



Arbuscular mycorrhizal fungi-weeds interaction in cropping and unmanaged ecosystems: a review

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Abstract

Weeds are the cause of substantial yield loss and extinction of some native species resulting from competition with the associated species for water, sunlight, nutrients and space. Due to the widespread occurrence of arbuscular mycorrhizal fungi (AMF) and their important role in communities and ecosystems, the interaction between weed species and AMF might have an important role in ecosystem functioning. The present review characterizes AMF-weeds interactions, targeting natural and crop ecosystems. In agroecosystems, AMF have the potential to contribute to weed control (i) directly by suppressing growth of many weeds belonging to families that are non-mycorrhizal, or (ii) indirectly by enhancing competitive ability of crop species to the detriment of both mycorrhizal and non mycorrhizal weeds. Some advantages conferred by AMF-weed interaction to associated species make evidence of the importance to identify weed species that can play an important role in ecosystem performance. In unmanaged ecosystems, AMF could play a crucial role in invasive plants control through enhancing the competitive ability of local species to the detriment of invasive ones. Additional methodologies are required to manage highly mycorrhizal invasive species.

Keywords Agroecosystems · Arbuscular-mycorrhizal fungi (AMF) · Invasive plants · Unmanaged ecosystems · Weeds

Abbreviations

AMF Arbuscular Mycorrhizal fungi
M Mycorrhizal
NM Non-Mycorrhizal

1 Introduction

Weeds are unwanted species that infest natural and managed areas and presumably compete with neighboring plants for water, nutrients, sunlight and space. In agricultural ecosystems, weeds represent a serious problem for crop production (Oerke and Dehne 1997). They could reduce global yields of major crops by around 34% (Oerke 2006). Yield losses in cereal crops due to competition from weed species in mediterranean area can reach up to 80% (Izquierdo et al. 2003).

Definitions of ‘weed’ in the scientific literature vary, but one common theme is that weed species “[interfere] with the objectives or requirements of humans” (Holzner and Numata 2013). The Weed Science Society of America defines a weed as a plant that causes economic losses or ecological damage, creates health problems for humans or animals, or is undesirable where it is growing. In natural areas, species presenting weedy traits are invasive plants that may threaten biodiversity through causing the extinction of some native species. Invasive plants are defined by Lincoln et al. (1998) as organisms undergoing a mass movement or encroachment from one area to another.

Agricultural weeds and invasive plants are both unwanted species. However, the main difference between the two kinds of species is that related to their respective ecosystems. Agricultural weeds occur in species-poor systems under heavy human control whereas invasive plants occur in multi-species systems that tend to self-regulate. Different methods can be used to control weeds and invasive plants including: manual or mechanical removal, grazing, biocontrol, herbicides, prescribed fire, solarization, and flooding. Each technique has advantages and disadvantages in terms of its effects against weeds, risks to human health and safety, impacts on biodiversity and costs. Herbicides are the main method to control both

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weeds and invasive plants. However, many problems are related to the use of herbicides, among which are: i) the phenomenon of resistance to herbicides: about 200 weed species were reported to express a resistance to a broad range of herbicides (Heap 2012); ii) the high cost of herbicides; iii) the restriction of the use of many chemical products to protect human health and environment; iv) the reduction of biodiversity through the effects of herbicides on some non-target species (Relyea 2005). However, if the use of herbicides is restricted, the dependence on tillage will be accentuated, which could have important negative environmental impacts and could result in crop damage in the case of high soil moisture (Peruzzi et al. 1997).

Biological control appears as a reliable and growing method to limit the proliferation of unwanted species. Biological control includes using rhizospheric bacteria, fungi or viruses (bioherbicides) to control weeds. Bioherbicides are considered to have less environmental impact than classical herbicides due to their increased target specificity, the rapid degradation of residual biological agent metabolites, and the inability to propagate without human assistance (Harding and Raizada 2015). This approach can provide permanent control with a very favorable cost-benefit ratio, especially considering the increased interest by consumers for agricultural practices that does not use chemical herbicides.

Many fungal species are widely used as biocontrol agents and more specifically, arbuscular mycorrhizal fungi “AMF” (Malik and Charaya 2013). AMF live as obligate symbionts within the roots of about 80% of land plants, including plants in most natural and agricultural ecosystems (Gianinazzi-Pearson et al. 1996). It is widely recognized that AMF symbiosis has positive effects on plant growth through enhancing water and nutrient absorption (especially phosphate) and enabling protection against biotic and abiotic stresses (Gianinazzi-Pearson et al. 1996). The fungus benefits in return by receiving carbohydrates from the host (Sylvia 1998). A large range of plant responses to AMF colonization was obtained in studies of many plant species (Bever et al. 1996; Wilson and Hartnett 1998; Van Der Heijden et al. 1998a; Watts-Williams et al. 2019). Some plants do not exhibit any benefit upon AMF inoculation while others even are negatively affected by AMF colonization (Johnson et al. 1997; Klironomos 2003). In fact, not all plants are mycorrhizal, some plant taxa do not usually form recognizable mycorrhizas (Tester et al. 1987) very likely due to the fact that the cost is higher than the benefit. Estimates vary, but plants have been shown to allocate between 4% and 20% of photoassimilates to mycorrhizal roots (Graham 2000). Some species on the other hand are facultative mycorrhizal species which, in contrast to obligate plants depend on mycorrhizae only in the case of a deficiency of nutrients in the soil (Janos 2007).

