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REVIEW PAPER

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INTERACTIONS OF ARBUSCULAR MYCORRHIZAL FUNGI WITH PLANTS AND SOIL MICROFLORA

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ABSTRACT

Mycorrhizal symbiosis is known since the 19th century and has been described as the coexistence of fungus with the roots of vascular plants. Root colonization by endomycorrhizal fungi causes changes in the quantity and quality of exudates produced by roots. The mycorrhiza may also affect plants' health status, their competitiveness and succession in eco-systems, and the formation of soil aggregates. The presence of a symbiont in the roots of plants causes a direct and indirect effect on rhizosphere microorganisms, fixing free nitrogen and transforming compounds constituting nutrient substrates for plants. The physiological and morphological relations of AMF with the plant promote its vitality and competitiveness by increasing resistance to abiotic and biotic stresses. Effective activation of the plant immune responses may occur, not only locally but also systemically. Mycorrhizal fungi, through the change of the composition and amount of root exudates, have influence on the development and activity of the communities of soil microorganisms. Certain soil bio-controlling microorganisms frequently showing synergism of the protective effect on plants together with AMF. In some cases, however, no positive interaction of selected microorganisms and endomycorrhizal fungi is observed. Double inoculation with the some species of bacteria and the mycorrhizal fungus can cause a decrease in the yielding the plants. Mycoparasitism of AMF spores and hyphae is also encountered in interaction between saprophytic fungi and AMF. This phenomenon is based on the lytic abilities of some fungi species which can lower the level of colonization and the effectiveness of mycorrhizal symbiosis with plants. Good knowledge of plant symbiosis with endomycorrhizal fungi and activity of these fungi in soils is necessary for their use in plant production.

Key words: mycorrhiza, AMF, soil microorganisms, biological control

Terrestrial ecosystems are dominated by plants living in symbiosis with mycorrhizal fungi. Thanks to that, plants are more competitive and productive, due to the easier access to components from the soil. This kind of symbiosis was discovered over 100 years ago. In 1882 Kamieński described coexistence of plant and fungi roots on the basis of anatomical studies of *Monotropa hypopitys* L. He found out that the whole root, especially the meristematic zone, are surrounded by a thick layer of mycelium. In 1885 a German botanist A. B. Frank called this phenomenon "mycorrhiza". However, it is only the research methods that are applied now, especially genetic ones, which made it possible to develop studies on mycorrhiza in the taxonomic, ecological and morphological aspects as well as in the aspect of the mecha-

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nisms of this phenomenon (physiological, biochemical and genetic ones). Since the discovery of mycorrhiza, a considerable number of scientific articles and monographic papers as well as textbooks concerning this phenomenon have appeared [Helgason et al. 1999, Parniske 2008, Smith and Read 2008, Zuccaro et al. 2014].

The most important function of mycorrhizal fungi (MF) is their ability to create a "bridge" between the soil and the plant. Mycorrhizal fungi hyphae take part in the formation of the soil structure. They improve the ability to penetrate the soil through the roots and they increase the flow of water and nutrient between the soil and the plant. Fungi, on the other hand, take up carbohydrates produced in the process of photosynthesis from the plant. Mycorrhizal fungi, through the change of the composition and amount of root exudates, have influence on the development and activity of the communities of soil microorganisms. In certain cases contact with MF may be harmful to the host plant and cause the growth inhibition [Finlay 2008]. The phenomenon of mycorrhizal symbiosis, therefore, does not always bring the expected effects because it depends on soil and environmental factors [Bücking et al. 2012].

Classification of mycorrhizas. Basing on the morphological and ecological aspects of the mycelium can be divided two forms of mycorrhizas: ectomycorrhiza and endomycorrhiza. This the last type of mycorrhiza is formed by arbuscular mycorrhizal fungi (AMF). Arbuscular mycorrhiza (AM) is formed by fungi from phylum Glomeromycota and class *Glomeromycetes.* Glomeromycota taxonomy was largely morphologically driven up to the end of the last millennium. Actually their classification is based on molecular, biochemical and morphological identification. Recently the system of classification of fungi forming or considered to form arbuscular mycorrhiza are placed in four orders: *Archaeosporales*, *Diversisporales*, *Glomerales*, and *Paraglomerales*, comprising ten families and thirteen genera [Schüßler et al. 2001, Oehl and Sieverding 2004, Walker and Schüßler 2004, Sieverding and Oehl 2006, Spain et al. 2006, Walker et al. 2007, Palenzuela et al. 2008, Oehl et al. 2011, Błaszkowski 2012]. The most frequently AMF species in the soils are *Glomus* spp. Other relatively frequently revealed fungi in the soil are genera *Scutellospora*, *Ambispora*, *Acaulospora*, *Archaeospora* [Wang et al. 2008, Leal et al. 2009, Kowalczyk and Błaszkowski 2011, Torrecillas et al. 2012, Quin et al. 2015].

