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Для оформления обложки использованы изображения арбускулярной микоризы (сканирующая электронная микроскопия, © Jozsef Racsko, Mycorrhizal Applications, LLC) и золотарника канадского (© Сергей Удалов, ФГБНУ ВИЗР). Изображения иллюстрируют объекты, описываемые в рукописи Малыгина и др. стр. 144–152.

For the title page design, the images of arbuscular mycorrhiza (scanning electron microscopy, © Jozsef Racsko, Mycorrhizal Applications, LLC) and Canadian goldenrod (© Sergei Udalov, All-Russian Institute of Plant Protection) were used. The figures are given to illustrate objects, mentioned in the manuscript by Malygin et al., pp. 144–152.

DOES ARBUSCULAR MYCORRHIZA FAVOR INVASION OF SOME ASTERACEAE TRIBES?

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Invasive species, including more than three dozen Asteraceae, such as *Solidago canadensis*, *Leucanthemum vulgare*, *Senecio inaequidens* etc, pose serious threat to ecosystem health. Arbuscular mycorrhizal symbiosis is a key factor for distribution of invasive species of some Asteraceae tribes, including Astereae, Anthemideae, Senecioneae, Gnaphalieae, Cardueae, and Cichorieae. The formation of invasion-friendly plant communities has occurred through increasing nutrient and water availability, hormonal regulation, production of bioactive compounds, and mycorrhiza-induced resistance of host plants. Native species are displaced through the influence on soil microbiota, mycorrhizal and nutrient status of neighboring plants, and several other parameters. Allelopathic influences and symbiotic interactions with bacteria and other fungi can inhibit these processes. Understanding the mycorrhizal status of invasive weeds, in our opinion, is a necessary condition for their successful control.

Keywords: common mycorrhizal networks, invasive weeds, Cardueae, Astereae, Anthemideae, Senecioneae, Cichorieae

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Invasive weeds, including more than three dozen species of Asteraceae, pose serious threat to ecosystem health (Medve, 1984; Mehraj et al., 2021). An important feature of Asteraceae, which often manifests itself alongside allelopathic effects, is the ability to form arbuscular mycorrhiza (AM) and common mycorrhizal networks (CMN) (Bongard et al., 2013; Yuan et al., 2014; Li et al., 2016; Chagnon et al., 2019; Qin, Yu, 2019). For invasive species like *Solidago canadensis* (Astereae), *Helianthus tuberosus* (Heliantheae), and *Echinops sphaerocephalus* (Cardueae), it was shown that AM and CMN contribute to their distribution and introduction successes (Bongard et al., 2013; Dong et al., 2015, 2021, Awaydul et al., 2018, Řezáčová et al., 2020, Nacoon et al., 2021). Analysis of scientific literature has established four tribes (Anthemideae, Astereae, Cardueae and Senecioneae) that rely on AM in their distribution (Table 1, Fig. 1). In addition, the analysis of about 40 thousand nucleotide DNA sequences of fungi from 32 genera in Asteraceae family contained in NCBI database and including the most noxious weeds was carried out. The percentage of AMF occurrence among all fungi associated with these plants was calculated. The soil mycobiota of Senecioneae, Anthemideae, Astereae, Gnaphalieae, Cichorieae, and Cardueae tribes was represented by AMF in more than 50% of the cases. It was also revealed that the mycobiota of monophyletic Senecioneae, Anthemideae, Astereae, and Gnaphalieae tribes contain AMF species belonging to four orders (Paraglomerales, Archaeosporales, Diversisporales, and Glomerales). In contrast, the Cichorieae and Cardueae tribes are associated mainly with Glomerales (Malygin, Sokornova, 2021). We believe that AM is the key factor for invasion of the species belonging to these tribes.

Senecioneae, Anthemideae, Astereae, and Gnaphalieae tribes originated in South Africa (Mandel et al., 2019). It is

possible that mycorrhiza helped them to spread around the world.