The beneficial effect of AMF in the control of biotic and abiotic stresses is well documented and has been the subject of numerous publications and reviews in scientific and

popularization journals (Berruti et al. 2016). Interesting reviews concerned with the interaction between AMF and weeds or invasive plants were published recently (Bunn et al. 2015; Harding and Raizada 2015; Li et al. 2016; Menzel et al. 2017). However, to our knowledge there are no studies gathering the characterization of the interaction between AMF and unwanted species in unmanaged and crop ecosystems. The main goal of this review is to summarize existing research about the interaction between AMF and weeds in a short term (crop cycle) and between AMF and invasive plants in a long term (natural areas). Understanding these interactions could help to assess the potential of using AMF to manage weeds and invasive plants. Our objectives are to determine: i) the suppressive effects of AMF on weeds along with the hypothesized implied mechanisms, ii) the positive AMF-weeds interaction effects, iii) the traits of AMF-weed interaction in the case of organic agroecosystems, and iv) the repercussions of AMF-invasive plants interaction on the structure of AMF and invasive plants communities in unmanaged systems. Elucidating these topics is necessary to set-up optimal weed control strategies with the goal of looking for an equilibrium between the control of damage caused by weeds and invasive plants and the conservation of biodiversity, ecosystem functioning and soil quality.

2 Suppressive effects of AMF on weeds

2.1 Direct effects

About 95% of the world’s species of higher plants are mycorrhizal (M) (Quilambo 2000). The remaining 5% do not form generally recognizable mycorrhizas due likely to the lack of any recognition enabling the establishment of a functional symbiosis (Giovannetti and Sbrana 1998). Weeds in the families Chenopodiaceae, Amaranthaceae, Polygonaceae and Brassicaceae are non-mycorrhizal (NM) (Glenn et al. 1985). Many experiments have shown reduced biomass, growth and survival of NM weeds upon AMF colonization (Vatovec et al. 2005; Rinaudo et al. 2010; Veiga et al. 2011, 2013; Li 2017). Table 1 summarizes some weed species that exhibited suppression due to AMF effect. For example, AMF colonization reduced the growth and biomass of the weed *Stellaria media* eight-fold (Veiga et al. 2012). Jordan et al. (2000) reported that AMF reduced biomass production in *Amaranthus retroflexus* and *Chenopodium album* by 90% and 80%, respectively. AMF has been shown to suppress also mycorrhizal weeds. For instance, greenhouse experiments have shown a reduced biomass due to AMF colonization for M species *Abutilon theophrasti* and *Setaria lutescens* (Vatovec et al. 2005), *Echinochloa crus-galli* (Rinaudo et al. 2010) and *Verbascum thapsus* (Francis and Read 1995). Reduced biomass, growth rate and survival were obtained in the case of

Table 1 Some weed species exhibiting growth suppression induced by AMF

Mycorrhizal status	Weed species	AMF Genre/species	Reference	
Non Mycorrhizal	<i>Amaranthus retroflexus</i>	unknown	Jordan et al. (2000)	
	<i>Amaranthus tuberculatus</i>	<i>Archaeospora</i>	Li (2017)	
	<i>Chenopodium album</i>	unknown	Jordan et al. (2000)	
	<i>Chenopodium album</i>	<i>Paraglomus</i>	Li (2017)	
	<i>Chenopodium album</i>	<i>Glomus intraradices</i> , <i>G. mosseae</i> , <i>G. coronatum</i>	Rinaudo et al. (2010)	
	<i>Stellaria media</i>	<i>Glomus intraradices</i>	Veiga et al. (2012)	
	<i>Salsola kali</i>	<i>Glomus etunicatum</i>	Johnson (1998)	
	<i>Rumex crispus</i>	unknown	Vatovec et al. 2005	
	<i>Rumex acetosella</i>	unknown	Francis and Read (1995)	
	<i>Brassica kaber</i>	unknown	Vatovec et al. (2005)	
	<i>Stellaria media</i>	<i>Rhizophagus irregularis</i>	Bilalis et al. (2011)	
	<i>Avena sterilis</i>	<i>Rhizophagus irregularis</i>	Bilalis et al. (2011)	
	<i>Fumaria officinalis</i>	<i>Rhizophagus irregularis</i>	Bilalis et al. (2011)	
	<i>Arabidopsis thaliana</i>	<i>Rhizophagus irregularis</i>	Veiga et al. (2013)	
	Mycorrhizal	<i>Setaria lutescens</i>	unknown	Vatovec et al. (2005)
<i>Setaria glauca</i>		<i>Archaeospora</i> <i>Glomus</i> <i>Paraglomus</i>	Li (2017)	
<i>Verbascum thapsus</i>		unknown	Francis and Read (1995)	
<i>Digitaria sanguinalis</i>		<i>Glomus intraradices</i> , <i>G. Mosseae</i> , <i>G. coronatum</i>	Rinaudo et al. (2010)	
<i>Echinochloa crus-galli</i>		<i>Glomus intraradices</i> , <i>G. Mosseae</i> , <i>G. coronatum</i>	Rinaudo et al. (2010)	
<i>Setaria viridis</i>		<i>Funneliformis mosseae</i>	Qiao et al. (2016)	
<i>Echium vulgare</i>		unknown	Francis and Read (1995)	
<i>Echinochloa crus-galli</i>		<i>Glomus intraradices</i> , <i>G. Mosseae</i> , <i>G. claroideum</i>	Veiga et al. (2011)	
<i>Setaria viridis</i>		<i>Glomus intraradices</i> , <i>G. mosseae</i> , <i>G. claroideum</i>	Veiga et al. (2011)	
<i>Solanum nigrum</i>		<i>Glomus intraradices</i> , <i>G. Mosseae</i> , <i>G. claroideum</i>	Veiga et al. (2011)	
<i>Abutilon theophrasti</i>		unknown	Vatovec et al. (2005)	
<i>Abutilon theophrasti</i>		<i>Archaeospora</i>	Li (2017)	
<i>Sida spinosa</i>		<i>Glomus</i>	Li (2017)	
Mycorrhizal-Non Mycorrhizal		<i>Reseda luteola</i>	unknown	Francis and Read (1995)
		<i>Spergula arvensis</i>	unknown	Francis and Read (1995)

Echium vulgare, *Reseda luteola* and *Spergula arvensis* (Francis and Read 1995).