Occurrence of AM in the world of plants. Arbuscular mycorrhiza is widely spread in terrestrial plants [Hart et al. 2003]. The ability to create this type of symbiosis was found in many species of thallophytes (*Thallophytes*), ferns (*Pteridophytes*), the majority of gymnosperms (*Gymnospermae)* and angiosperms (*Angiospermae)*, which proves permanent participation of AMF in phytogenesis of terrestrial plants [Smith and Read 2008]. It is assumed that from 85% to 90% of more than 231 000 species of terrestrial plants establish symbiosis with AMF. The arbuscular mycorrhiza predominates in green plants although some of those plants can create symbioses with ectomycorrhizal fungi [Wang and Qiu 2006, Tahat et al. 2010]. Plants which are resistant or little susceptible to colonization by AMF include numerous species from the families of *Equisetaceae*, *Polygonacea*, *Cyperaceae*, *Caryophyllaceae*, *Plumbaginaceae*, *Brassicaceae*, *Chenopodiaceae*, *Papaveraceae* and *Amaranthaceae.* Root colonization of plants belonging to those families is observed only incidentally in definite soil and biotic conditions [De Mars and Boerner 1995].

Importance of AM for plants and soil microflora. The basic role in the signaling functions between the symbionts play the liquid and volatile root exudates of plants, especially phenolic derivatives (flavonoids) [Tahat and Sijam 2012]. Stimulation of spore germination and contacts between AMF and the plant can also be supported by metabolites of soil microorganisms, especially certain saprophytic bacteria and fungi, which provided the basis to distinguish them as a group "Mycorrhizal Helper Bacteria" (MHB) [Joseph and Sivaprasad 2012, Ząbkiewicz et al. 2014]. Endomycorrhizal fungi colonize epidermal and cortex tissues but they do not penetrate vascular and meristematic tissues. Roots colonized by AMF can change the colour, ranging from light yellow to brown. It is connected with the ageing of arbuscules and the production of a characteristic yellow pigment in the plant root tissue [Klingner et al. 1995]. In favourable conditions vegetative hyphae of AMF can colonize intercellular spaces at 60–90% of the length of the plant's root system. A lot of plants colonized by AMF produce thicker roots with a smaller number of root hairs as compared to control plants. The surface of the roots of mycorrhizal plants is often considerably larger than for non-mycorrhizal ones [Derkowska et al. 2015]. Root colonization by endomycorrhizal fungi causes changes in the quantity and quality of exudates produced by roots, in the manner of distributing carbon in the leaves, stems and roots of plants, in the level of supplying nutrients to plants, especially phosphorus, nitrogen and microelements, as well as in plants' tolerance or resistance to the content of heavy metals in the soil [Jakobsen et al. 2003]. The occurrence of mycorrhiza may also affect plants' health status, their competitiveness and succession in eco-systems, and the formation of soil aggregates. The presence of a symbiont in the roots of plants also causes a direct and indirect effect on rhizosphere microorganisms, fixing free nitrogen and transforming compounds constituting nutrient substrates for plants [Birhane et al. 2012]. Rhizosphere microorganisms can have a positive and negative influence on plants. This consists in both releasing and transforming nutritive substrates as well as in excreting their own, in addition to detoxication of secondary plant metabolites, frequently harmful to plants [Vázquez et al. 2000].

The physiological and morphological relations of AMF with the plant promote its vitality and competitiveness by increasing resistance to abiotic and biotic stresses. During mycorrhiza establishment, modulation of plant defence responses occurs upon recognition of the AMF in order to achieve a functional symbiosis. As a consequence of this modulation, a mild, but effective activation of the plant immune responses may occur, not only locally but also systemically [Pozo et al. 2009].

AMF also create favorable conditions for the activity of rhizosphere microorganisms that have a positive effect on plants [Zarea et al. 2011]. The specific rhizosphere microflora, on the other hand, performs important functions in the activation of spores and mycorrhizal colonization of roots. Pectinolytic properties of *Pseudomonas fluorescens* strains can be a factor facilitating penetration of hyphae and the formation of mycorrhizas [Vásquez et al. 2000]. Bacteria promoting the germination of AMF spores and mycorrhizal colonization of plant roots are MHB [Biró et al. 2000]. The group capable of promoting the growth of plants also includes symbiotic *Rhizobium* and free-living *Azotobacter* and *Azospirillum* as well as certain saprophytic bacteria having the properties of Plant Growth-Promoting Rhizobacteria (PGPR) from genera *Pseudomonas*, *Bacillus*, *Serratia* and *Streptomyces* [Bashan and Houlgin 1997, Biró et al. 2000, Artursson et al. 2006, Mugabo et al. 2014]. In many cases, however, no positive interaction of isolates of bacteria included with PGPR with endomycorrhizal fungi was observed, or their effect on the plant depended on the species of AMF colonizing the roots [Wyss et al. 1992, Isopi et al. 1995]. Interesting facts were observed in the interactions between isolates of *Bacillus* sp. and *Glomus mosseae.* It was observed that after being applied to the rhizosphere of non-mycorrhizal pea, this strain did not affect its yielding while showing considerable abilities to aggregate the soil. After 8 weeks of vegetation, a double inoculation with the bacteria and the mycorrhizal fungus caused a decrease in the yielding by 30%, but at the same time the degree of soil aggregation was remarkably increased [Andrade et al. 1995].

