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Agricultural University of Athens, Greece

*CORRESPONDENCE

Irene Pagliarani

✉ irene.pagliarani@phd.unipi.it

†These authors share first authorship

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The nonhost mycorrhizal status of weeds and its relevance to weed management in agroecology

Irene Pagliarani^{*†}, Arianna Grassi[†], Monica Agnolucci,
Alessandra Turrini, Luciano Avio and Manuela Giovannetti

Department of Agriculture, Food and Environment, University of Pisa, Pisa, Italy

The implementation of agroecological practices aims at promoting productivity and reducing environmental impacts due to the excessive use of mineral fertilizers and pesticides. It relies on soil microbiota beneficial activities, such as the efficient use of water and natural soil resources and the provision of important ecosystem services. This review will focus on arbuscular mycorrhizal fungi (AMF) and their role in weed management. AMF are soil beneficial microorganisms establishing mutualistic symbiotic associations with the roots of most food crops and playing key roles in plant growth, nutrition and health. Several plant species are unable to form functional mycorrhizal symbioses (nonhost plants), lacking “symbiotic-specific” genes, as shown by genomic, transcriptomic and phylogenomic analyses. The majority of nonhost plants belong to families encompassing some of the world’s worst agricultural weed species, such as *Chenopodium album*, *Raphanus raphanistrum*, *Rapistrum rugosum*, *Capsella bursa-pastoris* and *Sinapis arvensis*. The nonhost mycorrhizal status entails adverse effects on nonhost weeds due to attempted fungal colonisation, leading to reduced plant survival, growth and nutrient acquisition, particularly when grown in the presence of active AMF extraradical hyphae originating from host plants. These effects have been attributed to the activation of plant root defenses diverting resources from plant growth. This review provides qualitative and quantitative data on the interactions between AMF and nonhost weeds and on the mechanisms underlying weed fitness reduction. The lack of extensive field studies highlights the need for experimental works under real crop conditions to determine whether the combination of AMF with cover crops – a weed management practice adopted in agroecology – could serve as a valuable strategy for weed control, promoting the agroecological transition towards low-input, safe, and resilient agroecosystems.

KEYWORDS

nonhost weeds, arbuscular mycorrhizal fungi, plant root defenses, mycorrhizal networks, agroecological practices

1 Introduction

The main challenge for global agriculture in the years to come is represented by the safe production of high-quality food for a growing world population, while conserving natural resources for future generations, reducing the use of pesticides and chemical fertilizers and protecting biological soil fertility. Even more so, when considering climate change and global warming, which have a negative impact on food security, mainly due to increasing heat and drought (IPCC, 2023).

The implementation of novel agroecological practices may enhance soil structure and biodiversity, improve ecosystem services and nutrient cycling, while promoting productivity and reducing environmental impacts caused by the excessive use of mineral fertilizers and pesticides. Such practices rely on the beneficial activities of the soil microbiota, which is related to the efficient use of water and natural soil resources, the modulation of soil biochemical, biological and nutritional processes, and the provision of ecosystem services that are of great economic importance for agriculture, forestry and society (Philippot et al., 2013; Azcón-Aguilar and Barea, 2015; Wang and Qiu, 2006).

Among soil beneficial microorganisms, the most significant groups are represented by arbuscular mycorrhizal (AM) fungi (AMF, Glomeromycota), that establish mutualistic symbiotic associations with the roots of about 71–80% of land plants, including most staple food crops, i.e. wheat, rice, maize, sorghum, potatoes, soybeans, cassava, the majority of horticultural plants and fruit trees, and many economically important industrial crops, such as sunflower, cotton, flax, tobacco, sugarcane (Wang and Qiu, 2006; Smith and Read, 2010; Brundrett, 2017). AMF play key roles in plant growth and nutrition, facilitating the uptake and transfer of mineral nutrients from the soil to the host plants, by means of an extensive network of extraradical hyphae. In exchange, they receive plant organic compounds, mainly sugars and lipids, on which they depend as chemoheterotrophic organisms (Smith and Read, 2010; Helber et al., 2011; Luginbuehl et al., 2017). Moreover, AMF are fundamental factors in soil nutrient flows and biogeochemical cycles, enhancing also carbon sequestration and water supply, and plant tolerance to biotic and abiotic stresses (Gianinazzi et al., 2010). Given their multifunctional roles in soil fertility and health, AMF have recently been included in the specific agricultural products category of biostimulants by the EU Regulation 2019/1009 of the European Parliament and of the Council (European Union, 2019).

Many works reported that AMF may act as determinants of weed community structure and composition, reducing the development and fitness of several agricultural weed species, mainly those unable to establish a functional mycorrhizal symbiosis (nonhost species) (Li et al., 2016). Although weed communities can sometimes contribute to agroecosystem services and provide diverse benefits (Gazoulis et al., 2024), their excessive growth represents a major problem in agriculture, responsible for 31–34% of global crop yield loss (Oerke, 2006; Kubiak et al., 2022), despite the growing use of herbicides, whose global application

increased by 121 percent since the 1990s (FAO, 2024). Such a large utilisation of herbicides and the resulting selective pressure on weeds, which led to the development of herbicide resistance in many aggressive species, have boosted the search for innovative non-chemical weed management practices, including crop competition, the adoption of cover crops (Peterson et al., 2018; Little et al., 2021) and AMF, which negatively affect the survival and growth of several pernicious and widespread weeds in agriculture (Li et al., 2016). Thus, it is fundamental to gather existing knowledge on AMF-weeds interactions that could lead to weed growth control, with the aim of advancing their implementation as biocontrol agents, in order to reduce herbicide utilization in agroecology. Weed responsiveness to AMF is related to two main factors: weed symbiotic competence, producing negative growth responses in nonhost species, and the performance of the diverse AMF taxa, which differentially affect plant growth and nutrition (Rinaudo et al., 2010; Veiga et al., 2012; Sälé et al., 2022).

In this review AMF-weeds interactions are discussed, in relation to i) the main developmental steps leading to the establishment of the mycorrhizal symbiosis, ii) the nonhost mycorrhizal status of weeds, iii) the growth responses of nonhost weeds and the direct and indirect mechanisms underlying such responses. The main and final objective of the review is to provide insights into the research directions aimed at implementing innovative strategies for weed management in agroecology.

2 AMF life cycle and symbiosis establishment

Knowledge of the complex life cycle of AMF is fundamental in order to understand some of the mechanisms possibly involved in their interactions with weeds. Indeed, the development of the different fungal structures essential for root colonization may be hindered by nonhost weeds, which may trigger diverse defence mechanisms to control, avoid or restrict fungal root penetration, with implications for plant growth and functioning (Delaux et al., 2014; Fernández et al., 2019).