AM is the most ancient and frequent type of mycorrhiza. It is suggested that mycorrhiza helped first plants to leave water and adapt to the aridity of land about 450 million years ago (Provorov, Shtark, 2014; Redecker et al., 2000; Rich et al., 2021).

Assessment of host specificity in mycorrhizal communities is difficult due to the large phylogenetic diversity of plants and fungi that can form AM. Earlier, it was believed that AMF are associated with a wide range of plants (Molina et al., 1992). However, more and more data are now emerging that reveal the association of different genotypes of AMF with geographic regions or/and host-plant species (Alguacil et al., 2019). Changes in AMF composition of the soil biome occur simultaneously with the development of plant communities (Öpik et al., 2013; Mony et al., 2021).

AM can significantly improve plant nutrition, water availability, soil structure and fertility, as well as stress resistance and tolerance (Augé, 2001). For example, AM reduces stress consequences caused by pathogens, heavy metals, and soil salinization (Jentschke, Godbold, 2000; Harrier, Watson, 2004; Whipps, 2004; Smith, Read, 2008). Plants do not receive large benefits from AM when there is high availability of nutrients, but AM enhances plant development under conditions of nutrient deficiency (Höpfner et al., 2015). Depending on the timing of *S. canadensis* invasion in arid habitats, the relative abundance of the two dominant AMF species significantly varied. For example, on the Chongming island, China, in dry habitats AMF colonization rate increased with distribution of *S. canadensis* but in lowland habitats there was no such effect (Jin et al., 2004). AMF can stimulate seed germination, enhance growth, and improve the synthesis of biologically active compounds of plants. For example,

Table 1. Distribution and proven ability to form AM of some species of Asteraceae family