Certain soil microorganisms can be a bio-controlling factor of plant pathogens, frequently showing synergism of the protective effect on plants together with AMF. Some amino acids, ethylene, proteins and isoflavonoids can be mediators between the positive rhizosphere microorganisms and AMF [Tahat and Sijam 2012]. The formation of the mycorrhizosphere modifies growth conditions for microorganisms in the root zone of plants (mechanisms of competition and selection in the rhizosphere) and the plants are protected against harmful microorganisms [Cordier et al. 1998, Amer and Abou-El-Seoud 2008, Al-Askar and Rashad 2010]. Root colonization by AMF can also cause defense reactions of plants by inducing the accumulation of phytoalexins and production of antioxidant enzymes in plants [Morandi 1996, Yang et al. 2015]. Another mechanism of the protection of the mycorrhizal plant from fungal pathogens can be an increase of the accumulation of non-soluble polysaccharides and lignins in the cell walls of plant roots as well as the very presence of the mycorrhizal fungus hyphae in the root tissue, which can constitute a physical barrier for the infection of fungal pathogens [Amer and Abu-El-Seoul 2008]. The protective effect of AMF is also dependent on the genetically controlled susceptibility of a given species or cultivar to fast and effective colonization of the roots by the endomycorrhizal fungus [Mark and Cassels 1996]. The phenomenon of bio-control of fungal pathogens of plants by endomycorrhizal fungi has been observed [Hage-Ahmed et al. 2013]. The best protection was secured by fast symbiosis with the mycorrhizal fungus – before the root infection by the pathogen [Yao et al. 2002, Sharma et al. 2007]. The effect of biological protection by means of AMF depends on a number of environmental and soil factors which can equally affect both the development and activity of AMF as well as pathogenic and saprophytic ones. As a result, they can limit the possibility of the synergetic bio-control of pathogens, with a simultaneous use of mycorrhiza and saprophytic fungi [Smith and Read 2008]. The studies on the influence of beneficial fungi *Trichodrema harzianum* and AMF (*Glomus intraradices*, *G. mosseae*, *G. claroideum* and *G. constrictum*) on melon crops growth showed that AMF-inoculated plants were effective in controlling Fusarium wilt and *G. mosseae*-inoculated plants showing the greatest capacity for reduction of disease incidence. Co-inoculation of plants with the AMF and *T. harzianum* produced a more effective control of Fusarium wilt than each AMF inoculated alone, but with an effectiveness similar to that of *T. harzianum*-inoculated plants [Martinez-Medina et al. 2011].

Interesting results were obtained in the studies on the effect of microorganisms on the plant, where additionally another microorganism was used besides inoculation with AMF. It had a bio-controlling effect on the tested pathogen. The bio-controlling fungi towards *Pythium ultimum* was *Gliocladium virens*, which effectively protected cucumber seedlings thanks to the ability of that fungus to mycoparasitism and production of metabolites inhibiting the growth of pathogenic fungi. It was shown that the fungus did not inhibit the activity of the mycorrhizal fungus, which creates possibilities to obtain synergism in the bio-control of the pathogen through double inoculation – with AMF fungus and the bio-controlling fungus [Joseph and Sivaprasad 2012].

The synergistic stimulation of the plants' growth was shown in the rhizosphere of mycorrhizal plants of maize after the application of microbial inoculants *Azospirillum*, *Pseudomonas*, *Trichoderma* and which increases enzyme activities in the rhizosphere [Vázquez et al. 2000]. Positive interactions were also observed with simultaneous inoculation of the seeds of white clover with fungus *Aspergillus fumigatus*, which dissolves organic phosphorus, and of the soil – with species *Glomus mosseae.* The plant's uptake of phosphorus was far more effective in the case of double inoculation as compared to the series where the studied fungi were tested separately [Tarafdar 1995]. Mycoparasitism of AMF spores and hyphae is also encountered in interaction between saprophytic fungi and AMF. This phenomenon is based on the lytic abilities of some fungi species which can lower the level of colonization and the effectiveness of mycorrhizal symbiosis with plants [Dumas-Gaudot et al. 1994].

Recognizing the requirements and scope of the bio-controlling effect of microorganisms in the rhizosphere environment of various plants as well as using nutritious synergism of different groups of saprophytic microorganisms with AMF can be a way for their practical application aimed to improve the yielding and protection of cultivated plants [Finlay 2008].

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