Different mechanisms could explain the suppressive effect of AMF on weeds. Direct antagonistic effects of AMF on weed species could be attributed to:

-parasitism AMF inoculation of NM weed species results usually in AMF root colonization although at very low percentages and arbuscular structures are often observed as noted in the works of Rinaudo et al. (2010) and Veiga et al. (2011). The classical explanation of the antagonistic effect of AMF on some weed species (NM species and sometimes M ones), is that the energetic cost of the symbiosis can be greater than the nutritional benefits, leading to plant growth depression. This is thus said to be caused by fungal carbon cost to the

host that outweigh any benefits that might be produced by nutrient transfer via the fungus. The AMF will essentially be acting as a weak parasite in this case as suggested by Johnson et al. (1997).

Explaining growth depression induced by AMF-infected weeds by parasitism may, however, be incomplete. Indeed, Li et al. (2008) demonstrated, in the case of plants exhibiting reduced growth due to AMF colonization, that more than 50% of phosphorus (P) in the roots is absorbed by external AMF mycelia even when more P is added to the soil. The amount of P absorbed by AMF mycelium was shown to be not correlated with growth and total P uptake. Substantial P uptake (determined using labeled P) via the external AMF mycelium is observed in many species (Smith et al. 2003, 2004; Zhu et al. 2003; Facelli et al. 2009). This suggests that weeds still

benefit from the association with AMF at least in terms of P supply (Jones and Smith 2004). The interaction between incompatible species (AMF and NM weeds) may inactivate direct P uptake through the epidermis and root hairs (Smith et al. 2010) reducing P uptake efficiency. Moreover, changes from one pathway (epidermis and root hairs) to another (AMF mycelium) for P uptake by AM plants may generate additional costs decreasing thus the benefits of the association with AMF (Li et al. 2008).

-defense Allen et al. (1989) observed cell browning and death upon AMF colonization of roots of *Salsola kali* reflecting a defense response of this weed species (García-Garrido and Ocampo 2002). In fact, the lack of mutualistic association between incompatible partners (NM plant and AMF) in this case was indicated by the browning of the plant roots. The growth depression observed in weeds could be explained by the allocation of plant reserves to ensure defense against unrecognized fungi. A similar defense response was also reported in the case of M weeds: *Echium vulgare* exhibited swellings and distortion of the meristems of lateral roots upon infection by AMF (Francis and Read 1995).

-developmental stage The suppressed growth of weeds due to AMF colonization could be a result of an early developmental stage of the seedling that, for being young, the high carbon cost prevents the establishment of a symbiosis with AMF species. Young hosts may invest carbon in mycorrhizal networks but receive no benefit in return although this situation can change within a short time of the host life. In fact, many studies show growth depressions in some AM plants species during the first several weeks of seedling development which disappear shortly thereafter (Koide 1985; Ronsheim 2012).

Regardless of the mechanisms by which AMF could suppress the performance of weeds, it seems that it is a useful method to fight against weeds particularly those belonging to the NM species. In addition to the mechanisms mentioned above, it is also possible that the negative effects could result from combined effect of many factors (synergistic effect). Antagonistic effects of AMF on some weed species were obtained in greenhouse conditions. Therefore, some of the findings may be an artefact of the experimental conditions, and they may not accurately reflect what actually happens in the field in the presence of other plant species and soil microorganisms. Antagonistic effects of AMF obtained in greenhouse experiments could be partially attributed to the low light or to the limited space for root development in pots (Li et al. 2008). However, in crop systems, in the presence of associated species (crop), the antagonistic effect of AMF colonization on weed performance was demonstrated to be more pronounced (Cameron 2010) -as we will discuss in the following section- suggesting actually a suppressive effect and that AMF could be a useful tool to control weeds.

2.2 Indirect effects (triple interaction AMF-weeds-crop species)

In this section, indirect antagonistic effects of AMF in the case of the triple interaction AMF-weed-crop species will be reviewed. Figure 1 represents a diagram summarizing this triple interaction making separation between NM and M weeds.

2.2.1 NM weeds

Rinaudo et al. (2010) have demonstrated that AMF can suppress NM weeds benefiting an M crop plant species. Their study showed suppression of the weed species *C. album* while benefiting the crop plant *Helianthus annuus* (sunflower) via enhancing P nutrition. Also, strong antagonistic effects of AMF colonization on the growth of weed species was obtained in the case of *Arabidopsis thaliana* inoculated with *Glomus intraradices* in the presence of host plant ryegrass (*Lolium perenne*) or clover (*Trifolium arvense*) (Veiga et al. 2013). The NM weed in this case may have a reduced access to nutrients, especially in the conditions of nutrients deficiency, because these are preferentially taken up by AMF and transported to host crop species enhancing thus crop competitiveness. On the other hand, NM weeds absorb nutrients less efficiently because the direct pathway of P uptake (via the epidermis and root hairs) may be inactivated (Smith et al. 2010) due to AMF infection whereas M crop species can absorb nutrients, in addition to the direct pathway, through the fungal mycelium that delivers nutrients to the root cortex through the arbuscules.

The enhanced suppressive effect of AMF on NM weed growth in the presence of associated species could somewhat be underestimated due to the effect of crop plant density. Crop density could be an important interfering factor in the case of the triple interaction (AMF-weed-associated species). In fact, positive growth responses of M plants compared with NM controls decrease with increasing plant density (number of plant individuals per unit soil volume) (Schroeder-Moreno and Janos 2008). So, when plant density increases, competition for P among the AMF hyphae decreases the benefits of the AMF inoculation because the competition for P among the M plants will equal that among NM control plants. Therefore, the enhanced decrease of NM weeds due to AMF effect in the presence of M associated species, should take into consideration the decrease of M associated species growth due to the competition between individuals.