Species	Tribe	Geographic origin	Establishment and spread of invasive species	AM	Reference
<i>Anthemis arvensis</i>	Anthemideae	Europe, Northern Africa	North and South Americas, Australia, New Zealand, Africa	+	Symbio data
<i>Anthemis cotula</i>	Anthemideae	Mediterranean Europe, Northern Africa	North and South Americas, Australia, North-East Asia, Europe, Siberia	+	Shah et al., 2008
<i>Anthemis tinctoria</i>	Anthemideae	Northern part of Eurasia	Southern Europe, Eastern Asia, North America	+	Symbio data
<i>Artemisia campestris</i>	Anthemideae	Eurasia, North America	—	+	Symbio data
<i>Artemisia maritima</i>	Anthemideae	Europe, Siberia	—	+	Symbio data
<i>Artemisia verlotiorum</i>	Anthemideae	China	Eurasia, Africa, Australia, New Zealand, North America	+	Kempel et al., 2013
<i>Artemisia vulgaris</i>	Anthemideae	Eurasia, Northern Africa	North America	+	Symbio data
<i>Leucanthemum vulgare</i>	Anthemideae	Europe, Central Asia	China, India, North America, southern part of South America, South Africa, Australia, New Zealand	+	Noori et al., 2014
<i>Tanacetum vulgare</i>	Anthemideae	Eastern and Central Europe	Western Europe, Eastern Asia, Australia, New Zealand, North America, southern part of South America	+	Lucero et al., 2020
<i>Tanacetum cinerariifolium</i>	Anthemideae	Balkan Peninsula	—	+	Waceke et al., 2002
<i>Tanacetum parthenium</i>	Anthemideae	South-West Europe	Europe, North America, Chile	–	Symbio data
<i>Tripleurospermum inodorum</i>	Anthemideae	Eurasia	North America	+	Symbio data
<i>Tripleurospermum maritimum</i>	Anthemideae	Northern Europe	—	+	Symbio data
<i>Erigeron annuus</i>	Astereae	North America	Western Europe, China	+	Gucwa-Przepióra et al., 2016
<i>Erigeron canadensis</i>	Astereae	North America	Eurasia, Australia, New Zealand, North Africa	+	Řezáčová, 2020
<i>Erigeron karvinskianus</i>	Astereae	Central America	North America, northern and eastern parts of South America, Africa, South-West Asia, Australia, New Zealand	+	Oliveira et al., 2005
<i>Solidago canadensis</i>	Astereae	North America	Europe, Russia, China, India, Australia, New Zealand, Brazil	+	Awaydul et al., 2018
<i>Solidago gigantea</i>	Astereae	North America	Europe, Asia	+	Harkes et al., 2021
<i>Solidago nemoralis</i>	Astereae	North America	—	+	Cumming, Kelly, 2009
<i>Solidago virgaurea</i>	Astereae	Europe	—	+	Betekhtina et al., 2016
<i>Symphotrichum x salignum</i>	Astereae	Europe	Western Siberia, Far East of Russia, Japan	+*	Pendergast IV et al., 2013
<i>Symphotrichum subulatus</i>	Astereae	Southern USA, Mexico, South America	China, Iran, South Korea	+	Wang et al., 2021
<i>Arctium lappa</i>	Cardueae	Eurasia	North America, Australia, New Zealand	+	Symbio data
<i>Carduus nutans</i>	Cardueae	Eurasia	North America, Argentina, Australia, New Zealand	–	Wardle et al., 1998
<i>Centaurea cyanus</i>	Cardueae	Central Europe	Eurasia, North America, Australia	+	Symbio data
<i>Centaurea maculosa</i>	Cardueae	Eastern Europe	North America, New Zealand, Western Europe	+	Mummey et al., 2006
<i>Centaurea melitensis</i>	Cardueae	Northern Africa, Southern Europe	USA, New Zealand, Australia, South America	+	Callaway et al., 2001
<i>Centaurea solstitialis</i>	Cardueae	Mediterranean Europe, Northern Africa	Eurasia, North America, Southern South America, Australia, New Zealand	+	Waller et al., 2016
<i>Cirsium arvense</i>	Cardueae	Southeastern Europe	Eurasia, Australia, New Zealand, South Africa, North America	+	Eschen et al., 2010
<i>Echinops sphaerocephalus</i>	Cardueae	Southeastern Europe	Europe, USA	+	Řezáčová et al., 2020
<i>Cichorium intybus</i>	Cichorieae	Eurasia, North Africa	Australia, New Zealand, South Africa, North and South America	+	Awaydul et al., 2018
<i>Hieracium alpinum</i>	Cichorieae	Europe	—	+	Symbio data
<i>Hieracium bifidum</i>	Cichorieae	Europe	—	+	Symbio data
<i>Hieracium lachenalii</i>	Cichorieae	Europe	North America, Australia	+	Symbio data

