



Arbuscular Mycorrhiza Symbiosis as a Factor of Asteraceae Species Invasion

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Abstract: Invasive weeds of the Asteraceae family are widespread in the world. Arbuscular mycorrhiza (AM) is one of the main factors contributing to the successful distribution of these species that is most clearly manifested in the subfamily Asteroideae. The benefits of plant-AMF symbiosis are most significant under unfavorable biotic and abiotic conditions. The specificity of the relationship between arbuscular mycorrhizal fungi (AMF) communities and plants and is determined at the presymbiotic stage. The AMF colonization level is higher in invasive species than in native ones, but AMF communities associated with Asteraceae invasive species are less diverse. AMF communities of Asteraceae invaders often include fewer common species (e.g., species belonging to Diversisporales). Invaders also reduce native AMF species richness in new areas. Arbuscular mycorrhizal fungi can form mycorrhizal networks that allow the redistribution of nutrients in plant communities. The most significant influence of AMF associated with invasive Asteraceae plants is seen in the formation of soil and rhizosphere microbiota, including the suppression of beneficial soil bacteria and fungi. This review could be useful in the development of practical recommendations for the use of AMF-based fertilizers.

Keywords: arbuscular mycorrhizal fungi community; invasive weeds; Asteraceae; common mycorrhizal networks; *Glomeromycota*; biotic and abiotic factors

1. Introduction

In the context of world economic globalization and the rapid increase in food demand due to world population growth, invasive weeds have become a serious threat to various ecosystems worldwide. Such invasions become a significant economic and ecological risk factor, providing irreparable damage to agricultural biocenosis. Among the most harmful invasive plants, there are more than three dozen Asteraceae species [1,2]. Many invasive weeds not only produce allelopathic compounds and allergenic species themselves but also may be hosts for pests and pathogens, which are transferred to agricultural crops from these new habitats [3]. One of the features of most invasive Asteraceae species, including dangerous and quarantine plants such as *Ambrosia artemisiifolia* L., *Ambrosia trifida* L., *Bidens frondosa* L., *Helianthus tuberosus* L., *Solidago canadensis* L., *Solidago gigantea* Aiton, etc., are arbuscular mycorrhizal fungi (AMF) mutualism and mycorrhizal networks formation which facilitates their successful distribution and anchoring in new territories (Table 1) [4–8].



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Asteraceae Species	Life Cycle	AMF Colonization Level *	Invasive/Native	References
	Care	dueae		
Carduus acanthoides L.	biennial/perennial	medium	native	[9]
Carduus tenuiflorus Curtis	annual/biennial	medium	native	[10]
Centaurea scabiosa L.	perennial	medium	introduced	[11]
Centaurea stoebe (=Centaurea maculosa) L.	biennial/perennial	medium	invasive	[12]
	Cich	orieae		
Cichorium intybus L.	perennial	high	native/introduced	[13]
Lactuca serriola L.	annual/biennial	medium	native	[14]
Sonchus arvensis L.	perennial	low	pres	[15]
<i>Taraxacum officinale</i> (L.) Weber ex F.H.Wigg.	perennial	high	pres	[16]
	Seneo	rioneae		
Senecio vernalis Waldst. and Kit.	biennial	low	native	[17]
Tussilago farfara L.	perennial	medium	native	[18]
	Anthe	mideae		
Achillea millefolium L.	perennial	medium	native	[19]
Artemisia vulgaris L.	perennial	medium	native	[18]
Matricaria discoidea (=Matricaria matricarioides) DC.	annual	medium	native/introduced	[20]
Tanacetum vulgare L.	perennial	high	native	[21]
	Ast	ereae		
Aster squamatus (Spreng.) Hieron.	annual	medium	introduced	[14]
Baccharis halimifolia L.	perennial	low	native	[22]
Erigeron annuus (L.) Desf.	annual	high	invasive	[23]
Erigeron bonariensis (=Conyza bonariensis) L.	annual	medium	introduced	[15]
Erigeron canadensis (=Conyza canadensis) L.	annual	medium	invasive	[23]
Solidago canadensis	perennial	high	invasive	[23]
Solidago gigantea	perennial	high	invasive	[24]
Solidago nemoralis Aiton	perennial	medium	native	[25]
	Mill	erieae		
Galinsoga quadriradiata (=Galinsoga ciliata) Ruiz and Pav.	annual	medium	invasive	[26]
Galinsoga parviflora Cav.	annual	low	invasive	[27]
	Eupa	torieae		
Ageratina adenophora (Spreng.) R.M.King and H.Rob.	perennial	medium	invasive	[28]
	Coreo	psideae		
Bidens frondosa	annual	low	native	[29]
	aiiiluai	high	invasive	[23]

Table 1. AMF colonization level of different Asteraceae species.