2.2.2 M weeds

In response to AMF effect, M weeds also showed an enhanced suppressive effect in the presence of associated species. *E. crus-galli* growth decreased in response to AMF when

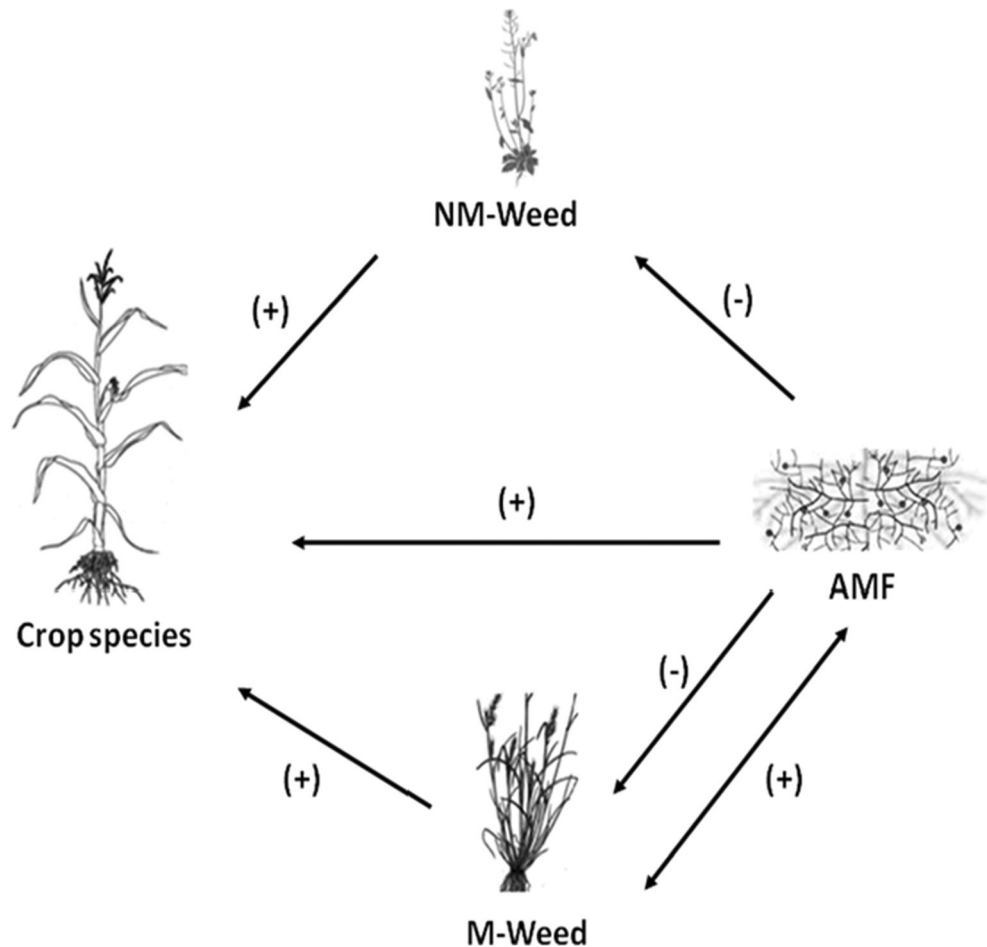
coexisting with maize (Veiga et al. 2011). Root colonization was also significantly enhanced due to the suppressive effect of AMF. Although many factors depending on both associated species and weed traits may be involved in the suppressive effect of AMF, there are many evidences that competitive ability of M weed species is decreased thus benefiting associated species. The competitiveness of associated species conferred by AMF colonization may be due to nutrient availability in the soil. In conventional agricultural cropping systems characterized by high nitrogen and phosphorus input, strong M crops had a higher positive response to AMF than strong M weeds (Li et al. 2016, a meta-analysis). This could be attributed to the fact that the sinks created by the growth of host crop (dominant species) are higher than the sinks created by the growth of host weed. AMF preferentially allocate nutrients to the crop (the big sink) rather than weed (Bethlenfalvai et al. 1996). Thus, crop species govern mineral absorption from the soil through AMF especially in conditions of relatively high nutrient availability.

In conditions of low nutrient availability, Qiao et al. (2016) showed within an intercropping system, an enhanced growth of some M dependent crop species (maize and faba bean

(*Vicia faba*)) due to AMF colonization, while the growth of the M weed species *Setaria viridis* was suppressed. Also, Li et al. (2016) demonstrated that the growth of strong M crop species was higher than that of weak M weed species in conditions of low phosphorus and nitrogen. Furthermore, some studies suggest that the outcome of the plant-plant interaction may depend on the responsiveness of the dominant species. When dominant “crop” species are highly M-responsive, the presence of AMF may result in suppression of the subordinate species “weeds” (O’Connor et al. 2002).

The suppressive effect in the case of the triple interaction could be attributed both to direct effects of AMF on weeds and to indirect effects that result from enhancing competitive ability of crop species. Breeding programs must take into account the indirect effects of AMF in order to select highly M responsive crop varieties. This should minimize yield loss due to competition with weeds through conducting studies aiming to compare plant varieties. In fact, commercial crops tend to have lower competitiveness due to the selection of cultivars highly adapted to artificial conditions (Altieri 1999). On the other hand, M colonization of some weed species could vary depending on the identity of the associated species

Fig. 1 Diagram of the triple interaction: Arbuscular Mycorrhizal Fungi -weed- crop. In the case of the non-mycorrhizal (NM) weed, the triple interaction results in the suppression of weeds which could benefit indirectly crop species. In the case of the mycorrhizal (M) weed, the triple interaction could result in a suppression of weeds which exhibit decreased competitive ability (-) or an enhanced growth of weeds (+). Weeds have the advantage to increase the diversity and abundance of AMF in the soil which will in turn benefits crop species



(Massenssini et al. 2014). So, the relationship of AMF-weed-crop species should be properly characterized in order to obtain best results of weed management using AMF.