Table 1 continued

Species	Tribe	Geographic origin	Establishment and spread of invasive species	AM	Reference
<i>Hieracium oistophyllum</i>	Cichorieae	Europe	—	+	Symbio data
<i>Hieracium umbellatum</i>	Cichorieae	Eurasia, North America	—	+	Symbio data
<i>Pilosella aurantiacum</i>	Cichorieae	Europe	North America, Russia, Mongolia, Japan, Australia, New Zealand	+	Weed Control..., 2013
<i>Pilosella officinarum</i>	Cichorieae	Europe, South-West Asia	North America, Argentina, New Zealand	+	Höpfner et al., 2015
<i>Sonchus arvensis</i>	Cichorieae	Europe	Asia, Australia, New Zealand, North America, few regions of Africa	+	Symbio data
<i>Taraxacum officinale</i>	Cichorieae	Greece	Eurasia, North and South America, South Africa, Australia, New Zealand	+	Mariotte et al., 2012
<i>Bidens frondosa</i>	Coreopsideae	North America	Eurasia, New Zealand, Morocco	+	Stevens et al., 2010
<i>Bidens pilosa</i>	Coreopsideae	South and Central America	North America, Africa, Western Europe, South-West Asia, Australia, New Zealand and islands across Indian and Pacific oceans	+	Zhang et al., 2018
<i>Coreopsis drummondii</i>	Coreopsideae	North America	North and South Korea, Japan	+	Chen et al., 2007
<i>Coreopsis grandifolia</i>	Coreopsideae	North America	Europe	+	Yanfang et al., 2012
<i>Ageratina adenophora</i>	Eupatorieae	Central Mexico	South and South-East Asia, Australia, New Zealand, Western Europe, few regions of Africa	+	Li et al., 2016
<i>Praxelis clematidea</i>	Eupatorieae	South America	China, Thailand, Australia	–	Intanon et al., 2020
<i>Gnaphalium californicum</i>	Gnaphalieae	USA	—	+	Vogelsang, Bever, 2009
<i>Gnaphalium supinum</i>	Gnaphalieae	Eurasia, North America	—	+	Symbio data
<i>Gnaphalium sylvaticum</i>	Gnaphalieae	Europe, North America	—	+	Symbio data
<i>Gnaphalium uliginosum</i>	Gnaphalieae	Eurasia, North America	—	+	Symbio data
<i>Ambrosia artemisiifolia</i>	Heliantheae	North and Central America	South America, Eurasia, Australia, New Zealand, North and South Africa	+	Fumanal et al., 2006; Zhang et al., 2018
<i>Ambrosia psilostachya</i>	Heliantheae	Western North America	Europe, India, Japan, Australia, South Africa	+	Montagnani et al., 2017
<i>Helianthus annuus</i>	Heliantheae	North America	—	+	Symbio data
<i>Helianthus tuberosus</i>	Heliantheae	North America	Eurasia, southern part of South America, Australia, New Zealand	+	Nacoon et al., 2021
<i>Senecio jacobaea</i>	Senecioneae	Eurasia	North America, Brazil, Australia, New Zealand	+	Symbio data
<i>Senecio vulgaris</i>	Senecioneae	Eurasia, northern Africa	North America, southern part of South America, Australia, New Zealand	+	Symbio data

* AM was detected in the parental form *Symphyotrichum novae-angliae*.

multifaceted effects on herbivores and growth of host plants were demonstrated (van der Heijden et al., 1998; Bennett, Bever, 2007; Smith, Read, 2008).

Success of mycorrhizal colonization of plants may also depend on the soil state. In the case of invasive *Ambrosia artemisiifolia*, for example, the most intensive mycorrhizal colonization was observed in disturbed areas such as roadsides and wastelands while the minimal percentage of mycorrhizal colonization occurred in cultivated areas. This may be due to the differences in physicochemical properties of soils (soil texture, moisture, pH, nutrients) or to the cessation of agricultural methods such as application of fungicides or soil tillage (Fumanal et al., 2006). Moreover, the unfavorable ecological factors (acid precipitation, soil contamination by heavy metal ions, herbicides, etc.) can promote an invasion enhanced by AM (Richardson, Pyšek, 2012).

AM can inhibit soil pathogens such as *Aphanomyces*, *Cylindrocladium spathiphylli*, *Fusarium*, *Macrophomina phaseolina*, *Phytophthora*, *Pythium*, *Rhizoctonia*, *Sclerotinium*, *Verticillium*, and *Thielaviopsis basicol*, as well as nematodes

such as *Heterodera*, *Meloidogyne*, *Pratylenchus* and *Radopholus* (Harrier, Watson, 2004; Zhang et al., 2009; 2011). The soil microbiota in this case depends on the plant species and AM genotype. AMF are also able to induce nonspecific immune responses in their host plants (Qu et al., 2021). In turn, bacterial soil community can inhibit the development of AMF. For example, analysis of microbial community of *Arctium lappa* (Asteraceae) rhizosphere showed exceptionally low level (0.05%) of AMF in presence of a diverse bacterial community (Xing et al., 2020).