Asteraceae Species	Life Cycle	AMF Colonization Level *	Invasive/Native	References
Bidens tripartite L.	annual	medium	introduced	[30]
	He	liantheae		
Ambrosia artemisiifolia	annual	medium	invasive	[31]
Helianthus annuus L.	annual	high	invasive	[21]
Helianthus tuberosus	perennial	medium	introduced	[32]
		high	invasive	[23]
Parthenium hysterophorus L.	annual	medium	native	[27]
Rudbeckia laciniata L.	perennial	high	invasive	[24]
Xanthium albinum (Widder) Scholz and Sukopp	annual	high	invasive	[23]

Table 1. Cont.

* low (<30%), medium (30–70%), high (>70%); assessed by histochemical method, based on counting the number of arbuscules, vesicles, and the length of mycelium.

The arbuscular mycorrhiza (AM) is formed by the fungi of the subphylum Glomeromycotina in the phylum Mucoromycota [33]. Their phylogeny has changed several times in the last two decades [33,34]. Earlier most of the AMF belonged to the major genus *Glomus*, but now many former *Glomus* species are assigned to other genera [35]. Nevertheless, this order Glomerales, which includes most of these genera, is still major in AMF communities (>70%).

There are lots of plant–AMF association benefits. First of all, it has better nutrient delivery, including phosphorus, nitrogen, sulfur, and microelements [36–41]. Mycorrhized plants are also more resistant to fungal diseases and pests [42–44]. One of the key factors affecting the effectiveness of mycorrhizal protection is the environmental conditions [42,45–47]. Under favorable environmental conditions and high availability of nutrients, arbuscular mycorrhiza does not have a significant effect on plant development, however, under adverse conditions of various nature, its effect becomes significant [8,47–49]. Symbiosis with arbuscular mycorrhizal fungi affects plant growth, increases their immunity, and helps them better tolerate drought, flooding, soil salinization and heavy metal pollution [26,48,50–53].

Research conducted on Chongming island, China, showed that the spread of Canadian goldenrod *S. canadensis* in arid areas was accompanied by increased AMF colonization, while such an effect was not observed in wet lowlands [48]. The success of plant AMF colonization may also depend on soil conditions. In the case of invasive ragweed *A. artemisiifolia* the highest degree of root mycorrhization was observed in disturbed areas, such as roadsides and wastelands, while the minimum percentage of mycorrhization was observed in natural conditions and in cultivated areas [54].

Invasive plants are colonized with AMF better compared to native plants. This was shown in *A. artemisiifolia*, *R. laciniata*, and *S. gigantea* [24,55]. The AMF community can influence the invasion of species by changing the competitive relationship between invasive and native species through changes in the abundance of AMF and their species composition. The invasion of some plants is usually accompanied by a decrease in the diversity of AMF species, but these remaining fungi help the invader. That was also shown in Asteraceae in the field [24,55,56]. As a result, native plants, dependent on mycorrhizal symbiosis, reduce or even lose their competitive advantage in the invaded area. Moreover, depending on the phytobiome and other biotic factors, the competitiveness of either invasive or native species may increase [57–59].

It is worth noting, that along with the physiological features of the development of invasive species (lengthening of the growing season, increase in the size of leaves, the number and viability of seeds, the formation of monodominant thickets, etc.), the synthesis of allelopathic compounds and other factors, and the success of expansion into new ter-