3 Positive effects of AMF-weed interaction

AMF-weeds interaction does not result always in suppressive effects of weeds (Fig. 1). Many weed species exhibit positive effects upon AMF colonization, generally reflected in enhanced biomass and growth of weeds. Vatovec et al. (2005) studied the effect of AMF colonization on the growth of 14 weed species of temperate field-crop agroecosystems. In spite of the great variability in the results obtained, they found a clear significant positive effect of AMF inoculation in the case of *Ambrosia artemisiifolia* and *Cirsium arvense* (the average of growth increase was 50% and 68% respectively). The enhanced competitive ability might be due to a higher degree of responsiveness of some weed species to AMF inoculation (Kurle and Pflieger 1994) or to a higher AMF availability around the roots (Hendrix et al. 1995). Another aspect of positive effects of AMF colonization is the vigor observed in the offspring of some weed species. Offspring of M mother plants of wild oat exhibited higher nutrient content of the roots and shoots, greater leaf area and number of seeds by spikelet and P content of seeds than offspring of NM mother plants. This suggest a potential effect of AMF colonization in increasing the vigor of their host's offspring (Koide and Lu 1992). This fact could have the effect of strengthening weak hosts from generation to generation, with its consequent effect of changing weed community structure. Thus, the ecological significance of maternal M effect on offspring performance might be very high. In fact, some studies suggest that initial size advantages of some species could be very important under competitive conditions because small differences will be greater with time due to competition between species (Weiner 1990).

Similarly, M weeds could have beneficial effects on the diversity and abundance of AMF. Weeds enhance AMF propagule density in the soil by enhancing sporulation or root colonization compared to crop species (Kurle and Pflieger 1994) and could induce differences in dominant AMF species enabling a wider spectrum of AMF to colonize crop roots (Radić et al. 2012). The high proportion of AMF in the soil and therefore the development of extra-radical mycelium will enable an early colonization of the following crop (Kubota et al. 2015). In fact, during crop rotations that involve a low mycotrophic species (wheat, for example) or a non AM crop such as brassica, rape, beet or kale; mycorrhiza formation is inhibited in subsequent mycotrophic species (Hayman et al. 1975; Powell 1982; Plenchette 1989). Moreover, it could take more than two successive growing seasons with a mycorrhizal host to re-establish AMF population to the original level (Harinikumar and Bagyaraj 1988; Duponnois et al. 2001). On the other hand, fallow periods provoke a reduction in the

number of mycorrhizal spores and infective mycelium as reported by several studies (Karasawa and Takebe 2011; Schnoor et al. 2011). However, Plenchette (1989) observed that when weeds are not controlled, mycorrhizal infectivity is maintained. It was also reported that minimal rotation to non-host crops and the continual presence of a host plant such as a winter cover crop or perennial weed provide conditions favourable to AMF colonization (Jordan et al. 2000; Koide and Kabir 2000). All this suggest a substantial role of weeds in maintaining AMF populations in the soil.

NM weeds could also play an important role in stabilizing the population of AMF in the soil, even they are not colonized with AMF. For example, Schmidt and Reeves (1984) found that till six months, the NM *S. kali* does not have a negative effect on the number of viable *G. fasciculatum* propagules in the soil, but enhanced the survival of the AMF.

AMF-weed interaction could benefit associated plant species. In fact, some M grasses showed an increased ability to extract water from the soil in the presence of both AMF and annual NM weeds although no differences in the nutrients levels of the plants attributable to M associations was detected (Allen and Allen 1986). Also, in the case of the *Euphorbia hirsuta*, some amount of its leaf extract was suggested to be beneficial for eggplant crop species growth which could result in synergism with AMF and benefiting thus the crop species (Elhag et al. 2015).

We can conclude that in spite of the positive effects of AMF on the growth of some weed species, those could have a positive feed-back on AMF communities in the soil. The abundance and diversity of AMF could have further positive effect on competitive ability of crop species against problematic weeds (Fig. 1). Furthermore, AMF interaction with weeds may improve soil quality and favor beneficial organisms (Jordan et al. 2000). So, attention should focus on identifying weed species that can play an important role in maintaining beneficial effects of AMF on ecosystem functioning.

The aforementioned beneficial effects show that suppression but not eradication of weeds could be a more appropriate practice in cropping systems and especially recommended in organic agriculture as we will discuss in the following section.

4 Weed-AMF interaction in organic agroecosystems

Weeds represent a serious problem in organic culture practice since organic systems tend to harbor 2.3–2.8 times more weed seed densities and 1.3–1.6 times more weed species compared with conventional systems (Kubota et al. 2015). Cultivation is the most common direct form to control weeds as the use of herbicides is not allowed. However, the overuse of tillage may reduce soil quality and destroy AMF hyphae (Peruzzi et al. 1997, Curaqueo et al. 2010, Säle et al. 2015). Thus, the use of

bioherbicides including AMF is of great significance. Organic systems are characterized by a lower concentration of total and available soil P than equivalent traditional systems (Gosling and Shepherd 2005) which could be more favorable to AMF abundance. Although the continuous shift of available P from organic to inorganic form could result in a greater P availability to AMF than to roots alone, this shift is gradual in time and could not result in an excess of P availability in the soil compared to mineral fertilizers (Magdoff 1995).

The management of weeds in organic agriculture takes a different perspective from that of conventional one. The former treats the problem of weeds in an extended time domain whilst in conventional agriculture, weed control management aims to prevent or minimize immediately (during the crop cycle) yield loss. Organic weed management practices promote suppression of weeds rather than their eradication keeping thus weeds at minimal level. Relationships between weeds and AMF have a dual significance in organic cropping systems: we could manage weeds to enhance AMF proportion and diversity in the soil and in turn manage AMF to control the growth of problematic weeds (Vatovec et al. 2005). M weeds may serve to maintain diversity and agronomically beneficial taxa of AMF (Kubota et al. 2015). In return, AMF can strongly affect plant community composition, and may thus provide some degree of biological control for weeds.

Available data on weed management via AMF effects in organic farms is limited. Vatovec et al. (2005) obtained high variability between species studied and concluded that there is little evidence that AMF in different cropping systems has differential effects on weed growth. On the other hand, Bilalis et al. (2011) found that organic cultural practices significantly increase weed biomass and AM root colonization of competitive weeds whereas there was no difference in the case of non-competitive weeds studied. The challenge to study the AMF-weed interaction in organic farming is that the soil is richer in microorganisms than conventional areas due basically to the destructive effect of soil biota by pesticides, herbicides and fungicides. This higher underground and above-ground diversity in organic farming systems makes the study of AMF-weed relationship complex: the increased number of factors and order interactions makes difficult the characterization of such relationship. The main strategy to maximize yields in organic systems is selecting cultivars that maintain high yield rates in conditions of severe weed stress (Kubota et al. 2015) and enhancing crop competition where AMF could play a key role as has been shown in conventional agroecosystems.