There is a relationship between AM and the synthesis of plant phytohormones (Hanlon, Coenen, 2011). Sometimes, allelopathic effects on native flora were observed along with AM. Classic examples of such Asteraceae plant invasions are those of *Solidago canadensis* (Astereae) and *Centaurea maculosa* (Cardueae) (Yang et al., 2007; Abhilasha et al., 2008; Zhang et al., 2009; Yuan et al., 2013). However, there are also examples of invasions that rely on allelopathic effect only, including *Carduus nutans* (Cardueae), *Praxelis clematidea* (Eupatorieae), and *Mikania micrantha* (Eupatorieae) (Wardle

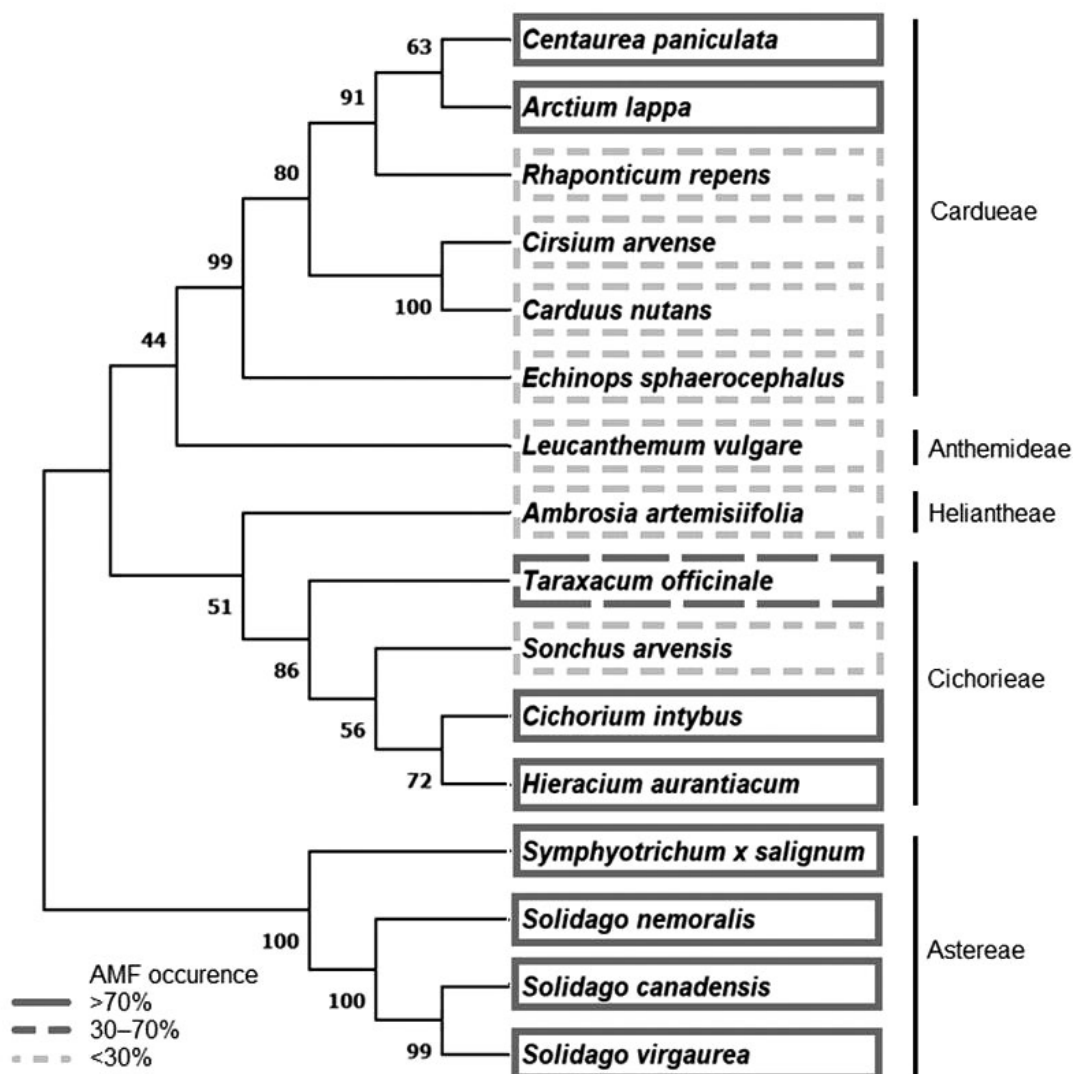


Figure 1. The occurrence of AMF among Asteraceae tribes. Phylogenetic relations of weed species representing the respective tribes are inferred from a 342 bp long rDNA sequence dataset (18S ribosomal RNA gene, partial sequence; internal transcribed spacer 1, 5.8S ribosomal RNA gene, and internal transcribed spacer 2, complete sequence) using the Maximum Likelihood method based on the Tamura-Nei model. The bootstrap consensus tree is obtained using 400 replicates in MEGA7 (Kumar et al., 1993). Branches corresponding to partitions reproduced in less than 40% bootstrap replicates are collapsed

et al., 1998; Chen et al., 2017; Intanon et al., 2020). AM can influence foliar fungal endophyte community, as it was shown *in vitro* for *Cirsium arvense* (Eschen et al., 2010).

Competitiveness of invasive and native plants can be influenced by CMN, which simultaneously colonize root systems of several plants, affecting ecosystem processes and dynamics of plant communities (Selosse et al., 2006; Horton, van der Heijden, 2008; van der Heijden, Horton, 2009; Horton, 2015). A necessary condition for the formation and functioning of a mycorrhizal network is the ability of neighboring plants to be colonized by CMN (Lucero et al., 2020). Structures of mycorrhizal networks depend on the composition of plant species in a given area (Chagnon et al., 2019). The formation of mycorrhizal network was demonstrated for *Tanacetum vulgare*, *S. canadensis*, and *Cichorium intybus* (Awaydul et al., 2018; Lucero et al., 2020).

