to acquire soil resources and improve their competitive ability than others. The improved resource uptake by the more AM fungal dependent plant can come at a cost to the neighbouring plants as resources are depleted. For instance, both Scheublin et al. (2007) and Wagg et al. (2011b) showed that the presence of AM fungi changed the competitive relationship between a grass and a legume species, favoring the more AM-dependent species, the legume, to the detriment of the grass. AM mediated plant-plant competition might also explain why negative effects of AM fungi on the growth of non-mycorrhizal plants (or mycorrhiza-defective mutants) are frequently observed when they co-occur with a mycorrhizal species (e.g. Sanders and Koide 1994; Facelli et al. 2010; Veiga et al. 2012, 2013, see Fig. 7.5 for an example). This mechanism is probably one of the

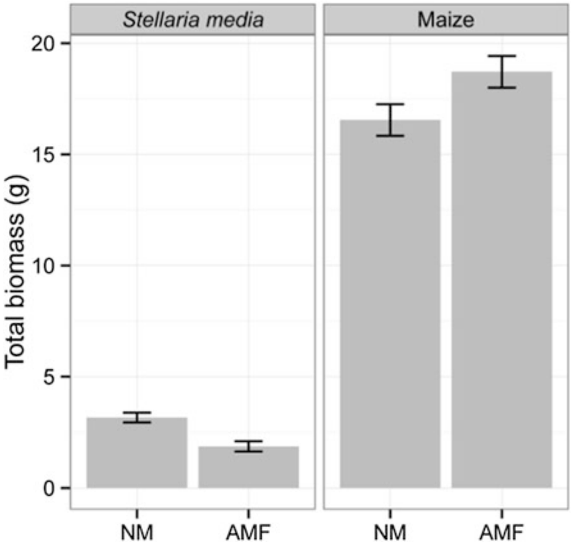

Fig. 7.5 Example of a growth depression of a non-host plant (*Stellaria media*) in the presence of an AM fungal (*AMF*) network supported by a co-existing host species (*Zea maize*). Roots of the two plant species were separated by a hyphal mesh (30 μm in size) to restrict direct root competition (see Veiga et al. 2011 for similar Methods). *Bars* represent the means ± SEM ($n = 7$) *of S. media* or maize in the presence (*AMF*) or absence (NM) of AM fungi. The total biomass of *S. media* in the presence of an *AMF* network supported by maize was lower ($P < 0.05$) than the control *S. media* plants grown in the absence of AM fungi. By contrast, the host plant maize grew better ($P = 0.05$) when AM fungi were present. This suggests that the host, maize, benefited from AM fungi through increased access to soil resources that, consequently, became unavailable to the neighbour non-host, *S. media*. (R. Veiga Unpublished data.)

primary mechanisms for plant growth depressions in a mixed plant community in the presence of AM fungi (Fitter 1977; Hartnett et al. 1993; Zobel and Moora 1995; Urcelay and Diaz 2003; Scheublin et al. 2007; Collins and Foster 2009; Wagg et al. 2011a; Veiga et al. 2011).

It is known that soil microbes can compete with plants for soil resources such as nitrogen (Kaye and Hart 1997; Schimel and Bennett 2004; Dunn et al. 2006; Harrison et al. 2007). In a similar manner, AM fungi compete with plants by taking up soil nutrients for their own growth and development (Treseder and Allen 2002; Hodge and Fitter 2010). For instance, AM fungi may compete with plants for N as considerable amounts of N have been found in mycorrhizal fungal networks (Hodge and Fitter 2010). Therefore AM fungal nutrient immobilization may also have a deleterious effect on plant performance.

7.3.3 AM Fungal Allelopathy and Activation of Defence Responses

Less explored avenues by which AM fungi may be antagonistic is through the release of toxic compounds and/or by activating plant defence responses. For instance, Francis and Read (1994, 1995) observed that aqueous extracts of soil containing AM mycelium had a direct inhibitory effect on the development of non-mycorrhizal seedlings, suggesting that AM fungi may produce allelopathic compounds. However, recently, by using two different methods Veiga et al. (2012) found no evidence that AM fungi produce compounds that suppress the growth of AM non-hosts.

In addition to growth depressions and seedling mortality, some studies have reported abnormal root structures and root development of non-mycorrhizal species in the presence of AM fungi. Allen et al. (1989) observed that inoculation of the non-host *Salsola kali* with AM fungi resulted in browning and death of infected root segments while Francis and Read (1995) reported swellings and distortion of the meristems of several non-host roots in the presence of AM mycelium. Such effects resemble a hypersensitive-like plant response (García-Garrido and Ocampo 2002), probably to limit colonization by the fungus. Such a response could directly impair the plants' capacity to take up soil resources. Furthermore, it is known that defence responses can entail costs derived from trade-offs between investment in defence and allocation of resources to plant growth and development (Walters and Heil 2007). Therefore, activation of defence responses could be another mechanism explaining growth depression and abnormalities in the non-host plants in the presence of AM fungi. This hypothesis has not been further investigated in any great detail. Interestingly however, there are indications that similar antagonistic effects of AM fungi can be reproduced on the non-host *Arabidopsis thaliana*, which is the model organism for plant molecular biology and genetics (Veiga et al. 2013). *Arabidopsis thaliana* may thereby in the future serve as a valuable tool in unravelling the molecular basis of incompatible plant—AM fungi interactions.

7.4 Concluding Remarks and Future Considerations

The facilitative and antagonistic interactions between plant communities aboveground and AM fungal communities and networks belowground are more dynamic and context dependent than previously thought. Unravelling the complexities of such interactions are pertinent for the remediation of grassland biodiversity and agricultural management. This entails understanding the functional compatibility between plants and AM fungi. The way forward in attaining a predictive understanding of AM fungal antagonistic and facilitative effects for ecological application may be in the assessment of phylogenetic and functional changes in the AM fungal community after anthropogenic disturbance. For instance, tillage damages the richness of AM fungi and potentially results in the loss of some of the services AM fungi provide to agriculturally desirable plant hosts. The phylogenetic under dispersion in an AM fungal community, indicated by the presence of few AM fungal genera or families, could be used as an indicator of where AM fungal communities may be limited in functional diversity, if phylogeny can be linked with functional complementarity and AM fungal coexistence (e.g. Maherali and Klironomos 2007). Finally, the application of niche theory and temporal community dynamics to AM fungal communities would greatly improve the knowledge base as to how environmental heterogeneity may support AM fungal diversity and thus the overall facilitative effects of an AM fungal community. Nonetheless, although the facilitative, and to a lesser extent antagonistic effects of AM fungi have been long studied, the mechanisms that control them in a predictable fashion for future ecological application have yet to be fully realized.

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