5 Effect of AMF taxa on weed management

Individual plant hosts can form mycorrhizae with many AMF taxa (Helgason et al. 1999), although they may exert some

degree of control over the fungal community composition by selecting more beneficial symbionts. Numerous pot studies have demonstrated variations in the growth rate of plants inoculated with different AMF species (Mosse 1972; Bever et al. 2001). AMF influence on plant competition and on the relative abundances of the competitors was also shown to depend on the specific AMF isolate (Scheublin et al. 2007). Streitwolf-Engel et al. (1997) showed that colonization by different isolates of AMF differently affect reproductive allocation by two *Prunella* species. Some isolates stimulated clonal propagation through stolons, while other isolates stimulated sexual reproduction through flowering. *Hieracium pilosella* differs greatly in its growth response to several and to a mixture of AMF species (Van Der Heijden et al. 1998a). Othira et al. (2012) demonstrated that the *Glomus* spp. had the largest effect in suppressing *Striga hermonthica* in maize compared to *Gigaspora* and *Scutellospora* genera.

Some studies in contrast, did not show any effect of AMF taxa on weed performance. Rinaudo et al. (2010) showed that the effects of different AMF taxa on weed growth were not significant (only *C. album* from other five weed species responded differently to different AMF species) and that AMF diversity (three AMF taxa versus one) did not lead to a reduced weed biomass. The same result was obtained in the case of *Bromus erectus* (Van Der Heijden et al. 1998a) and *Medicago truncatula* (Derelle et al. 2015).

The lack of the effect of AMF taxa may be explained by the fact that there is no, or little variation between species of AMF used. The two AMF species used by Derelle et al. (2015) belong to the same genus, *Rhizophagus*, (*R. irregularis* and *R. clarus*) whereas the species used by Rinaudo et al. (2010) are *Glomus* spp. It seems that variation in growth effects by different AMF taxa is at the genus level and not at the species or isolate level (Hart and Klironomos 2002). However, Gworgwor and Weber (2003) studied the effect of five *Glomus* species (*G. mosseae*, *G. intradices*, *G. albidum*, *G. fasciculatum* and *G. etunicatum*) to control *S. hermonthica* within sorghum crop species. They found that *G. mosseae* was the only AMF species that was effective in improving plant growth and in controlling *Striga*. Furthermore, Xavier et al. (2001) studied the effect of four *Glomus* species (*G. clarum*, *G. etunicatum*, *G. intradices* and *G. mosseae*) on the interaction between two cultivars of wheat and between those and the weed species *Avena fatua*. They obtained a different level of competitiveness and growth response depending on AMF species. This suggests that differences exist also between AMF species within the same genus.

Mixed AMF species influences the response of weeds to AMF infection. Li et al. (2016) reported that mycorrhizal growth responses were lower in weak host weeds than strong host crop and this difference was more pronounced under mixed AMF inoculum and low nutrient availability. On the other hand, van der Heijden et al. (1998b), using microcosm

plant communities in which species diversity, varied from two to fourteen AMF species, demonstrated that plant community diversity and ecosystem productivity increased with increasing AMF species diversity, regardless of which AMF species was present. These results suggest that possible synergism may exist between different AMF species, especially when they belong to different genera (De la Providencia et al. 2005). The possibility of functional complementarity among AMF species must be taken into consideration when choosing AMF species to manage weeds and/or invasive species.

6 AMF-invasive plants interaction in unmanaged ecosystems

Invasive plants are one of the major threats to the natural environment. They may decimate the native plant community and threaten rare species or influence ecosystem properties (Razaida et al. 2008). Due to the widespread occurrence of AMF and its important role in communities and ecosystems (Brundrett 1991), the interaction between invasive species and AMF might have an important role in ecosystem functioning in natural habitats.

AM symbioses play important roles in plant coexistence and in ecosystem management programs that aims to preserve native species diversity (Sanon et al. 2009). They could also play a determining role in succession after a disturbance (Allen and Allen 1984, 1988; Gange et al. 1990, 1993). The AMF community is more diverse in natural areas (Hawkes et al. 2006; Oehl et al. 2010; Souza et al. 2016) and this diversity is a key contributor to the diversity and productivity of plant communities in natural environments (Van Der Heijden et al. 1998b). Thus, AMF-invasive plants interaction studies could elucidate our understanding about underground biotic factors that affect plant fitness and ecosystem performance. It could more specifically help in determining the potential of using AMF to deal with invasive plants in natural areas.

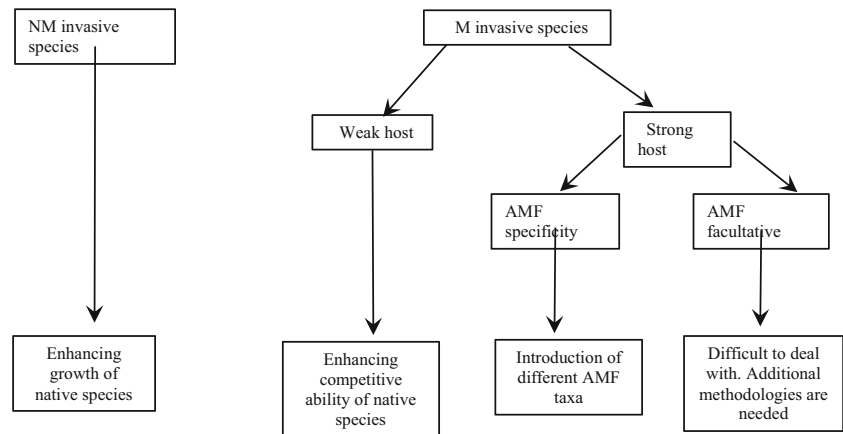
Invasive plants could impact adversely the abundance and diversity of AMF in the case of NM or low AMF dependent species. Invasive plants could affect indigenous AMF through exudation of allelochemicals inhibiting native mutualisms (Stinson et al. 2006). On the other hand, invasive plants that have a preference for a specific AMF species could enhance the abundance and proliferation of a particular AMF. Consequently, this will generate a positive feedback on the growth of invasive plants, enhancing thus its competitiveness at the expense of the native species (Zhang et al. 2010). Some studies by contrast, have found no change in AMF communities following plant invasions or the shift was judged not enough to be of ecological importance (Bunn et al. 2015).

