

INTERRELATIONS BETWEEN THE MYCORRHIZAL SYSTEMS AND SOIL ORGANISMS

BALAEȘ TIBERIUS¹, TĂNASE CĂTĂLIN¹

Abstract: The mycorrhizae are largely spread in natural ecosystems, and the proportion of plants that realise mycorrhizas is overwhelming, this relation involving advantages for both partners. The presence or absence of mycorrhizae, the rate and intensity of mycorrhiza formation are aspects with ecological importance, but also present importance in modern agriculture. The research results published on international literature which views the principal relations between mycorrhizae and soil microbiota, the way in which these relations affect the intensity of mycorrhizae formation and also the efficiency of mycorrhizae under the influence of soil organisms are synthesized and commented in this paper. The relations between mycorrhizae and different categories of bacteria, protozoa or microfungi, as well the influence of invertebrates through interactions of them with microorganisms are also being analyzed.

Key words: mycorrhizae, interrelations, rhizosphere

Introduction

The presence of mycorrhizae makes possible the coexistence of symbiotic organisms in hostile environment or in places where the competition is very strong. In this way, the mycorrhizal partners present advantages and benefits that allow them to develop or reproduce in underoptimal conditions or to become competitive, being able to survive. These are natural constant mutualistic associations between the roots of plants and soil fungi. The purpose of these relations is to obtain anorganic nutrients by the plants and organic nutrients by the fungi in an easily and efficiently way. Fungal species that form mycorrhizae are taking up to 25% from photosynthesis products of plants and they can contribute with P and N up to 80% of plant necessary [MEYER & al. 2010].

Mycorrhizae are morphological and physiological different, and the interactions between mycorrhizal species are also different. The mycorrhizae types and the distribution of them in terrestrial bioms are being influenced by the climatic factors, soil composition and participant species, as well by the composition of soil organisms communities. The influence of mycorrhizae over the distribution in ecosystems of plant species is major, playing an active role in qualitatively and quantitatively modelling the ecosystems structure. In nature, the mycorrhizal species establish extremely complex relations with soil organisms, the formation of mycorrhizae often leads to qualitative and quantitative modifications of soil biota, the process being reciprocal, so soil organisms may play a decisive role on the way and intensity of mycorrhiza formation. As plants are a valuable source of nutrients for many categories of

¹ "Alexandru Ioan Cuza" University of Iași, Bd. Carol I, no. 11, 700 506, Iași – Romania
e-mail: tiberius_balaes@yahoo.com, tanase@uaic.ro

INTERRELATIONS BETWEEN THE MYCORRHIZAL SYSTEMS AND SOIL ORGANISMS

soil organisms, they represent the centre of different types of interrelations, competition or cooperation, in order to gain access to these nutrients.

The fungal symbiont occupies a special position in these relations, its presence in rhizosphere leading to profound modifications of microrrhizosphere community structure. According to the effects of soil microorganisms on mycorrhiza formation and functioning, they can be beneficial, neutral or they can negatively affect the functionality of mycorrhizae.

There is a possibility of using some microorganisms that can significantly reduce negative effects of the pathogens or microorganisms that directly or indirectly stimulate plants growth and development (through stimulation of mycorrhiza formation). In order to use it, it is necessary to elucidate the complex mechanisms established between mycorrhizal species and other categories of microorganisms on a hand, and on the other hand to elaborate the efficient schemes and methods of utilisation such beneficial microorganisms in agriculture, forestry, ecological reconstruction etc.

The researches of Roumanian specialists concerning mycorrhizae were initiated half century ago [ŞESAN & al. 2010]. These researches approached the symbiosis in general and mechanisms determined by mycorrhizae (ALDEA, ZARNEA, ZAMFIRACHE, TOMA, MAXIMILIAN, CARASAN etc.). Some authors (CHIRA, IORDACHE, NEAGOE etc.) were highlighting particular aspects of ecto- or endomycorrhizae. ALDEA, CHIRA, BRĂILOIU etc. had studied the mycorrhizal impact to the economical important plants.

The concerns of researchers regarding the interactions between mycorrhizal species and soil microorganisms had generally targeted the plants protection and the reduction of frequency and severity of the phytopathogens attack [IACOMI & al. 2010]. It has been discovered that some microorganisms are frequently associated with mycorrhizae, their action being positive in relation with fungal symbiont, protecting the plant against the pathogens. In the last decades, the interest concerning elucidation of the mechanisms involved in establishing the complex interactions of the mycorrhizosphere and their role in protecting and stimulating plant development had increased.

The mycorrhizal systems – clarification

The mycorrhizae are symbiotic association, during which specific fungi are colonizing plants rootlets. In this type of relation, pathogenity and lesion of root structures are normally missing and the fungal invasion is blocked by the plant. Mycorrhizal plants are better developed than non-mycorrhizal plants. In this relation, plants are providing organic compounds for the fungal symbiont, and receive, in exchange, anorganic nutrients absorbed by hyphae. Due to the small size of hyphae, the absorptive surface and the explored volume of soil are very large, and the formation of root hairs is no longer necessary. Thus, the functions of mycelium become complementary to the root function.

The mycorrhization represents a common phenomenon in ecosystems and it is characteristic for very different taxa, from the bryophytes to angiosperm. It is estimated that over 90% of terrestrial plants realise vesicular-arbuscular mycorrhizae [ENE & al. 2010], adding to them the plants that realise other types of mycorrhizae. A few groups of vascular plants do not realise mycorrhizae at all, these usually living in wet habitats. The fungal invasion is limited by the plant, being located to the cortex level, in intercellular position (at ectomycorrhizae) and with intracellular ramification (at endomycorrhizae).