AMF life cycle can be completed only after the establishment of the mycorrhizal symbiosis (Figure 1). AMF show an apparently inconsistent behaviour as obligate symbionts, since their spores lack of host-regulated germination, being able to germinate in the soil even in the absence of a host plant. Germlings are not capable of extensive independent development and cease growth within 8–20 days (Giovannetti et al., 2010). Prior to physical contact with plant roots, a complex chemical and molecular dialogue takes place, as the fungal symbiont release signals – a mixture of sulphated and non-sulphated simple lipochitooligosaccharides (LCOs, called Myc factors) – which stimulate the expression of genes allowing mycorrhizal establishment (Maillet et al., 2011; MacLean et al., 2017). On the other side, plant roots secrete particular signalling molecules, represented by carotenoid-based phytohormones called strigolactones, able to reorient the direction of hyphal elongation to their source – the roots – and to trigger a differential hyphal

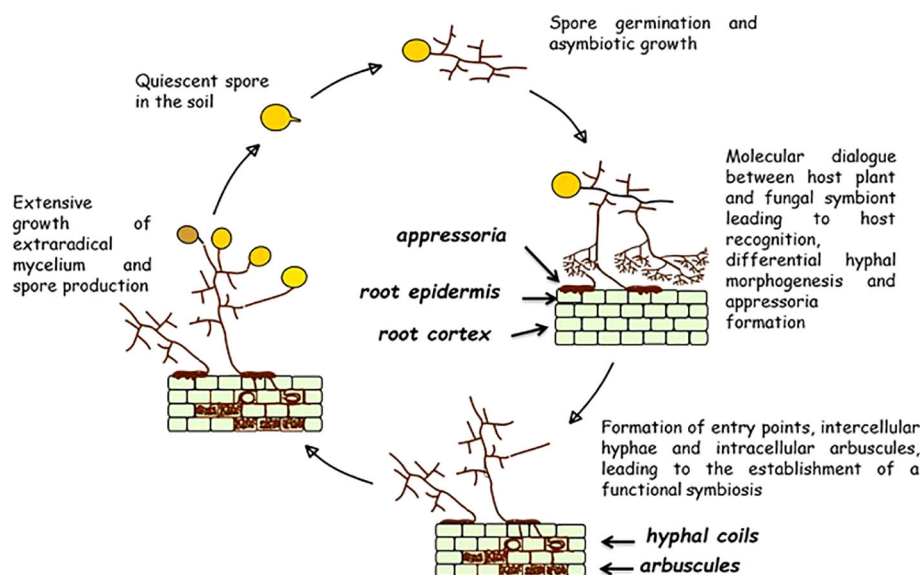


FIGURE 1

Flow diagram representing the life cycle of obligate biotrophic arbuscular mycorrhizal fungi and the key developmental steps leading to the establishment of the mycorrhizal symbiosis. Source: Modified from Giovannetti (2000), courtesy of Kluwer Academic Press.

morphogenesis and branching, facilitating the location of plant roots and successive adhesion and colonization (Giovannetti et al., 1993, 1994; Akiyama et al., 2005; Besserer et al., 2006). At the same time, plant “symbiosis-specific” genes produce the cascade of events leading to the development of the mycorrhizal symbiosis (Delaux et al., 2014; MacLean et al., 2017).

The large adhesion structures, appressoria (called also hyphopodia), are formed as early as 36 h after the first contact (Giovannetti and Citernes, 1993). The role of appressoria is essential not only for the establishment of the symbiosis, but, more importantly, for plant nutrition, as they are the only fungal structures connecting soil-based to root-based hyphae, through which the transfer of P, N and other mineral nutrients from extraradical hyphae to the host plant can be accomplished (Pepe et al., 2020). Appressoria germinate producing entry points (called also infection pegs) and intraradical hyphae, which colonise the roots by forming intracellular hyphal coils and growing intercellularly, before producing, in the inner cortex, intracellular highly branched tree-like structures, similar to haustoria, named arbuscules. Arbuscules are the structures where nutrient exchanges between host plants and fungal symbionts are realized, as at their level plant carbon and lipids are released to the symbionts, while mineral nutrients imported by the extraradical hyphae are released to the hosts (Kiers et al., 2011; Wyatt et al., 2014). Moreover, several AMF taxa form intraradical spore-like lipid-rich vesicles, considered as storage organs.

Once established in their distinctive ecological niche and after obtaining host carbon, AMF grow from the host roots into the surrounding soil, developing wide networks of interconnected extraradical mycelium (ERM), which are real extensions of the absorbing root system, capable of long-term survival in the soil, independent of the host plant’s lifespan (Pepe et al., 2018). Besides

increasing the uptake of soil mineral nutrients and transferring them to the host plant, ERM can establish belowground interconnections among plants by means of hyphal fusion (anastomosis) (Giovannetti et al., 2004) and translocate soil nutrients from one plant to another (Mikkelsen et al., 2008; Weremijewicz et al., 2016; Řežáčová et al., 2025). Eventually, AMF life cycle is completed by the formation of asexual spores by extraradical hyphae, that germinate and give rise to a new cycle (Figure 1).

3 The nonhost mycorrhizal status of weeds

Many plant species are unable to establish functional AM symbioses and are considered nonhost or non-mycorrhizal plants. They represent an estimated 18% of all vascular plants and mainly belong to the families Amaranthaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Cyperaceae, Polygonaceae and Proteaceae (Harley and Harley, 1987; Tester et al., 1987; Brundrett, 2002, 2009; Wang and Qiu, 2006). Nonhost plants encompass some of the world’s worst agricultural weed species, such as *Chenopodium album*, reported amongst the ten most problematic weeds having developed a wide-scale herbicide resistance, *Raphanus raphanistrum*, which developed multiple herbicide-resistant populations, *Rapistrum rugosum*, a highly competitive weed rapidly increasing worldwide, the cosmopolitan *Capsella bursa-pastoris* and *Sinapis arvensis* widely distributed around the world with a persistent seedbank (Baskin et al., 2004; Walsh et al., 2004; Manalil et al., 2018; Singh et al., 2022).

The nonhost mycorrhizal status entails the absence of arbuscules, that are the defining feature of the physiological

functionality of AM symbioses (Koide and Schreiner, 1992; Brundrett, 2009). Thus, plants are considered nonhosts even in cases where low levels of hyphal root penetration and/or vesicles formation occur (Hirrel et al., 1978; Harley and Harley, 1987; Tester et al., 1987; Wang and Qiu, 2006; Brundrett, 2002, 2009, 2017). In addition, it has long been known that nonhost plants do not elicit the differential hyphal morphogenesis that is the first sign of fungal recognition of a host plants (Giovannetti et al., 1994; Akiyama et al., 2005; Akiyama and Hayashi, 2006; Besserer et al., 2006).