ritories by these species is determined by the ability to form arbuscular mycorrhiza and mycorrhizal networks [4–8]. Allelochemicals reduce the survival and regeneration of native plants and have a significant impact on the microbial community of the rhizosphere, due to the processes of decomposition, metabolization of labile and recalcitrant substrates, modifications of soil enzyme activity, etc. [60-67]. It was shown that allelochemical compounds, produced by S. canadensis, inhibit the colonization of native plants Echinochloa crusgalli, *Kummerowia striata*, and *Ageratum conyzoides* by AMF and change the AMF community [68]. Traditionally, allelopathy is considered to be a separate, independent mechanism of plant invasion. However, we suppose that in the case of invasive Asteraceae species this may be a first step in the two-step invasion. Thus, the release of allelochemical compounds leads to the weakening of the native flora, both directly—allelopathically and indirectly—through the suppression of their mycorrhizal symbiosis [68-70]. This leads to a change in the composition of the AMF community, which, in turn, may allow invasive plants to form their own effective symbiosis with AMF, further increasing their competitive potential. The main objective of the study was to determine the effects of AMF in symbiosis with plants on the spread of invasive Asteraceae weeds and to define its features. We compared AMF communities in native and invasive Asteraceae species, identified features of symbiotic relationships between AMF, and assessed their soil microbiota.

2. Invasive Asteraceae Species Associated with AMF

In Central Europe and European Russia, there are such associated AMF invasive species of the Asteraceae family such as fleabane *E. canadensis*, ragweed *A. artemisiifolia*, Jerusalem artichoke *H. tuberosus*, stickseed *B. frondosa*, goldenrod *S. canadensis*, pineapple weed *M. discoidea*, daisy *Symphyotrichum* x *salignum* (Willd.) G.L.Nesom, common cocklebur *Xanthium orientale* L., quick weed *Galinsoga parviflora*, spherical muzzle *Echinops sphaerocephalus* L., and others [32,71–76]. It is important to point out that the majority of noxious invasive Asteraceae species belong to the subfamily Asteroideae (Figure 1). It was shown that these species have the highest level of AMF colonization among other subfamilies [20,24].

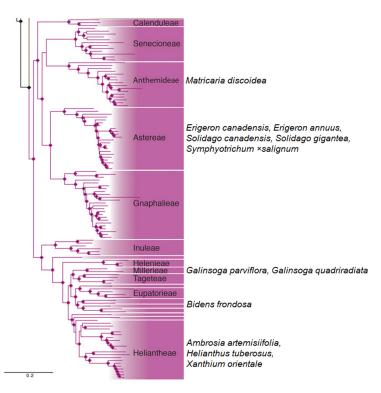


Figure 1. Phylogenetic tree of some dangerous invasive plants of subfamily Asteroideae according to Mandel et al., 2019 [77].

Depending on abiotic factors, host–plant species, and the presence of other species, the types of relationships may vary from mutualism to parasitism [46,78]. For invasive Asteraceae species, it is a powerful symbiosis. The nature of these interactions is determined by the plant species and the AMF community [79]. An analysis of the occurrence of fungal species associated with plants of the Asteroideae subfamily showed that invasive species from the tribes Anthemideae, Astereae, Cardueae, Gnaphalieae, Cichorieae, Senecioneae, and Heliantheae are often associated with such genera as *Glomus, Claroideoglomus, Rhizophagus, Septoglomus, Funneliformis, Paraglomus, Diversispora, Acaulospora, Archaeospora, Scutellospora*, and *Pacispora* [80]. This hypothesis is confirmed by data on a high level of arbuscular mycorrhizal fungus colonization of invasive Asteraceae species obtained in the Czech Republic, including *E. canadensis, S. canadensis, R. laciniata, G. parviflora, A. artemisiifolia*, etc. [20].

Along with widespread species of fungi, there are fewer common representatives of the Diversisporales order. The most frequent AMF associated with Asteraceae plants belongs to the genus *Glomus*. However, the AMF community of the invasive Asteroideae weeds in most cases contains Diversisporales in the field (Table 2). We suppose that the species of Diversisporales may be the key partners in the mutualistic relationships between invaders and AMF.