CMN serve as conductor of various signaling and allelochemical compounds (Barto et al., 2011; Babikova et al., 2013; Johnson and Gilbert, 2015). They also participate in the

distribution of mineral nutrients between the plants (Walder et al., 2012; Merrild et al., 2013; Weremijewicz, Janos, 2013; Fellbaum et al., 2014; Jakobsen, Hammer, 2015; Walder, van der Heijden, 2015; Weremijewicz et al., 2016, 2017). For example, CMN promotes the growth of *Linum usitatissimum* (Linaceae) by transferring nitrogen, phosphorus, and carbon from *Sorghum bicolor* (Poaceae) (Walder et al., 2012). It is interesting to note that the functioning of the CMN depends on physiological characteristics of participating plants as well. For example, some AM fungi supply nitrogen preferentially to large light-loving plants (Weremijewicz et al., 2016). CMN of the invasive *S. canadensis* enhances the uptake of nitrogen and phosphorus and, consequently, enhances the growth of this plant by decreasing the uptake of these elements by *Kummerowia striata* (Fabaceae). Thus, CMN influence on intraspecific and interspecific competition via unequal distribution of mineral nutrients between plants.

Plants connected through CMN can quickly change their behavior in response to external factors. This is manifested

by a change in the growth rate of roots and shoots, in the processes of photosynthesis and nutrition, and in the plant defense reactions. It was shown that *Tanacetum vulgare* in association with *Solidago canadensis* was less attacked by insects and tolerated losses of biomass to a greater extent than the association-free plants (Lucero et al., 2020). The process of CMN development by an invasive plant can affect plant communities, including intra- and interspecific interactions, species coexistence, and biodiversity. These changes are wave-like (Gorzela et al., 2015).