The absence of mycorrhizal colonization and the lack of arbuscules and successful entry points has been reported in several weeds, such as *Arabidopsis thaliana*, *Amaranthus retroflexus* (Amaranthaceae), *Brassica campestris*, *B. napus*, *B. nigra*, *C. bursa-pastoris*, *Sinapis arvensis*, *Sisymbrium altissimum* (Brassicaceae), *Stellaria media* (Caryophyllaceae), *Chenopodium album* (Chenopodiaceae), *Urtica dioica* (Urticaceae) inoculated with either of the species *Rhizophagus fasciculatus*, *Rhizophagus intraradices*, *Funneliformis mosseae*, *Funneliformis coronatum*, *Gigaspora margarita* and *Gigaspora gigantea* (Glenn et al., 1985; Fontenla et al., 1999; Rinaudo et al., 2010). Moreover, a large experimental survey of 646 taxa within the Brassicaceae family inoculated with *R. intraradices* reported that only 122 (19%) showed root penetration, represented by intraradical hyphae and vesicles, while no arbuscules were observed across the 3,230 root sections examined (Demars and Boerner, 1996). Accordingly, no arbuscules were detected in any of the 7,200 root segments examined of *C. bursa-pastoris* and among 8 nonhost weeds from two field sites (Demars and Boerner, 1994; Wang et al., 2021).

Investigations on a number of Brassicaceae and Chenopodiaceae species showed that no root colonization occurred after AMF inoculation when grown alone, while when a mycorrhizal companion host plant was present, the fungus was able to penetrate the roots, in some cases dead or senescing ones, producing only intercellular hyphae and vesicles, but no functionally active arbuscules (Hirrel et al., 1978; Ocampo et al., 1980, 1986; Demars and Boerner, 1995; Veiga et al., 2013; Fernández et al., 2019). Such a phenomenon was explained by the vigorous activity of extraradical hyphae spreading from mycotrophic plant roots growing nearby (Koide and Schreiner, 1992; Francis and Read, 1995; Lambers and Teste, 2013). This type of endophytic colonization in nonhosts by AMF has been classified as Glomalean Fungus Colonisation (GFC), or rudimentary arbuscular mycorrhizal (RAM) phenotype, in order to discriminate such fungal penetration from well-established functional symbioses in host plants (Brundrett, 2009, 2017; Cosme et al., 2018) (Table 1).

Alas, many of the quoted works did not follow the dynamics of the colonization process, which was reported in a detailed early investigation on the development of root colonization in the host *Trifolium subterraneum* and the nonhost *Brassica napus* (Tommerup, 1984). After 4 weeks' growth no arbuscules were formed in the nonhost, compared with the 86 of the host, while the hyphal swellings developed on the root surface of the nonhost produced few penetration pegs, some of which ceased growth, retracted the cytoplasm and formed septa separating living from dead hyphal parts (abortive entry points). This latter cellular event

was detected in other nonhost weeds, such as *Sinapis arvensis* and *Chenopodium album*, the latter showing also the formation of rare abortive arbuscules (Rinaudo et al., 2010; Daisog et al., 2012) (Figure 2).

Such findings, reported also in successive studies with diverse nonhost plants, suggested that plant resistance to fungal colonization is expressed after adhesion, resembling defence responses, such as the production of thick cell wall appositions and intense yellow root autofluorescence indicative of phenolic depositions in incompatible interactions, causing root browning and in some cases root death (Tommerup, 1984; Glenn et al., 1985; Allen et al., 1989; Gollotte et al., 1993; Giovannetti et al., 1994; Veiga et al., 2013) (Figure 3).

4 Direct and indirect mechanisms underlying the nonhost mycorrhizal status

The phenomenon of nonhost plants sparked interest into the mechanisms underlying the hindering of mycorrhizal development (Tester et al., 1987). One prevalent hypothesis of a role played by inhibitory compounds, such as root glucosinolates, was ruled out by investigations on different cultivars of *Brassica* spp. containing genetically determined levels of such compounds, whose different concentrations were not correlated with AMF ability to colonise the roots (Glenn et al., 1988). More recent data showed that AMF colonization of transgenic *Arabidopsis* lines differing in indolic glucosinolates levels was limited to vesicle formation, few intraradical hyphae and no arbuscules (Anthony et al., 2020).

Successive genomic, transcriptomic and comparative phylogenomic analyses revealed that the inability to establish the mycorrhizal symbiosis resulted from the multiple loss of "symbiotic-specific" genes (*NFP*, *DMI2*, *CASTOR*, *DMI3*, *IPD3*, *RAM1*, *RAM2*, *VAPYRIN*, *STR*, *STR2*, *PT4*), operating as regulators of the key steps of plant/AMF interactions, such as presymbiotic dialogue, fungal entry into the root, intraradical hyphal proliferation and arbuscule development (Delaux et al., 2014). Such loss was reported to have occurred independently in different plant lineages (Delaux et al., 2014; Bravo et al., 2016; MacLean et al., 2017). It is important to note that the nonhost plants lacking the "symbiotic toolkit" included the weeds *Arabidopsis thaliana*, *Brassica rapa*, *Camelina sativa*, *Reseda odorata*, *Thlaspi arvense* (Brassicaceae), *Cleome spinosa* (Cleomaceae), *Utricularia gibba* (Lentibulariaceae), *Cuscuta pentagona* (Cuscutaceae) and also species of the genus *Lupinus*, the only non-mycorrhizal legume (Delaux et al., 2014) (Figure 4). Actually, recent RNA-seq transcriptome analyses revealed that in the nonhost weed *A. thaliana* symbiosis-related genes were not expressed and diverse defence-related genes were upregulated (Fernández et al., 2019). These data clearly showed that the fungus was recognized as a potential enemy, whose root colonisation triggered the activation of plant defence responses, possibly leading to negative effects on plant growth (see next section).

TABLE 1 Type of AMF structures in the roots and growth responses of nonhost weeds, as assessed in microcosms inoculated with selected AMF or in the field (dash indicates no information on AMF occurrence in the roots or on growth responses).

