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The Role of Arbuscular Mycorrhizal Fungi in Exotic Plant Invasion

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Abstract

The invasion success of exotic plants is largely determined by their invasiveness, which is influenced by soil abiotic properties and soil biota. Among these, arbuscular mycorrhiza fungi (AMF) can symbiosis with more than 80% of terrestrial plants and may be crucial to the successful invasion of exotic plants. Although many studies indicated that AMF can enhance the growth and competitiveness of invasive plants, some studies have also reported that AMF does not actually increase the invasiveness of invasive plants, and even inhibits it. This inconsistency is frequently attributed to the interactions between AMF and soil abiotic properties, especially soil nutrients like nitrogen and phosphorus, which significantly affect the symbiotic relationship between AMF and host plants. Here, we summarize the common hypothesis on invasion mechanisms, the relationship between AMF and host plants, the AMF's role in plant invasion, the control of invasiveness by soil abiotic properties, the interaction between AMF and soil abiotic properties, which benefits our understanding for the prevention and control of exotic invasive plants and the remediation of the soil at the invaded site.

Keywords: Exotic plants, Invasion mechanism, Soil nutrients, AMF

1. Introduction

Biological invasion can decrease the biodiversity of native species and destroy agriculture, forestry, animal husbandry and fishery production, and human health. Especially, plant invasion is threatening the survival of native species, and the structure and function of global ecosystems (Van Kleunen et al., 2020; Wu, 2019; Seebens, 2021), which commonly bring serious ecological and economic losses (Xu et al., 2018). It is thus crucial to effectively prevent and control the growth and spread of invasive plants. A precise comprehension of the plant invasion mechanism forms the foundation for identifying the consequences of invasion, minimizing the risk of invasion, and effectively preventing and controlling invasive plants.

2. Mechanistic Hypothesis for the Successful Invasion of Exotic Plants

With the development of invasion ecology, ecologists have put forward many hypotheses to decipher the intrinsic mechanism of plant invasions. Due to the complexity and uncertainty of the plant invasion process, several hypotheses propose multiple potential drivers (Enders et al., 2020). These hypotheses mainly involve the invasiveness of exotic plants, habitat invisibility, and their combination as the fundamental mechanisms for the successful invasion.

2.1. Invasiveness of Exotic Plants

Exotic invasive plants acquire to improve functional traits over native plants by modifying their growth and physiological characteristics and regulating nutrient acquisition and resource allocation strategies. Such traits include larger leaf area, higher photosynthetic rate, nitrogen use efficiency, water use efficiency, growth rate, and higher root biomass percentage, etc. These advantages allow exotic plants to adapt better and gain competitive dominance. For example, the nitrogen allocation hypothesis (NAH) suggests that in the absence of nature enemies, invasive plants will improve their nitrogen allocation to adapt to the environment and evolve trait advantages to enhance invasiveness.

The propagule pressure hypothesis (PPH) proposes that invasive plants frequently display superior reproductive traits than native plants, such as a reduced maturation period, an extended period of flowering, more seeds, both sexual and asexual reproduction and rapidly expanding populations by taking advantage of reproduction (Tian et al., 2018). For example, the invasive plant, *Spartina alterniflora*, grew rapidly and demonstrated both sexual reproduction through seed dispersal and asexual reproduction through close tillering and rhizome diffusion. Its seedlings achieved maturation in only 3~4 months and exhibited exceptional resilience and competitiveness (Meng et al., 2020).

The phenotypic plasticity hypothesis proposes that invasive plants frequently exhibit greater phenotypic plasticity and stress tolerance, allowing them to adapt more effectively to various environments and enhance invasiveness (Davidson et al., 2015; Zhang et al., 2015). The invasive plant *Alternanthera philoxeroides* showed more heavy metal stress tolerance than the native plant *Alternanthera sessilis* (Wang, Chen, et al., 2021; Wang, Xiong, et al., 2021). The invasive plant *Plantago virginica* demonstrated high plasticity in altering nitrogen supply, with increased biomass, inflorescence, and seed production (Luo et al., 2019).