Host-Plant Species	Associated AMF Community	References
Brown knapweed <i>Centaurea jacea</i> L.	Glomus sp. Claroideoglomus sp. Diversispora sp. ** Acaulospora sp. ** Archaeospora sp.	[81]
Thistle Cirsium purpuratum (Maxim) Matsuma.	Acaulospora sp. ** Rhizoglomus sp. Rhizophagus sp. Diversispora sp. **	[82]
Canadian fleabane Erigeron canadensis (=Conyza canadensis)	Glomus versiforme Funneliformis caledonius F. mosseae Rhizophagus intraradices Septoglomus constrictum Claroideoglomus claroideum C. etunicatum Diversispora eburnean ** Diversispora sp. **	[23,83,84]
Canadian goldenrod <i>Solidago canadensis</i>	Septoglomus constrictum Funneliformis mosseae F. geosporus Claroideoglomus claroideum C. etunicatum Oehlia diaphana Glomus versiforme Acaulospora excavate ** A. mellea Diversispora sp.	[23,75]
Shaggy soldier Galinsoga quadriradiata	Glomus spp. Claroideoglomus claroideum Funneliformis mosseae Septoglomus constrictum *	[23]

Table 2. Asteraceae plant species whose distribution is enhanced by AMF.

Host-Plant Species	Associated AMF Community	References
Crofton weed Ageratina adenophora (=Eupatorium adenophorum)	Claroideoglomus etunicatum Funneliformis geosporus Rhizophagus aggregatum Diversispora arenaria **	[85,86]
Annual forb Bidens pilosa	Septoglomus viscosum Septoglomus constrictum Glomus perpusillum	[31]
Devil's beggarticks Bidens frondosa	Claroideoglomus claroideum Claroideoglomus drummondii Septoglomus constrictum Diversispora sp. **	[23]
Common ragweed Ambrosia artemisiifolia	Funneliformis mosseae Glomus reticulatum * Glomus perpusillum Septoglomus constrictum * Septoglomus viscosum Unundentidied spores	[31 <i>,</i> 55]
Jerusalem artichoke Helianthus tuberosus	Funneliformis mosseae Claroideoglomus claroideum Septoglomus constrictum Diversispora sp. **	[23]
Cutleaf coneflower Rudbeckia laciniata	Glomus macrocarpum Acaulospora cavernata** Claroideoglomus claroideum Funneliformis mosseae Pacispora franciscana ** Rhizoglomus fasciculatum Scutellospora dipurpurescens ** Septoglomus constrictum	[24]
Cocklebur Xanthium albinum	Funneliformis mosseae Claroideoglomus claroideum Septoglomus constrictum Rhizoglomus microaggregatum	[23,87]

Table 2. Cont.

* soil samples. ** genera of order Diversisporales.

2.1. The Nature of Symbiotic Relationship between Invasive/Native Plants and AMF Communities

The plant–AMF symbiosis is mediated through plant and fungal metabolites (primary and specialized metabolites, phytohormones) that ensure partner recognition, colonization, and the establishment of a symbiotic association. During pre-symbiotic communication, root released quercetin and 2-hydroxy fatty acids lead to compound-specific morphological AM fungal responses. Then strigolactone and cutin monomers (1,16-hexadecanediol and 16-hydroxyhexadecanoic acid) trigger hyphopodium development on the root surface. It has been established that the specificity of the relationship between AMF communities and plants is determined at the presymbiotic stage [78,79]. Phytohormones are involved in the plant-AMF regulation interactions as signaling molecules. They act from the early recognition of AMF in the soil to the final formation of mycorrhiza as strigolactones, auxins, abscisic acid, brassinosteroids, and gibberellic acid [88-92]. Auxin is necessary both for the early stages of fungal growth and for the differentiation of arbuscules, while gibberellic acids modulate the formation of arbuscules [91]. During the initial colonization, plant-AMF interactions are facilitated through the regulation of signaling and carotenoid pathways. Phytohormones can modulate plant immunity by altering the balance of jasmonate and salicylic acid signaling pathways, to promote phytohormone gibberellic acid. The AMF

symbiotic association influences the primary metabolism of plants to increase the level of sugars and metabolites of the tricarboxylic acid cycle and to facilitate photosynthates sharing.

Along with the changes in the primary metabolism, the formation of arbuscular mycorrhiza also affects the synthesis of specialized metabolites. AM has a positive effect on the production of specialized metabolites either by increasing plant biomass or by stimulating metabolite biosynthetic pathways. AMF–plant symbiosis provides benefits for sucking pests by altering the plant immunity with phytohormones and influencing primary and specialized metabolites [93,94]. For example, pyrrolizidine alkaloids—the major defense compounds of plants in the *Senecio* genus, are synthesized in response to AMF colonization.