Families and species of nonhost weeds	AMF inoculum	AMF structures in the roots	Responses of nonhost weeds to AMF	References
AMARANTHACEAE				
<i>Achyranthes aspera</i>	Native soil AMF	H, V No arbuscules	–	Neeraj et al., 1991
<i>Alternanthera sessilis</i>	Native soil AMF	H, V No arbuscules	–	Neeraj et al., 1991
<i>Amaranthus gracilis</i>	Native soil AMF	H, V No arbuscules	–	Neeraj et al., 1991
<i>Amaranthus spinosus</i>	Native soil AMF	H, V No arbuscules	–	Neeraj et al., 1991
<i>Amaranthus retroflexus</i>	<i>R. intraradices</i>	0	Mortality ↑ Biomass ↓	Sanders and Koide, 1994
<i>Amaranthus retroflexus</i>	Multispecies AMF inoculum	–	Biomass ↓	Jordan et al., 2000
<i>Amaranthus retroflexus</i>	Native AMF inocula	0	No responses	Vatovec et al., 2005
<i>Amaranthus retroflexus</i>	<i>F. coronatum</i> , <i>F. mosseae</i> , <i>R. irregularis</i>	H, V No arbuscules	No responses	Rinaudo et al., 2010
<i>Alternanthera philoxeroides</i>	Native soil AMF	H, V No arbuscules	–	Wang et al., 2021
ARACEAE				
<i>Acorus calamus</i>	Native soil AMF	H, V No arbuscules	–	Wang et al., 2021
<i>Pistia stratiotes</i>	Native soil AMF	0	–	Wang et al., 2021
ASTERACEAE				
<i>Arctium lappa</i>	Native soil AMF	0	–	Safari Sinegani and Elyasi Yeganeh, 2017
BORAGINACEAE				
<i>Echium vulgare</i>	Native soil AMF	H, No arbuscules	Mortality ↑ Biomass ↓	Francis and Read, 1995
BRASSICACEAE				
<i>Alliaria petiolata</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Alyssum alyssoides</i> , <i>A. desertorum</i> , <i>A. minus</i>	<i>R. intraradices</i>	0	–	Id.
<i>Arabidopsis thaliana</i>	<i>R. irregularis</i>	H, V No arbuscules	Biomass ↓	Veiga et al., 2013
<i>Arabidopsis thaliana</i>	<i>R. irregularis</i>	H, no arbuscules	Biomass ↓	Fernández et al., 2019
<i>Arabis glabra</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Barbarea orthoceras</i> , <i>B. verna</i>	<i>R. intraradices</i>	0	–	Id.
<i>Berteroa incana</i>	<i>R. intraradices</i>	0	–	Id.
<i>Brassica kaber</i>	Multispecies AMF inoculum	–	Biomass ↓	Jordan et al., 2000
<i>Brassica kaber</i>	Native AMF inocula	Negligible colonization	No responses/ Biomass ↓	Vatovec et al., 2005
<i>Brassica campestris</i>	<i>R. fasciculatus</i> E3	H, V No arbuscules	–	Ocampo et al., 1980

(Continued)

TABLE 1 Continued

Families and species of nonhost weeds	AMF inoculum	AMF structures in the roots	Responses of nonhost weeds to AMF	References
BRASSICACEAE				
<i>Brassica campestris</i>	<i>Gigaspora margarita</i>	0	–	Id.
<i>Brassica campestris</i>	Native AMF inocula	0	–	Id.
<i>Brassica campestris</i>	<i>F. mosseae</i>	H, V No arbuscules	–	Glenn et al., 1985
<i>Brassica campestris</i>	<i>Gigaspora gigantea</i>	0	–	Id.
<i>Brassica campestris</i>	<i>F. mosseae</i>	0	–	Fontenla et al., 1999
<i>Brassica campestris</i>	Native soil AMF	0	–	Yaseen et al., 2020b
<i>Brassica fruticulosa</i> , <i>B. juncea</i> , <i>B. nigra</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Brassica napus</i>	<i>R. fasciculatus</i>	0	–	Hirrel et al., 1978
<i>Brassica napus</i>	<i>R. fasciculatus</i> E3	H, V No arbuscules	–	Ocampo et al., 1980
<i>Brassica napus</i>	Native AMF inocula	H No arbuscules	–	Id.
<i>Brassica napus</i>	<i>F. caledonius</i>	H 1 abortive arbuscule/plant	–	Tommerup, 1984
<i>Brassica napus</i>	<i>F. mosseae</i>	H, V No arbuscules	–	Glenn et al., 1985
<i>Brassica nigra</i>	<i>R. fasciculatus</i>	H, V No arbuscules	–	Hirrel et al., 1978
<i>Brassica nigra</i>	<i>F. mosseae</i>	0	–	Fontenla et al., 1999
<i>Brassica nigra</i>	Native soil AMF	0	–	Yaseen et al., 2020a
<i>Cakile edentula</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Cakile maritima</i>	Native sand dune AMF	0	–	Giovannetti and Nicolson, 1983
<i>Camelina sativa</i>	Native soil AMF	0	–	Yaseen et al., 2020a
<i>Capsella bursa-pastoris</i>	Native soil AMF	H, V No arbuscules	–	DeMars and Boerner, 1994
<i>Capsella bursa-pastoris</i>	<i>R. intraradices</i>	H, V No arbuscules	–	DeMars and Boerner, 1995
<i>Capsella bursa-pastoris</i>	<i>F. mosseae</i>	0	–	Fontenla et al., 1999
<i>Cardamine hirsuta</i>	Native sand dune AMF	0	–	Ernst et al., 1984
<i>Cardamine impatiens</i> , <i>C. parviflora</i> ,	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Coincya monensis</i>	<i>R. intraradices</i>	0	–	Id.
<i>Coronopus didymus</i> , <i>C. squamatus</i>	<i>R. intraradices</i>	0	–	Id.
<i>Descurainia incana</i> , <i>D. sophia</i>	<i>R. intraradices</i>	0	–	Id.
<i>Diploaxis muralis</i> , <i>D. tenuifolia</i>	<i>R. intraradices</i>	0	–	Id.
<i>Erophila verna</i>	Native sand dune AMF	0	–	Ernst et al., 1984
<i>Eruca sativa</i> , <i>E. vesicaria</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Erucastrum gallicum</i>	<i>R. intraradices</i>	0	–	Id.
<i>Erysimum hieracifolium</i> , <i>E. inconspicuum</i>	<i>R. intraradices</i>	0	–	Id.