2.2. Habitat Invasibility

The success of exotic plant invasions is also significantly influenced by environmental conditions in the invaded habitat. Invasibility describes the susceptibility of a community to the invasion of exotic species, which is used to conduct a thorough evaluation of a community or region's proneness to biological invasions (Mack et al., 2000). The invasion is closely linked to the biodiversity, availability of resources, and soil nutrient status of the invaded site.

The empty niche hypothesis (ENH) describes the invasibility of habitats in terms of the variety of local ecosystems. This hypothesis considers that the lack of species biodiversity and the abundance of ecological resources in island ecosystems provide ecological niches for exotic species, causing island ecosystems to be more susceptible to invasive damage than terrestrial ones (Elton, 1977). Ample resources in invaded habitats present opportunities for invasive plants to expand and reproduce, potentially facilitating invasion. A similar hypothesis is the resource fluctuating hypothesis (RFH), which suggests that an increase in the resource availability of invaded habitats due to resource fluctuations may facilitate the successful invasion of native communities by exotic plants.

2.3. Comprehensive Effects of Invasiveness of Exotic Plants and Invaded Habitats

Invasions cannot be fully assessed solely by evaluating the invasiveness of the exotic plant or the invasibility of the invaded habitat. Throughout the invasion process, there is a complex interplay between invasive plants and local environments. Plant invasion is a continuous, dynamic process, but most previous invasion mechanisms and hypotheses have typically focused on explaining only a single factor during a given invasion phase. To better explain the plant invasion process, it is necessary to connect hypotheses based on the invasiveness of exotic plants to the invasibility of habitats (Lau & Schultheis, 2015). For example, the enemy release hypothesis (ERH) operates in tandem with the phenotypic plasticity hypothesis to clarify the mechanism behind plant invasion. It is believed that exotic plants are not subjected to natural predators, pathogenic microorganisms, or competition from native environments upon new invasion sites. Moreover, invasive plants exhibit better physiological and reproductive traits along with greater phenotypic plasticity than native plants, resulting in significantly greater competitiveness than the latter. The *Claviceps purpurea* (Fr.) Tul. in North America can infect the seeds of *S. alterniflora*, reducing seed production. The reproductive advantage of *S. alterniflora* is realized when it lacked the threat of this natural predator, thus greatly increasing the success of invasion in new habitats (Wang et al., 2008).

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3. The Role of Arbuscular Mycorrhizal Fungi in the Successful Invasion of Exotic Plants

3.1. Overview of Arbuscular Mycorrhizal Fungi

Arbuscular mycorrhiza fungi belong to the subphylum *Glomeromycotina*, and they have a symbiotic relationship with over 80% of terrestrial plants. They are extremely important functional microorganisms, closely associated with plants. The role of AMF in plant invasions has gained increasing attention in recent years (Dawson & Schrama, 2016; Dong et al., 2021). Based on the most current classification by Oehl (Oehl et al., 2011), AM fungi are classified into the phylum *Glomeromycota*, consisting of three orders (*Glomeromycetes*, *Archaeosporomycetes*, and *Paraglomeromycetes*) and five suborders (*Glomerales*, *Paraglomerales*, *Archaeosporales*, *Diversisporales*, *Gigasporales*), with a total of 14 families and 26 genera.

3.2. The Structure of the Arbuscular Mycorrhizal Fungi

The surface structures of AM fungi include entry points, hyphae on rot, external hyphae, spores, etc. The internal structures include internal hyphae, arbuscule, vesicles, etc. (Liu & Chen, 2007) (Figure 1). As shown in Figure 2, spores and sporocarps are the main propagules of AM fungi.