2.2. Arbuscular Mycorrhiza and Soil Microbiota

The most significant influence of arbuscular mycorrhiza is seen in the formation of soil and rhizosphere microbiomes. Thus, a community of certain microorganisms is formed in the hyphosphere of AMF (mycorrhizosphere). In this case, the mycorrhizosphere is a narrow area of soil around the hyphae, where physical, chemical, and biochemical conditions differ from the rest of the soil volume due to the influence of hyphal exudates [95]. This effect of AM fungi can be compared with the formation of the soil rhizosphere by plants. Due to their apparently close ecological interactions, mycorrhizospheric microorganisms can be assigned to the so-called «second genome» of AMF, which significantly contributes to the attraction and nutrient turnover [95]. The microbiome of the mycorrhizosphere is unique compared to other microbial communities and is characterized by less species diversity, but a larger number of cultivated bacterial species [96]. In turn, the taxonomic composition, abundance, and diversity of bacterial and fungal communities also influence the relationship between the host plant and mycorrhizal fungi. For example, the analysis of the rhizospheric microbial community of greater burdock Arctium lappa L. (Asteraceae) showed an exceptionally low ratio of AMF (0.05%) in the presence of a diverse bacterial community. According to the authors, the key factors that led to this result are a more diverse and numerous bacterial community and soil characteristics. For example, there are differences in the composition of the bacterial communities of Gigaspora margarita and *Gigaspora rosea*, as well as six strains of AMF belonging to the species *Funneliformis mosseae*, F. coronatum n Rhizophagus intraradices. No correlation between the taxonomic status of fungi has been established [97,98]. Bacteria of the mycorrhizosphere are divided by their functions into «mycorrhiza helper bacteria» (MHB), which promote spore germination, mycelium growth and mycorrhiza formation, and «plant growth-promoting rhizobacteria» (PGPR). The PGPR provide an increase in available nutrients, protection and resistance to stress plants, improving their growth characteristics, as well as bacteria that combine the characteristics of MHB and PGPR [99–105]. The presence of *Paenibacillus* sp. in the mycorrhizasphere of *Rhizophagus irregularis* led to an increase in the amount of nitrogen from chitin [64,66,67,106,107]. Under field conditions, the synergistic effects promote the growth of sunchoke H. tuberosus by Rhizophagus intraradices KKU-Wh and Klebsiella variicola UDJA102 \times 89–9 [32]. A growth-stimulating effect was also observed with the combined action of the endophytic Exserohilum rostratum NMS1.5 and AMF Glomus *etunicatum* (=*Claroideoglomus etunicatum*) UDCN52867 [108]. It is interesting to note that a decrease in the proportion of arbuscular mycorrhiza fungi was accompanied by an increase in the proportion of asco- and basidiomycetes [65]. In general, invasive plants have a significant impact on local soil pathogens, which, in turn, affects the success of their spread in new territories [43]. There are soil bacteria that can inhibit the development of extraradical mycelium of AMF. Thus, the influence of AMF on the ecosystem depends on the soil microbiome [109]. *Gigaspora rosea* (Diversisporales) suppresses the beneficial soil bacteria *Pseudomonas putida* and fungi *Trichoderma pseudokoningii* [110,111].

The increase in disease and pest resistance, as well as the increased growth of plants colonized by arbuscular mycorrhiza, is the result of complex interactions between plants, pathogens and AMF. For example, mycorrhized plants of various families showed resistance

to soil phytopathogens *Aphanomyces*, *Cylindrocladium spathiphylli*, *Fusarium*, *Macrophomina phaseolina*, *Phytophthora*, *Pythium*, *Rhizoctonia*, *Sclerotinium*, *Verticillium*, *Thielaviopsis basicol*, and nematodes *Heterodera*, *Meloidogyne*, *Pratylenchus* n *Radopholus* [42–44]. It was shown that the resistance of *Leucanthemum vulgare* (Vaill.) Lam. (Asteraceae) to pathogens is not associated with changes in the root architecture and depends on the species composition of the AMF community [112]. It is supposed that there are many possible mechanisms to exhibit plant immunity against pathogens and pests. For example, the resistance of mycorrhized plants to soil pathogens may be associated with a nonspecific immune response that occurs in host plants, changes in the hormonal status of plants, and the endophytic community of microorganisms [45,113,114]. Arbuscular mycorrhiza is involved in signaling between infected and healthy plants, thereby contributing to the expression of PR protein genes (PR1, PR2, PR5) in uninfected plants and the formation of immune responses in plants [115].