(Continued)

TABLE 1 Continued

Families and species of nonhost weeds	AMF inoculum	AMF structures in the roots	Responses of nonhost weeds to AMF	References
BRASSICACEAE				
<i>Hesperis matronalis</i>	<i>R. intraradices</i>	H, V No arbuscules	–	DeMars and Boerner, 1995
<i>Hirschfeldia incana</i>	<i>R. intraradices</i>	0	–	Id.
<i>Lepidium sativum</i>	Native soil AMF	0	–	Safari Sinegani and Elyasi Yeganeh, 2017
<i>Lepidium campestre</i> , <i>L. densiflorum</i> , <i>L. latifolium</i> , <i>L. perfoliatum</i> , <i>L. ruderales</i> , <i>L. virginicum</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Lunaria annua</i>	<i>R. intraradices</i>	0	–	Id.
<i>Malcolmia africana</i>	<i>R. intraradices</i>	0	–	Id.
<i>Matthiola incana</i>	<i>R. intraradices</i>	H, V No arbuscules	–	DeMars and Boerner, 1995
<i>Nasturtium microphyllum</i> , <i>N. officinale</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Raphanus raphanistrum</i>	<i>R. intraradices</i>	0	–	Id.
<i>Raphanus sativus</i>	<i>R. fasciculatus</i>	H, V No arbuscules	–	Hirrel et al., 1978
<i>Raphanus sativus</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Rapistrum perenne</i> , <i>R. rugosum</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Rorippa amphibian</i> , <i>R. austriaca</i> , <i>R. islandica</i> , <i>R. microphylla</i> , <i>R. nasturtium-aquaticum</i> , <i>R. palustris</i> , <i>R. sylvestris</i> , <i>R. teres</i>	<i>R. intraradices</i>	0	–	Id.
<i>Sinapis alba</i>	Native soil AMF	0	–	Fitter and Nichols, 1988
<i>Sinapis arvensis</i>	<i>F. coronatum</i> , <i>F. mosseae</i> , <i>R. irregularis</i>	H, V No arbuscules	No responses	Rinaudo et al., 2010
<i>Sinapis arvensis</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Sisymbrium altissimum</i> , <i>S. erysimoides</i> , <i>S. irio</i> , <i>S. loeselii</i> , <i>S. officinale</i> , <i>S. orientale</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Raphanus sativus</i>	<i>R. fasciculatus</i>	H, V No arbuscules	–	Hirrel et al., 1978
<i>Rorippa palustris</i>	Native soil AMF	H, V No arbuscules	–	Wang et al., 2021
<i>Sisymbrium altissimum</i>	<i>F. mosseae</i>	0	–	Fontenla et al., 1999
<i>Thlaspi arvense</i> , <i>T. perfoliatum</i>	Native soil AMF	0	–	Regvar et al., 2003
<i>Thlaspi perfoliatum</i>	<i>R. intraradices</i>	0	–	DeMars and Boerner, 1996
<i>Turritis glabra</i>	<i>R. intraradices</i>	0	–	Id.
CARYOPHYLLACEAE				
<i>Arenaria serpyllifolia</i>	Native soil AMF	H No arbuscules	Mortality ↑ Biomass ↓	Francis and Read, 1995
<i>Cerastium fontanum</i>	Native soil AMF	V, No arbuscules	–	Laursen et al., 1997
<i>Saponaria officinalis</i>	Native soil AMF	0	–	Zubek and Błaszczkowski, 2009

(Continued)

TABLE 1 Continued

Families and species of nonhost weeds	AMF inoculum	AMF structures in the roots	Responses of nonhost weeds to AMF	References
CARYOPHYLLACEAE				
<i>Spergula arvensis</i>	Native soil AMF	H, V No arbuscules	Mortality ↑ Biomass ↓	Francis and Read, 1995
<i>Stellaria media</i>	Native soil AMF	V, No arbuscules	–	Laursen et al., 1997
<i>Stellaria media</i>	<i>F. mosseae</i>	0	–	Fontenla et al., 1999
<i>Stellaria media</i>	<i>R. irregularis</i>	H, V No arbuscules	Biomass ↓	Veiga et al., 2012
CHENOPODIACEAE				
<i>Atriplex hortensis</i>	<i>R. fasciculatus</i>	0	0	Hirrel et al., 1978
<i>Chenopodium album</i>	<i>R. fasciculatus</i>	H, V No arbuscules	–	Hirrel et al., 1978
<i>Chenopodium album</i>	Native soil AMF	H, No arbuscules	Mortality ↑ Biomass ↓	Francis and Read, 1995
<i>Chenopodium album</i>	<i>F. mosseae</i>	0	–	Fontenla et al., 1999
<i>Chenopodium album</i>	Multispecies AMF inoculum	–	Biomass ↓	Jordan et al., 2000
<i>Chenopodium album</i>	Native soil AMF	0	–	Kasowska, 2002
<i>Chenopodium album</i>	Native AMF inocula	Negligible colonization	No responses	Vatovec et al., 2005
<i>Chenopodium album</i>	<i>F. coronatum</i> , <i>F. mosseae</i> , <i>R. irregularis</i>	H, V Few abortive arbuscules	Biomass ↓	Rinaudo et al., 2010
<i>Salsola kali</i>	<i>G. margarita</i> <i>R. fasciculatus</i> , <i>F. mosseae</i> , <i>G. microcarpum</i>	H, V Few abortive arbuscules	–	Allen et al., 1989
<i>Salsola kali</i>	<i>Entrophospora etunicata</i>	–	Biomass ↓	Johnson, 1998
<i>Salsola kali</i>	Native AMF inocula	–	Biomass ↓	Johnson, 1998
COMMELINACEAE				
<i>Commelina communis</i>	Native soil AMF	H, V No arbuscules	–	Wang et al., 2021
CYPERACEAE				
<i>Cyperus rotundus</i>	<i>R. aggregatus</i> , <i>F. geosporus</i> , <i>S. sinuosa</i>	H, V No arbuscules	Biomass ↓	Muthukumar et al., 1997
<i>Fimbristylis dichotoma</i>	Native soil AMF	0	–	Wang et al., 2021
MALVACEAE				
<i>Malva sylvestris</i>	Native soil AMF	0	–	Safari Sinegani and Elyasi Yeganeh, 2017
OXALIDACEAE				
<i>Oxalis pes-caprae</i>	<i>F. mosseae</i>	0	–	Parra-Garcia et al., 1992
PLANTAGINACEAE				
<i>Bacopa monnieri</i>	Native soil AMF	0	–	Wang et al., 2021
POACEAE				
<i>Agrostis capillaris</i>	Native soil AMF	0	–	Kasowska, 2002
<i>Agrostis stolonifera</i>	Native soil AMF	0	–	Kasowska, 2002

(Continued)