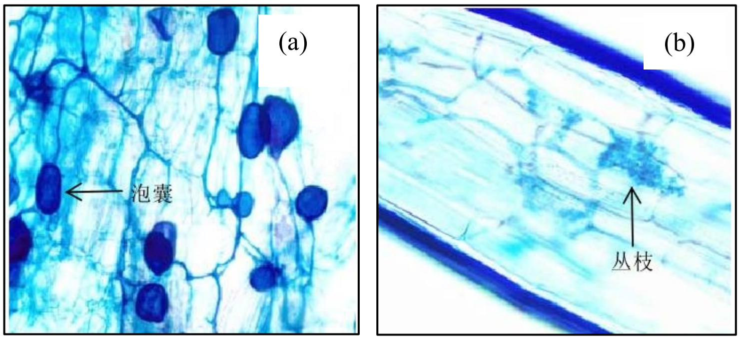

Figure 1. The arbuscular mycorrhizal structure formed by infecting the root system of *Robinia pseudoacacia* (He, 2016) (a) Formation of vesicles by inoculation with AMF; (b) Formation of arbuscule by inoculation with AMF

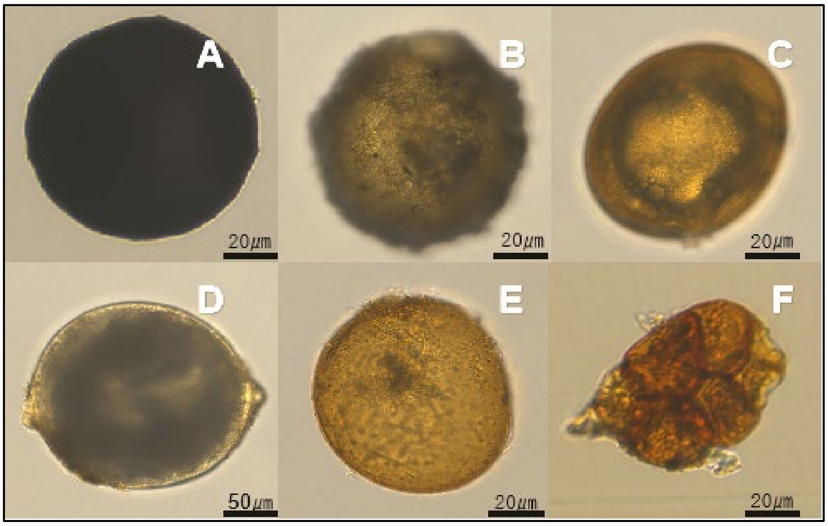

Figure 2. Main AMF spore morphology in the rhizosphere soil of *Solidago canadensis* (×20)

The arbuscular is a crucial structure of AMF as it serves as the endpoint for fungal extension into the inner cortical cell tissue of the root system. It is also a determining factor for the formation of mycorrhiza in AMF-infected root systems. The presence of mycelium not only expands the absorption area of the root system but also acts as a medium connecting the rhizosphere soil and host plant tissues (Liu & Chen, 2007).

3.3. The Role of Arbuscular Mycorrhizal Fungi in Plant Invasion Success

Arbuscular mycorrhizae are the earliest type of mycorrhizal fungi that form symbiotic relationships with plant roots through AMF infection (Shi et al., 2003). It has been recognized that most invasive plants are mycorrhizal and can establish mutually beneficial symbiosis with AMF (Callaway et al., 2011; Dawson & Schrama, 2016; Sun et al., 2022). AMF may directly provide exotic plants with a strong mutualistic advantage. Recent molecular studies have provided more evidence supporting the enhanced mutualism hypothesis (EMH), which suggests that exotic plants establish new interactions with highly effective local symbiotic fungi in invaded sites to facilitate their invasion. The presence of mycorrhizal symbionts can enhance the competitiveness of host plants. For instance, a study by Jin (Jin, 2004) demonstrated that the presence or absence of mycorrhizal symbionts had a significantly greater impact on the relative competitiveness of *S. canadensis* compared to *Artemisia lavandulaefolia*. The presence of mycorrhizae significantly increased the biomass of *S. canadensis*, thereby enhancing its relative competitiveness. AMF improves the host plant's ability to absorb and utilize soil water, nitrogen, phosphorus, and other mineral nutrients, thereby promoting their growth, development, and competitive advantage. For example, *Rhizophagus intraradices* can enhance phosphorus uptake in seven invasive plants of the *Asteraceae* family, thereby increasing their competitive ability against similar native species (Sun et al., 2022). AMF can enhance their tolerance to drought, nutrients, and heavy metals by improving photosynthesis and biomass, as well as mitigating the damage caused by environmental stresses. Additionally, AMF can increase the resistance of plants to stress and disease, thus enhancing the competitiveness of invasive plants (Yang et al., 2014).