2.3. Common Mycorrhizal Networks

AMF can also influence the dynamics of plant communities through the formation of mycorrhizal networks [116–119]. Mycorrhizal networks or common mycorrhizal networks (CMN) are networks of hyphae of mycorrhizal fungi that simultaneously colonize the root systems of some plants. A necessary condition for the formation and functioning of a mycorrhizal network is the ability of neighboring plants to be colonized by the same mycorrhizal fungi. The impact on intraspecific and interspecific competition is carried out due to the redistribution of mineral nutrients between plants, as well as the exchange of various signal and allelochemical compounds [120–130]. The structures of mycorrhizal networks depend on the species composition of plants growing in this area, and, in some cases, on their anatomical features (leaf size, etc.) [7,129]. Thus, a study conducted with 22 plant species formed in different communities showed that in the presence of several host plants, arbuscular mycorrhiza fungi prefer certain species [7].

The formation of arbuscular-mycorrhizal networks is shown for such Asteraceae plants as Canadian goldenrod *S. canadensis*, and common chicory *C. intybus* [72]. Plants connected by mycorrhizal networks exhibit greater plasticity in response to adverse external factors. This is manifested by a change in the growth rate of roots and shoots, the processes of photosynthesis and nutrition, and the occurrence of plant defense reactions. In the event of a stressor, plants associated with the CMN can exchange warning signals about the stress sources [131]. The laboratory experiments have shown the ability of mycorrhizal network, connecting invasive *S. canadensis* and native *Kummerowia striata* (Thunb.) Schindl. (Fabaceae), enhanced the growth of Canadian goldenrod and the influx of nitrogen and phosphorus compounds. At the same time, the growth and the number of available nutrients decreased in *K. striata* [72]. Thus, due to the uneven distribution of nutrients, arbuscular mycorrhizal fungi are able to change plant communities, facilitating the invasion of some species. It is interesting to note that nitrogen compounds are most often supplied by CMN to big photophilous plants [129].

3. Discussion

One of the important factors in the spread of invasive Asteraceae is the plant-associated AMF community. As a result of symbiotic relationships, weeds receive serious advantages over native species. These advantages are most significant under unfavorable biotic and abiotic conditions. The formation of arbuscular mycorrhiza improves nutrition (including phosphorus, nitrogen, sulfur, trace elements), and water supply, increases stress resistance of plants, and reduces their susceptibility to diseases and attractiveness for leaf-eating insects, including the increased synthesis of specialized plant metabolites. The influence of AMF and mycorrhizal networks on the soil microbiota, as well as the suppression of phytopathogens and nematodes, are important.

AMF communities associated with invasive and native plants have a number of significant differences. Firstly, the AMF community of Asteraceae invasive species is less diverse. Invaders also decrease AMF species richness in invaded ecosystems [24,56,132]. Secondly, the rate of AMF colonization of invaders is higher than that of native species [55]. Thirdly, AMF communities of Asteraceae invaders often include fewer common species (such as species of the order Diversisporales). Species of Diversisporales are quite difficult to identify by morphological features since the diversity of spores is high. The suppressive effect of Gigaspora rosea (Diversisporales) on soil bacteria and fungi was shown, while representatives of the order Glomerales generally demonstrate a synergetic effect on plants [110,111]. The question of whether there is an interaction between the AMF communities of invasive and native plant species remains open. Unfortunately, all commonly used approaches have some weaknesses. The classical histochemical method of assessment of fungal colonization through calculating the length of hyphae and the number of arbuscules and vesicles may reduce the value due to the fact that some AMF genera do not form arbuscles or form mainly exomycelium. These species are stably present in the AMF community associated with invasive weeds and may play a key role in the symbiosis. A discrepancy between the level of AMF colonization obtained by the histochemical method and the level of expression of genes, the products of which are involved in symbiosis, was revealed (Krukov unpublished). Therefore, the assessment of the level of colonization by physiological and biochemical plant parameters may lead to correction of existing conclusions and hypotheses.