TABLE 1 Continued

Families and species of nonhost weeds	AMF inoculum	AMF structures in the roots	Responses of nonhost weeds to AMF	References
POACEAE				
<i>Festuca ovina</i>	<i>Glomus</i> spp.	–	Biomass ↓	van der Heijden et al., 1998
<i>Poa annua</i>	Native soil AMF	0	–	Laursen et al., 1997
POLYGONACEAE				
<i>Polygonum aviculare</i>	Native soil AMF	0	–	Kasowska, 2002
<i>Polygonum lapathifolium</i>	Multispecies AMF inoculum	–	Biomass ↓	Jordan et al., 2000
<i>Polygonum lapathifolium</i>	Native soil AMF	0	–	Kasowska, 2002
<i>Polygonum lapathifolium</i>	Native AMF inocula	0	No responses	Vatovec et al., 2005
<i>Polygonum lapathifolium</i>	Native soil AMF	H, V No arbuscules	–	Wang et al., 2021
<i>Rumex acetosa</i>	<i>Septoglomus constrictum</i>	0	Biomass ↓	Grime et al., 1987
<i>Rumex acetosella</i>	Native soil AMF	H, No arbuscules	Mortality ↑ Biomass ↓	Francis and Read, 1995
<i>Rumex acetosella</i>	Native soil AMF	H, No arbuscules	–	Eriksen et al., 2002
<i>Rumex crispus</i>	Native soil AMF	0	–	Kasowska, 2002
<i>Rumex crispus</i>	Native AMF inocula	Negligible colonization	No responses/ Biomass ↓	Vatovec et al., 2005
<i>Rumex obtusifolius</i>	Multispecies AMF inoculum	–	Biomass ↓	Jordan et al., 2000
PORTULACACEAE				
<i>Portulaca oleracea</i>	Multispecies AMF inoculum	–	Biomass ↓	Jordan et al., 2000
<i>Portulaca oleracea</i>	Native AMF inocula	0	No responses/ Biomass ↓	Vatovec et al., 2005
SCROPHULARIACEAE				
<i>Verbascum thapsus</i>	Native soil AMF	H, No arbuscules	Mortality ↑ Biomass ↓	Francis and Read, 1995
URTICACEAE				
<i>Urtica dioica</i>	<i>F. mosseae</i>	0	–	Fontenla et al., 1999
<i>Urtica dioica</i>	Native soil AMF	0	–	Eriksen et al., 2002
ZYGOPHYLLACEAE				
<i>Zygophyllum fabago</i>	Native soil AMF	0	–	Safari Sinegani and Elyasi Yeganeh, 2017

The weed status of each plant species is reported in: Composite List of Weeds (Weed Science Society of America), <https://wssa.net/weed/composite-list-of-weeds/>.

5 Growth responses of nonhost weeds to AMF

Since the 1980s, scientists reported AMF adverse effects on nonhost plants by attempted colonisation, such as root damages and reduced plant survival, growth and nutrient acquisition, especially when grown in the presence of active AMF extraradical hyphae originated from a host companion plant. For example, the

nonhost *Brassica oleracea* showed decreases in dry weight and P content of 71 and 72%, respectively, when challenged by *F. mosseae* extraradical hyphae originated from mycorrhizal roots of the host *Sorghum vulgare* growing nearby (Ocampo, 1986). In experimental field plots where the mycotrophic weeds *Abutilon theophrasti* and *Setaria lutescens* were grown together with the nonhost weed *Amaranthus retroflexus*, AMF – both native and *R. intraradices* – reduced the growth and P content of the latter (Sanders and Koide, 1994), whose biomass was reduced also when challenged with

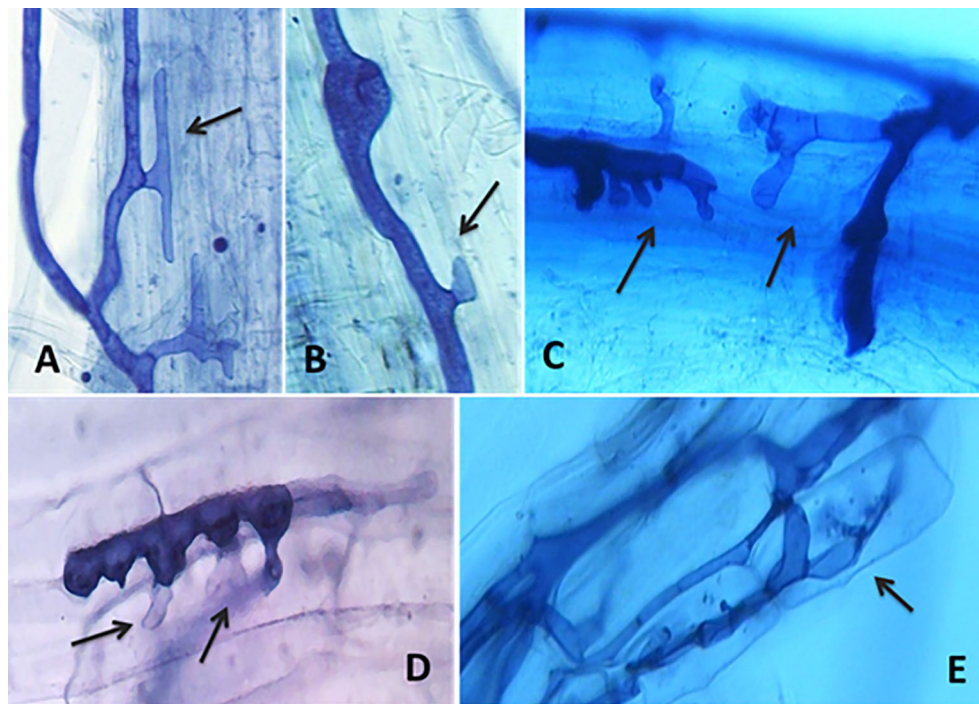


FIGURE 2

Light microscope pictures of the interactions between the arbuscular mycorrhizal fungus *Funneliformis mosseae* and roots of the nonhost weeds *Sinapis arvensis* and *Chenopodium album*, as shown by Trypan blue differential staining. (A) Hyphal swelling on the root surface of *S. arvensis*, ceasing growth and lacking cytoplasm (black arrow); (B–D) hyphal swellings and abortive entry points on the root surface of *C. album*, ceasing growth and lacking cytoplasm (black arrows); (E) a rare abortive arbuscule formed in the root of *C. album* (black arrow). Source: Courtesy of Dr. Valeria Rinaudo and Dr. Chandra Ramasamy Kamatchi

multispecies AMF inoculum (Jordan et al., 2000). On the other hand, no growth responses were found when *A. retroflexus* was inoculated with other AMF species, i.e. native AMF and *F. coronatum*, *F. mosseae* or *R. irregularis* (Vatovec et al., 2005; Rinaudo et al., 2010). Similar results were obtained with *Chenopodium album*, one of the most aggressive weeds, whose biomass was reduced by *F. mosseae*, *F. coronatum* or *R. irregularis* mycelium (Rinaudo et al., 2010) or by UK native soil AMF (Francis and Read, 1995), while no growth responses were shown when the weed was inoculated with native AMF inoculum of different geographic origin (Vatovec et al., 2005) (Table 1). Such inconsistent effects may be explained by the utilisation of diverse AMF taxa, which may show large differences among genera, species and also isolates, as evidenced by genome sequencing, transcriptomic data (Chen et al., 2018; Morin et al., 2019) and symbiotic performance studies (Lewandowski et al., 2013; Giovannini et al., 2020). Since only a small proportion of AMF have been investigated so far, further in-depth studies should explore the full potential of their wide interspecific and intraspecific physiological and functional diversity, particularly in relation to weeds growth, nutrition and health.