Similarly, AMF have been found to determine plant community composition and function (Smith and Read 2008).

Some experiments demonstrated that AMF could facilitate exotic plant invasions by increasing their competitiveness (Richardson et al. 1994). Stampe and Daehler (2003) found that the composition of the AMF community belowground reduces the success of a dominant species *Melinis repens*, which could promote invasion by the species *Bidens pilosa*. In some cases, AMF could promote certain invasive weeds by drawing assimilates from native species through AMF hyphae network (Marler et al. 1999) called “common mycorrhizal networks” (CMNs), while in other cases, AMF community could have a role in repelling plant invasion through alleviating allelopathic effects of invasive plants (Barto et al. 2010). This diversity in the outcome of the relationship between AMF, invasive and native species suggests that the potential of using AMF to manage invasive plants might depend on the degree of responsiveness to AMF colonization of both invasive and native species. As AMF associations were less frequently found among invasive plants than native species (Vogelsang et al. 2004; Pringle et al. 2009), the management strategy using AMF should focus on the mycorrhizal status of invasive plants (Fig. 2). For invasive plants that are not mycorrhizal or less dependent on AMF, native species could repel invasion upon AMF colonization through enhancing their competitive ability to the detriment of non-mycorrhizal invasive plants. With respect of mycorrhizal invasive plants, the traits to be determined should be firstly the degree of responsiveness to AMF colonization and secondly, the flexibility to be colonized by different AMF species. According to Moora et al. (2011) for example, the AMF-host symbiosis is relatively non-specific in terms of both plant and AMF partners. This low symbiosis specificity leads to suggest that a determined AMF species are, unlikely, to influence the invasion process because invading plants can form novel symbioses with universal AMF. However, the existence of specificity in the AMF-host relationship was also evidenced (Klironomos 2003; Stampe and Daehler 2003). Klironomos (2003) demonstrated that a mutualistic AMF-host relationship is more common in the case of interaction between locally adapted plants and AMF rather than if one partner (the plant or AMF species) is exotic. This suggests that the spread of invasive plants may be inhibited if required specific AMF species are lacking (Pringle et al. 2009). Therefore, AMF species could be useful to manage invasive plants (exotic species) in unmanaged ecosystems particularly if the invasive plants are characterized to be AMF host specific.

Invasive plants showing flexibility in the association with AMF species could be the most difficult species to deal with. So, a deeper understanding of the interaction between AMF and invasive plants, the interactions between AMF and native species as well as the interaction between AMF associated to native species and invasive plants, is needed. In fact, some weed species have been reported to have their specific microorganism community in the soil (Sarathchandra et al. 1997).

Fig. 2 Invasive species management based on mycorrhizal status and specificity towards AMF species



Comparative studies to characterize the triple interactions (AMF-invasive plants-native species) should be undertaken as sometimes invasive plants were observed to be more colonized by AMF when grown in indirect competition with native species (Bunn et al. 2015). Invasive species that are facultative are more advantageous for successful establishment and spread (Menzel et al. 2017) because they can use multiple ecological strategies. Additional methodologies could be applied in this case to fight against invasive species using different modes of action.

7 Weed/invasive species management using commercial AMF inoculum

Nowadays, some regions throughout the world are already integrating AMF in intensive agriculture (Cuba, Mexico, Bolivia, Canada and India) (Zimmerman et al. 2009) and some companies (in North America and India) are producing and selling AMF inoculum to farmers. In fact, the potential of a AMF inoculum to increase growth and crop yields has been largely demonstrated (Cely et al. 2016; Adeyemi et al. 2020). However, the efficacy of commercially available AMF inocula in agricultural systems remains controversial. Various constraints still existing regarding AMF application at a large scale, which are mainly related to mass production inoculum and the availability of an immediate methodology to assess AMF colonization in natural and managed ecosystems. In fact, it is not always possible for a commercial inoculum to establish in a given environment (Vosátka et al. 2012). This could be attributed to an incompatibility with host species, local conditions and/or indigenous microorganisms.

For an efficient application of AMF at large scale, the main approach is to select AMF isolates that should be beneficial to a determined host species (best compatibility) and that are more efficient against determined weeds/invasive species (as we already discussed in triple interaction (AMF-weed-host) section).

Also, it would be beneficial to consider the synergism that could exist between different AMF taxa (Jansa et al. 2008).

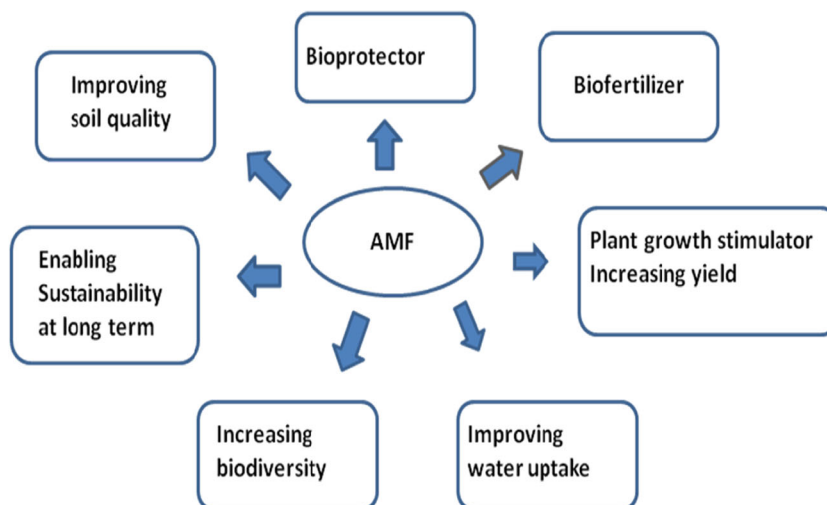
The second axis of investigation is that related to methodologies of mass production of AMF inoculum where the main hurdle lies in the fact that AMF have an obligate symbiont behavior. In spite of this, some advances are made regarding methods for large-scale production of AMF (Ijdo et al. 2011) and its coating on seed (Roy-Bolduc and Hijri 2012; Vosátka et al. 2012, Van der Heijden et al. 2015). The potential of using AMF as seed coating material to reduce significantly the amount of inoculum required is already reported (Oliveira et al. 2016).