Whereas some studies have also found that AMF reduced the invasiveness of exotic plants or had no significant effect (Pringle et al., 2009; Bunn et al., 2015; Dickie et al., 2017). The growth-promoting effect of AMF is generalized, but the growth-promoting effect is closely related to the species of AMF. For example, in a study on the competition between the invasive species *Flaveria bidentis* and the native species cotton, Li found that inoculation with *Glomus mosseae* increased the relative competitiveness of cotton and decreased the competitive advantage of the invasive species *F. bidentis*; and inoculation with *Glomus viscosum* increased the plant height and photosynthesis of *F. bidentis*, thereby enhancing its competitive advantage (Li, 2014). AMF also has a certain preference for plant host selection. In an experiment conducted by Yang et al. on the infection rate of AMF invasion in the field, the invasive plants were *F. bidentis*, *Ambrosia artemisiifolia*, and *Bidens Pilosa*, and the indigenous plants were *Setaria viridis*, *Melilotus officinalis*, and *Chenopodium album* (Yang et al., 2019). The study found that the main factors influencing AMF infestation rate were plant species, and the increase in species mainly affected the local plant root system AMF hyphae and their total infestation rate, which showed a decrease.

The symbiotic relationship between AMF and host plants and its effects are often influenced by a wide range of biotic properties (host plants themselves, growth status of local companion plant species, mycorrhizal status, mycorrhizal characteristics, etc.) and abiotic properties (nitrogen and phosphorus efficacy, soil acidity and alkalinity, water content, heavy metal content, etc.) (Aslani, 2019). Fu et al. (2011) found that there were differences in the growth effects of AM fungi inoculation *R. pseudoacacia* under different nitrogen application levels. In the study of *Astragalus memeranaceus* by He et al. (2009), it was also found that mycorrhizal effects could be maximized by moderate nitrogen application. Totally, to accurately evaluate the role of mycorrhizal fungi in the process of exotic plant invasion, it is necessary to consider the role of other influencing factors.

4. Influence of Soil Abiotic Properties on the Invasiveness of Exotic Plants

Significant interactions exist between soil abiotic factors and invasive exotic plants. When introduced into new habitats, exotic plants reproduce in large quantities under suitable conditions, drastically altering the soil biological and abiotic environment of the invading land, which in turn alters the plant community dynamics, that is, plant-soil feedback (PSF). The feedback effects of plant-soil microorganisms on invasive plants have been extensively studied (Yu et al., 2012), while the feedback effects of non-biological factors have been greatly ignored. However, soil abiotic properties significantly affect exotic plant invasiveness. For example, Wang et al. (2021) compared the reproductive characteristics of invasive and native species by manipulating soil nutrient levels. Nitrogen and phosphorus are both limiting nutrients for plant growth, and plant growth is co-regulated by both. Plants may utilize one element to gain access to the other, the nitrogen-phosphorus synergistic effect (Schleuss et al., 2020). Numerous studies have shown that nitrogen and phosphorus weights are redistributed during plant invasion. Tang et al. discussed the nutrient allocation strategy of the invasive plant *Parthenium hysterophorus* to different nitrogen and phosphorus levels, and within a certain phosphorus range, the aboveground biomass of the plant was higher than that of the underground part, and the leaf area and leaf biomass increased significantly (Tang et al., 2010). Chen et al. found that the invasive plant *B. pilosa* adopted the most effective nutrient allocation strategies for different habitats to enhance adaptation to heterogeneous environments, with low nitrogen conditions promoting phosphorus in the above-ground part of the plant, and high nitrogen-phosphorus conditions increasing phosphorus in the below-ground part (Chen et al., 2018).