AM is formed by fungi of the subphylum Glomeromycotina (phylum Mucoromycota) (Spatafora et al. 2016). Currently, species of Glomeromycotina are arranged in three classes, five orders, 16 families, and 41 genera (Goto, Jobim, 2018). The largest order is Glomerales, comprised by about 230 species (Bagyaraj, 2014; Spatafora et al., 2016). According to NCBI, plants in the subfamily Asteroideae are frequently associated with *Glomus*, *Claroideoglossum*, *Rhizophagus*, *Septoglossum*, *Funneliformis*, *Paraglossum*, *Diversispora*, *Acaulospora*, *Achaespora*, *Scutellospora*, and *Pacispora*.

There are certain difficulties associated with the identification of these fungi. AMF do not grow on artificial media. Therefore, traditional method for detecting AM is microscopic identification. There are many morphological types of mycorrhizas (Beck et al., 2007). Molecular research methods used for detection of AMF include nucleic acid amplification techniques, DNA sequencing, and next-generation sequencing (NGS). As many as ten pairs of primers are designed on the base of the LSU-ITS-SSU rDNA to perform phylogenetic analysis with species level resolution (Schwarzott, Schüßler, 2001; Da Silva et al., 2006; Walker et al., 2007; Gamper, Leuchtmann, 2007; Krüger et al., 2009;

Kohout et al., 2014; Morgan, Egerton-Warburton, 2017; Higo et al., 2020). By a high coverage reference transcriptome assembly of pea *Pisum sativum* mycorrhizal roots, gene markers of AM development were discovered (Afonin et al., 2020). The study of homologous genes can be used to develop methods for assessing the development of weed AM.

To explain the relationship between AM and invasive plants, two hypotheses have been proposed: the enhanced mutualism (Reinhart, Callaway, 2006) and the degraded mutualism (Vogelsang, Bever, 2009). The first one suggests that invasive plants enhance their competitiveness in the presence of AM. The second one assumes that invasive plants do not form AM, but disrupt mycorrhizal associations among native plants, thereby weakening them and facilitating the process of invasion. Even though researchers contrast the hypotheses of enhanced and degraded mutualism (Shah et al., 2009; Bunn et al., 2015), in our opinion, these are two sides of the same coin. We assume that both scenarios are realized in nature and the prevalence of one over another is determined by the host-plant species and features of ecosystem. Invasive plants of some Asteraceae tribes implement the enhanced mutualism scenario.

Thus, we suggest that AM and CMN favor invasion of Cardueae, Astereae, Anthemideae, and Senecioneae tribes of Asteraceae family. Benefits provided by AM and CMN allows alien species to successfully invade to new areas. Therefore, it is necessary to take this into account when developing measures to control the invasion of Asteraceae weeds. Suppression of AMF in soil may possibly help to control invasive plants of the Asteraceae family without affecting plants that are independent of AM.

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Мини-обзор

СПОСОБСТВУЕТ ЛИ АРБУСКУЛЯРНАЯ МИКОРИЗА ИНВАЗИИ ВИДОВ ASTERACEAE?

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Более трех десятков видов семейства Asteraceae, таких как *Solidago canadensis*, *Leucanthemum vulgare*, *Senecio inaequidens* etc, являются инвазивными и представляют серьезную опасность для экосистем. Арбускулярная микориза является ключевым фактором распространения инвазивных растений некоторых триб семейства Asteraceae, включая Astereae, Anthemideae, Senecioneae, Gnaphalieae, Cardueae, и Cichorieae. Формирование дружественного для инвазивного растения фитоценоза происходит, в том числе, за счет увеличения доступа питательных веществ и воды, гормональной регуляции и стимулирования неспецифического иммунного ответа растения-хозяина, изменения микоризного статуса окружающих видов, перераспределения между ними питательных веществ, подавления почвенной микробиоты и т.д. Аллелопатические воздействия на АМ со стороны почвенных микроорганизмов и других видов растений могут сдерживать этот процесс. Понимание микоризного статуса нежелательной растительности, на наш взгляд, является необходимым условием для успешного борьбы с ней.

Ключевые слова: арбускулярные микоризные сети, инвазивные сорные растения, Cardueae, Astereae, Anthemideae, Senecioneae, Cichorieae

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