The major role played by AMF in growth control of nonhost weeds was confirmed using one of the worst perennial weeds of agricultural crops worldwide, *Cyperus rotundus* (Muthukumar et al., 1997). In experimental microcosms the native AMF *Rhizophagus aggregatus*, *Funneliformis geosporus* and *Sclerocystis*

sinuosa significantly decreased shoot dry weight by 67% when *C. rotundus* was grown together with the mycotrophic plant onion, compared with reductions of 36% when grown alone. Interestingly, dry weights of the tubers, the organs perpetuating such weed species belowground, decreased by 94% when grown together with onions (Muthukumar et al., 1997) (Table 1). The importance of mycorrhizal mycelium of companion or “nurse” plants was revealed using experimental microcosms, where nonhost plants were challenged by AMF extraradical hyphae spreading from host plants growing nearby, but separated by a cylinder of nylon mesh with a pore size enabling only the passage of fungal hyphae. In such microcosms, the nonhost weeds *Arenaria serpyllifolia*, *Chenopodium album*, *Echium vulgare*, *Rumex acetosella*, *Spergula arvensis*, *Verbascum thapsus* were strongly inhibited in their growth by the presence of native AMF mycelium and showed lower survivorship, with *A. serpyllifolia* suffering severe mortality (Francis and Read, 1995) (Table 1). Other works utilized the same device, showing that the nonhost weed *Stellaria media* had an 8-fold biomass reduction when challenged with the active mycelium of *R. irregularis*, growing from neighboring wheat plants, which produced some root colonization, only represented by hyphae and vesicles, but no arbuscules (Veiga et al., 2012). The study excluded allelopathy as a mechanism responsible for such growth suppression, but could not assess other possible operative mechanisms (Lambers and Teste, 2013). A successive work confirmed the key role played by active extraradical mycorrhizal

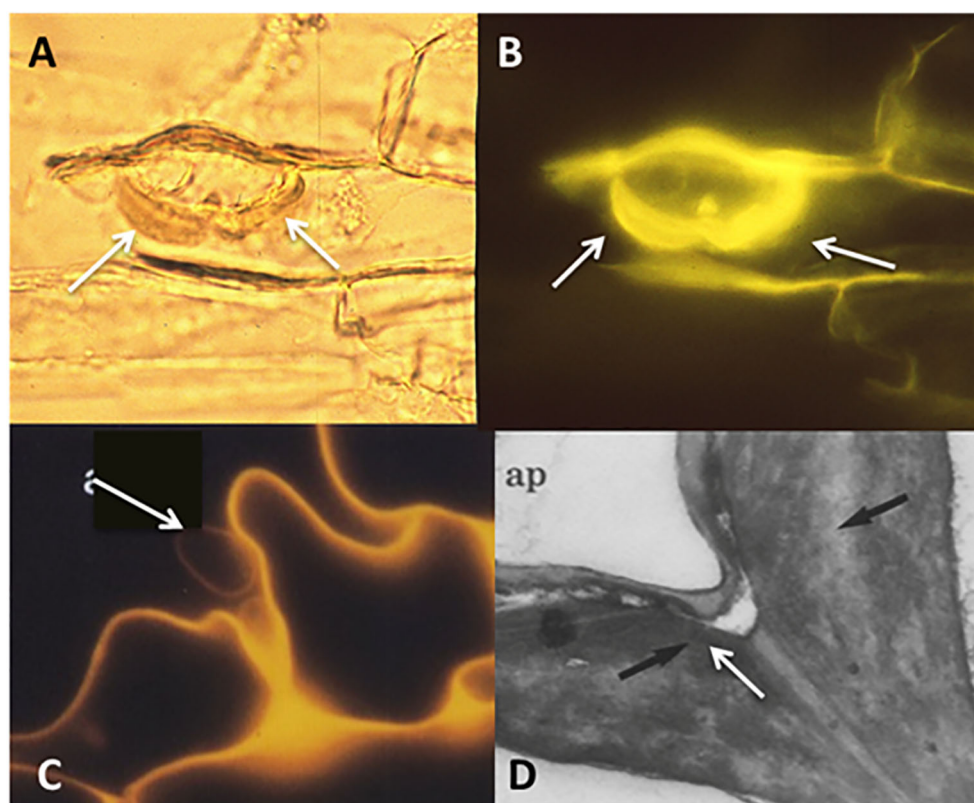


FIGURE 3

Micrographs of the interactions between *Funneliformis mosseae* hyphae in contact with the root surface of the nonhost *Pisum sativum* P2 mutant. (A–C) Wall thickenings below appressoria (A), showing strongly autofluorescence under epifluorescent microscope (B, C); (D) thickening of the plant cell wall below the appressorium (ap), visualised under transmission electron microscope. Source: (A, C, D) after Gollotte et al., 1993, courtesy of Springer-Verlag.

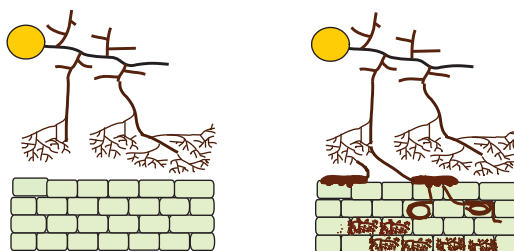
hyphae in growth control of the nonhost *A. thaliana*, whose biomass was reduced by more than 50% when grown together with both *T. pratense* and *Lolium multiflorum* inoculated with *R. irregularis*. Investigations on the cellular interactions between nonhost roots and the AMF fungus by confocal and transmission electron microscopy confirmed early findings by Allen et al. (1989), showing that root tissues colonised by AMF appeared senescent, with dead and partially collapsed cell walls, that appeared degraded at the point of contact with the fungal hyphae (Veiga et al., 2013) (Table 1). Utilizing a similar microcosm setup with *Medicago truncatula* as source of the active mycorrhizal network, Fernández et al. (2019) showed that the low (5%) hyphal colonization of *A. thaliana* roots by *R. irregularis* caused a 50% biomass reduction and was not associated with the expression of the symbiosis-related genes *GintPT*, *GintAMT2*, *GintMST2* and *GintMST4*, that are considered markers for a functional AM symbiosis. At the same time, the plant was able to recognise the fungus as an “unwanted invader” which activated root defences, possibly responsible of the growth decrease (Fernández et al., 2019). However, the specific mechanisms at the base of plant defence activation remain poorly understood, as well as the roles of certain fungal species in growth inhibition of diverse plant species. Further comprehensive studies are essential, including various crops, weeds and AMF species other than the model organisms *A. thaliana* and *R. irregularis*, as the

magnitude of responses may depend on the different plant/fungus combinations and also by the functional traits of each fungal species, in particular colonization ability and mutualistic performance (Giovannetti and Citeresi, 1993; Klironomos, 2003; Giovannini et al., 2020). Moreover, considering that most of the data collected so far have been carried out in microcosms/greenhouses (Table 1), field studies are needed under real crop conditions, as pH, organic matter, nutrient availability, edaphic factors and agricultural management can modulate the effectiveness of AMF in controlling nonhost weeds.