The integration of AMF inoculum to a large scale could imply an extra-cost to farmers. However, we should take into account: i) the large saving in fertilizers given the role of AMF in plant nutrition (especially P uptake), ii) the reported role of AMF in stimulating growth and iii) the role of AMF in defense against biotic and abiotic factors. Furthermore, just a small amount of AMF inoculum could be required, especially for productions that imply a transplant stage. Besides, it has been shown that AMF inocula could persist in roots for at least two years after introduction (Pellegrino et al. 2012) and could be prorated in the soil over the years (Barr 2010).

From an ecological perspective, the use of AMF inoculum could benefit projects of reforestation and land recovery, enabling a good soil quality and avoiding soil and water contamination due to crop residues which will contribute to a long term sustainability of ecosystems. AMF inoculum could be introduced in natural ecosystems in small areas that would develop gradually with time in a mycelium network covering larger areas. All those advantages could exceed in terms of benefits, the cost of a commercial AMF inoculum (Fig. 3).

Taking into consideration all constraints related to commercial AMF inoculum, the best strategy (independently of using or not commercial AMF) should be the preservation of native AMF populations, both in natural and managed ecosystems, through adopting AMF-friendly practices such as minimizing tillage (Säle et al. 2015), cover cropping (Lehman

Fig. 3 AMF benefits in agriculture and ecosystem sustainability that could balance the cost of a commercial AMF inoculum



et al. 2012), etc. In fact, indigenous AMF should have a better effect on weed and invasive species management in comparison to selected AMF species, for being well adapted to local conditions.

8 The management strategies of weeds and invasive plants using AMF: Conclusions and constraints

AMF could strongly affect the ecology of weeds and invasive plants. In fact, their growth could be promoted or suppressed depending on their mycorrhizal status and the degree of responsiveness to AMF colonization.

Antagonistic effect of AMF colonization was mostly obtained in the case of NM weed species. A strong antagonistic effect of AMF was observed in the case of the triple interaction AMF-weed-crop species which could be due to an increased suppression of weeds and/or to an enhanced growth of crop species. Indeed, AMF could enhance the competitive ability of M species (crop) by increasing nutrient acquisition, while NM weeds will be suppressed due to decreased nutrient availability in the soil and/or to increasing defense responses to AMF inoculation. The management of agricultural problematic weeds that are mycotrophic should be ensured by selecting crop varieties that are highly responsive to AMF colonization. Also, the specificity of the relationship in the case of the triple interaction should be taken into consideration to determine the best combination between AMF taxa, weeds and associated crop species.

It is noteworthy that the challenge of using AMF in agroecosystems lies in the fact that chemical compounds often used are very likely to kill microorganisms that are fundamentally important to plant functions, and could strongly affect plant population and community dynamics. The high amount of fertilizers will impact negatively AMF in two ways: i) in

terms of decreasing AMF root colonization (Johnson 2010; Johnson et al. 1997) reducing thus the carbon expense of the plant and ii) decreasing AMF diversity and abundance (Jordan et al. 2000). So, the use of AMF in agroecosystems should be combined with other methods within an integrated weed management program as AMF could be decimated due to artificial conditions. Another aim should be the determination of growing conditions that could not alter AMF quantity and quality.

In spite of causing substantial yield loss, weeds exhibit some advantages to ecosystem functioning in terms of preservation of AMF communities and plant species richness. Their suppression but not whole eradication must be the aim of weed management thus enabling some level of equilibrium between the control of parasitism and preservation of biodiversity. Another goal should be the identification of weed species that can play an important role in maintaining beneficial effects of AMF on plant performance and soil quality.

With respect to invasive plants, the management strategy should also depend on their mycorrhizal status. NM invasive plants could be managed through enhancing the competitive ability of native species using AMF. Mycorrhizal invasive plants that exhibit specificity towards AMF could be managed using different AMF species. Further studies are needed in this context and the main goal should be to determine the responsiveness of invasive plants to colonization by specific AMF species. Till date, the identification of species as hosts or non-hosts is based on experiments evaluating just root colonization. However, this could not enable to distinguish soundly between parasitism and mutualism (Johnson et al. 1997). Invasive plants that do not exhibit specificity towards AMF are the most difficult to control, so additional methods should be combined with the use of AMF. The challenge of using AMF in natural areas to fight against invasive plants is the high amount of inoculum required for large superficies.

Otherwise, the use of AMF to manage weeds and invasive plants should take into account the advantage of using mixed

AMF species that could result from synergism between different AMF taxa (Li et al. 2016). The possibility of the existence of a functional complementarity among AMF species must be taken into consideration when choosing AMF species to manage weeds and invasive plants.

We conclude that AMF could play important roles in alleviating the negative effects of unwanted species (weeds and invasive plants) both in highly managed systems in the presence of one species (crops) and in unmanaged systems with multi co-occurring species (natural ecosystems). The higher underground and aboveground diversity in natural areas makes difficult and complex the characterization of the triple interaction AMF-invasive plants-associated species due to the increased number of factors contributing to such interaction. More works should be done in this context to identify AMF species that could be used to manage specific invasive plants.

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Declarations

Conflict of Interest The authors declare no competing interests.

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