5. Arbuscular Mycorrhizal Fungi Interact with Soil Abiotic Properties

Arbuscular mycorrhizal fungi and soil abiotic properties often interact with each other and jointly influence plant growth and development. Firstly, the nutrient effectiveness in soil determines the mutualistic relationship between AMF and host plants. When nutrient effectiveness in the soil is low, the presence of AMF may be more beneficial to the host plant, leading to a reciprocal symbiotic relationship. Conversely, when soil nutrient effectiveness increases, AMF and host plants can change from a reciprocal symbiosis possibly to a parasitic relationship. (Johnson et al., 2015; Lekberg et al., 2021). For example, the invasive plant, *Conyza canadensis*, changed from parasitism to symbiosis with AMF and *C. canadensis* as abiotic properties such as moisture and nutrients in the soil changed from its native range to the invaded site, and the diversity and structure of the AMF community changed significantly (Sheng et al., 2022). In addition, different forms of nutrient elements (e.g., different forms of phosphorus) may also influence the effects of AMF on invasive plants, which may affect the competitive advantage between invasive and native plants (Chen et al., 2023). Therefore, the role of AMF in plant invasion can be regarded as a double-edged sword (Chen et al., 2020). On the one hand, AMF can enhance the nutrient absorption of host plants. For invasive plants, the presence of AMF may increase their absorption of nitrogen and phosphorus (Awaydul et al., 2019; Xia et al., 2020) or increase the absorption of phosphorus without increasing the absorption of nitrogen (Dong et al., 2021; Sun et al., 2022), suggesting that the regulatory mechanism of AMF on nitrogen and phosphorus absorption may be more complicated during plant invasion. On the other hand, abiotic properties such as soil pH, salinity, and alkalinity may also affect AMF community structure. In temperate grasslands in northern China, nitrogen addition can lead to soil acidification, which in turn affects AMF community structure (Wu et al., 2023). In general, plant invasion is the result of the synergistic effects of AMF and soil abiotic properties (Shannon-Firestone et al., 2015). Yet few studies have focused on their overall role or relative importance in a community context. Therefore, more research is needed to understand these interactions to better predict and manage plant invasion.

6. Summary and Prospect

Although the enhanced mutualistic symbiosis hypothesis and the resource fluctuation hypothesis have identified the role of AMF communities and soil nutrient changes in the successful invasion of exotic plants, previous studies have paid little attention to the relative importance of AMF communities and soil abiotic properties and the synergy between the two, and most of the previous studies have been conducted at the level of the individual or the population, therefore, it is necessary to explore the relative importance and synergy of the two from the community level closer to the real environment. This will help us to understand the successful invasion mechanism of exotic plants more comprehensively and provide an important reference for the prevention and control of invasive plants. The effects of invasive plants on the soil's biotic and abiotic environments can be long-lasting, and the legacy effects remain even after the plants are removed. Therefore, understanding the transformation of invasive plants in the soil environment can also provide important guidance for the remediation of invaded soils and the use of artificial planting soil.

In the complex relationship between plant, soil, and AMF, the change of anyone will drive the change of the remaining two, and the interaction of any two will also affect the third, but these changes are not constant. Therefore, we should continue to carry out more in-depth and comprehensive exploration, and comprehensive multi-factor invasion mechanism research, to provide deeper data support and theoretical evidence for revealing the success of exotic plant invasion.

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Declaration of Conflicting Interests

All authors declare that they have no conflicts of interest.

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