It should be noted that most studies on mycorrhiza are carried out in vitro by inoculating test plants or their seeds with a spore suspension of well-known arbuscular mycorrhizal fungi, such as *Funneliformis mosseae*, *Rhizophagus intraradices*, and several *Glomus* spp., which are commonly used in agricultural biotechnology. The relationships between them and agricultural plants are well studied, so they are often used as the basis for fertilizers [101,102,108]. Species of Diversisporales order are used for these purposes in rarely cases. The peculiarities of these interactions are studied poorly.

Although such studies show the positive effects of mycorrhiza on plants overall, due to the limited number of species used, they do not reflect situations in nature, especially in complex ecosystems with large numbers of potential interactions between their components (Figure 2). There are few studies that reveal the features of plant–AMF interactions in natural conditions. This is due to the complexity of the planning and methodological base of such experiments. In our opinion, a combination of several approaches is necessary, specifically histochemical, molecular and biochemical approaches.

It is also necessary to take into account the relationship of AMF with the soil bacterial community [117,118]. Despite the large number of articles pointing to the possibility of synergy with the simultaneous use of bacteria-based fertilizers and AMF, it is also important to consider which types of fungi and bacteria are used in the fertilizer. Otherwise, the opposite effect to the expected one can be achieved.

CMNs can greatly enhance the capabilities of invasive plants associated with AMF. For example, they may form friendly phytobiota, redistribute excess nutrients and water, or signal about threats [115,125–128]. The species composition of AMF involved in CMN is poorly understood. However, in our opinion, the data on the species composition is extremely important, since they determine the specificity of these relationships.

It should be noted that the identification of AMF species associated with invasive plants is rather complicated. It is difficult to distinguish them by morphological features, since they are located inside plant cells, and are capable of forming anastomoses. They also may not be cultivated on artificial nutrient media. When using molecular methods of AMF DNA identification, there is a risk of contamination with the genetic material of the soil mycobiota or the host plant. Another difficulty lies in the fact that the loci traditionally used for fungal identification have high interspecific and intraspecific genetic polymorphism [47,133,134]. Many authors associate the solution to these problems with a wider introduction of new generation sequencing (NGS) methods into the research process

and a more thorough analysis of genome and transcriptome data [135–137]. At the same time, the identification of key AMF genera associated with invasive plants, in our opinion, would make it possible to develop probes for their rapid identification and quantification by molecular methods. This is necessary to effectively control the number of AMF-associated invasive weeds.

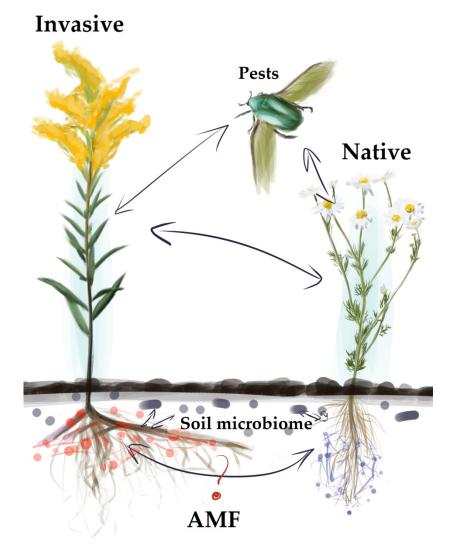


Figure 2. Interactions with invasive Asteraceae species in phytocenoses.

4. Conclusions

Thus, one of the important factors in the spread of invasive Asteraceae is the plantassociated AMF community. As a result of symbiosis, weeds receive serious advantages over native species. These advantages are most significant under unfavorable biotic and abiotic conditions.

It has been shown that the species of the host plant determine the species composition of the AMF communities. In turn, the AMF communities closely interact with soil biota. The influence of AMF communities on the phytocenoses as a whole is still insufficiently known. There is an opinion that AMF communities are rather «passengers» than «drivers» of Asteraceae invasions [138]. However, there are other opinions on this matter, and emerging data do not support this [57,132].

Cultivation of Asteraceae such as *H. annuus*, and *H. tuberosus* can affect the soil and rhizosphere microbiota. It is also necessary to monitor invasive Asteraceae weeds as *A. artemisiifolia*, *B. frondosa*, *S. canadensis*, etc. because these species have a significant impact on ecosystems. Thus, this factor of invasion must be considered while planning agrotechnical

measures to limit the distribution of weeds, developing measures for the conservation of native plants, and using AMF-based fertilizers.

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