6 Research directions in agroecology

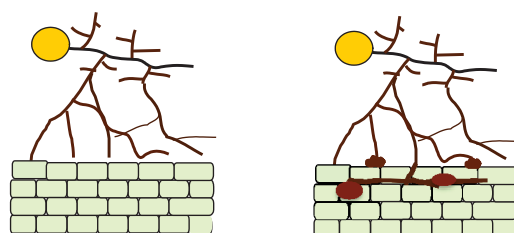
Altogether, all the experimental data obtained so far show that an active extraradical mycelium spreading from colonised host plants represents the main fungal factor responsible for negative impacts on nonhost weeds, ranging from biomass reduction to decreased survivorship. This is a very important, additional function of the soil mycorrhizal fungal networks, which are able to interconnect the roots of host plants belonging to different families, genera and species and transfer nutrients among them (Giovannetti et al., 2004; Mikkelsen et al., 2008; Weremijewicz et al., 2016; Wang et al., 2022; Řežáčová et al., 2025). In agricultural fields

Host root. 'Symbiotic toolkit' genes regulate the key steps of the interaction



Symbiotic-specific genes in host plants (*NFP*, *DMI2*, *CASTOR*, *DMI3*, *IPD3*, *RAM1*, *RAM2*, *VAPYRIN*, *STR*, *STR2*, *PT4*) regulate the key steps of plant/AMF interactions, such as presymbiotic molecular dialogue, appressoria formation, intraradical hyphal proliferation and arbuscule development, leading to the establishment of a functional mycorrhizal symbiosis.

Nonhost root. The absence of 'symbiotic toolkit' genes hinders the establishment of the symbiosis



The absence of symbiotic-specific genes in nonhost plants hinders pre-symbiotic molecular dialogue and the key steps of plant/AMF interactions. Occasionally hyphal swellings are formed on the root surface, with intraradical hyphal penetration, leading to the activation of plant-defense responses.

FIGURE 4

Schematic representation of the key steps of plant/AMF interactions regulated by symbiotic-specific genes, leading to the success or failure of mycorrhizal symbiosis establishment in host or nonhost plants.

AMF may produce differential effects on co-occurring species and alter the structure and functioning of plant communities, i.e. by favouring the growth and performance of host species, while simultaneously reducing the fitness and abundance of nonhosts. As to the biocontrol of nonhost weeds, it can be effective whenever crop plants are host species – such as most agricultural crops – able to produce extensive soil hyphal networks that may encounter the roots of nonhost weeds and lower their fitness by at least two diverse mechanisms. Firstly, hyphal root penetration in nonhost weeds without the formation of arbuscules – the site of nutrient transfer from the fungus to the host plant – does not provide any nutritional plant benefit, while the absence of “symbiotic-specific” genes can activate costly plant defence responses, diverting resources from plant growth (Delaux et al., 2014; Fernández et al., 2019). Secondly, the extraradical hyphal network may very efficiently uptake nutrients from the soil and transfer them to the host crops, promoting their growth, while reducing nutrient access by nonhost weeds. In this regard, the selection of crop genotypes with high AMF compatibility and able to produce extensive mycorrhizal networks may represent a good strategy in order to enhance weed control (Sawers et al., 2017; Giovannini et al., 2022).

The implementation of agroecological practices and the sustainable production of food crops, aimed at reducing chemical inputs into the soil, entail a careful and rational use of synthetic herbicides for weeds control. In this regard cover crops are increasingly being used as they provide many documented environmental benefits, including improved soil protection and health, enhancement of biodiversity and biological soil fertility, and the suppression of aggressive agricultural weeds (Adetunji et al., 2020; Haring and Hanson, 2022; Kumar et al., 2020; Tataridas et al., 2022). Mycorrhizal symbionts may boost cover crops performance, through the two main mechanisms already described. The first one concerns host cover crop species, which, when colonized by AMF, may benefit from the enhanced availability of soil nutrients provided by the extraradical hyphae and become more competitive against weeds. The second one involves nonhost weed species, whose growth may be negatively affected by AMF, due to the limited access to nutrients and to negative interactions involving plant defence responses activated in the absence of “symbiotic-specific” genes. Moreover, the AMF networks produced by mycorrhizal cover crops may represent a rich source of inoculum for the successive crops, contributing to the

maintenance of a high soil mycorrhizal potential, given the long-term survival of the extraradical mycelium (Pepe et al., 2018).

The detection of the best device to deliver AMF inoculum to crops and cover crops represents a tough challenge. One of the viable strategies to be adopted in agroecology could be represented by experimental seed inoculation with very infective and efficient AMF isolates, able to establish the mycorrhizal symbiosis immediately after seed germination, thus enhancing their competitive ability, in particular against host weeds. Seed inoculation could represent a strategy for broader use across agricultural systems, where viability and economic efficiency are of primary importance.

In order to understand whether the combination of cover crops with the use of beneficial AMF seed inoculation may represent effective agroecological tools for weed management, further work is underway within the framework of the research project Horizon Europe GOOD (AGroecology for weeDs, 101083589). In particular, we will study the possibility of enrichment cultures of autochthonous AMF to be reused for seed inoculation of a number of cover crops grown in rotation or as companion crops in the fields of annual main crops, such as wheat, rice, triticale, maize, soybean, cowpea, onion and perennial crops including pome and stone fruits, citrus, grapevine and olive. Such work is an example of the experimental studies to be performed under field conditions, needed in order to investigate AMF-cover crops-weeds interactions, implement innovative, systemic and sustainable strategies for weed management, and promote agroecological transition towards low-input, safe and resilient agroecosystems.

Author contributions

IP: Investigation, Writing – review & editing, Conceptualization. AG: Writing – review & editing, Investigation. MA: Data curation, Writing – review & editing. AT: Funding acquisition, Writing – review & editing. LA: Writing – review & editing, Writing – original

draft, Data curation. MG: Writing – original draft, Writing – review & editing, Investigation, Conceptualization.

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Conflict of interest

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