The hyphae are not colonizing tannins or calcium oxalate containing cells neither the organs apices. In the case of endomycorrhizae, arbuscules, vesicles and even hyphae are frequently lysed, their content being spilled in the cells of the host [ZAMFIRACHE &

TOMA, 2000]. Some mycorrhizal species are considered common and spread in different habitats, and other species considered rare are forming mycorrhizae only with some host plants [FODOR & al. 2010].

Interspecific signals in the mycorrhizal systems

The functions of the root can be influenced by mycorrhizae, in response to the rhizosphere action and soil fertility. These factors control the root architecture, reducing the ramification level and growing the dependency of plant for the symbiotic fungi [ZAMFIRACHE & TOMA, 2000].

The mycosymbiont becomes associated to the plant root and avoids the defence mechanisms. These processes are being initiated by the exchange of specific signals between both partners. The signalling is a process remarkably complex, involving different molecular mechanisms. In the early stages of the mycorrhiza formation, H_2O_2 plays a signalling role, and in a similar manner, the efflux of Cl^- and K^+ and the influx of Ca^{2+} and extracellular alkalization [HEBE & al. 1999]. The higher concentrations of monosaccharides at the root-soil interface are leading to the activation of some physiological modifications in the fungal metabolism which play a signalling role. On the other hand, the presence of nitrogen compounds with fungal origins induces some modifications in the radicular metabolism [HAMPP & al. 1999]. The degradation rate of the organic compound with N is controlled by the plants through the C resources given to fungi for extracellular enzymes synthesis [TALBOT & TRESEDER, 2009].

After these preparatory mechanisms of metabolic activation, is following a specific recognition phase mediated by phytohormones secreted by both the plants and the fungi, the process being bidirectional. Transport inhibitors of auxine and the compounds that release ethylene are activating the root ramification, a process that can be stopped by the ethylene synthesis inhibitors. In the mycorrhizal formation processes morphological modifications of root cells are interfering, modifications which are controlled through gene activity regulation by fungal or plant phytohormones (auxines, ethylene, abscisic acid). The root exudates secreted during fungal inoculation, induce defense mechanisms against the pathogens [DUCHESNE, 1989].

REQUENA & al. (2007) proved that some flavonoidic compounds from the root exudates are increasing the spores germination and the hyphal growth and development. Also, during the formation of the mycorrhiza, the fungi are influencing the expression of genes involved in phenylpropanoids, flavonoids and isoflavonoids radicular metabolism.

The rutin induces hyphal growth, and hypaphorine, an auxine analogous indolic compound, inhibits the root hairs elongation [NEHLS & al. 1998].

In the infective phase, proteosynthesis modifications take place, at least 50% from the both symbiotic partners proteins being synthesised in concentrations that differ from the concentration in which they are synthesised in a separate development of symbionts [DUCHESNE, 1989]. Some polyamines produced by fungal mycelium, have roles in the plants germination processes [NEHLS, 1998].

The hyphal adhesion is influenced by some hyphal wall compounds, as hydrophobines, cysteine-reached proteins, α -tubulin and actin [TIMONEN & al. 1996].

During the penetration of the root by the hyphae, low defensive responses are activated in plant organism, such as peroxidases production and proteins phosphorylation modifications. During a root infection made by a pathogenic fungal species, the plant reaction is strong and invariable, by contrary, the root infection made by a mycorrhizal

INTERRELATIONS BETWEEN THE MYCORRHIZAL SYSTEMS AND SOIL ORGANISMS

species is permitted by the plant. In physiological stress conditions, the production of such compounds increases, the fungal or plant metabolism being modified by them, with the purpose to adapt to the new conditions. The indol acetic acid of fungal origins controls the root morphological changes [GAY & al. 1994].

The types of mycorrhizae

The morphology of mycorrhizae can deeply vary along with the type of relations between plant-host and the fungal species and with the environmental condition. The endomycorrhizae do not have a varied external morphology, but the ectomycorrhizae have different colours, shapes, sizes, which are characteristic to the participating species. A particular type is represented by peritrophic mycorrhizae, this being a stable relation between partners, in which the fungi develop around the root and form a mycelial network without having a direct contact with them.

The ectomycorrhizae are symbiotic associations in which the fungal mycelium develops in strong contact with the roots, forming a mantle that covers the apice of the root. They are characteristic for many trees. There has been proposed different ectomycorrhizae classification systems based on morphological characteristics: colour (yellow, orange, red, brown, violet, black etc.) sizes, ramification types (non-ramificated, dichotomic branched, coralloids etc.) the sizes and shapes of rhizomorphs etc. A recent proposed criteria is based on the exploring type of substrate by the extramatrical mycelium, this having ecological importance [AGERER, 2001].

The ectoendomycorrhizae represent intermediate forms between ectomycorrhizae and endomycorrhizae, some authors placing them in the latter group.

The endomycorrhizae are formed on the young rootlets, presenting only intercellular hyphae, which have well developed haustoria in root cortical cells. The haustoria can be twisted or divided, being named arbuscules. In some cases, mycelial hyphae can get through the entire organism of a plant.

There are different categories of endotrophic mycorrhizae, some of them being characteristic for specific groups of plant: monotropoid mycorrhizae are present at *Monotropa hypopitys*, ericoid mycorrhizae found at species from Ericaceae and Epacridaceae, arbutoid mycorrhizae characteristic for species from Pyrolaceae and some species from Ericaceae, orchidean mycorrhizae present at Orchidaceae species. The vesicular-arbuscular mycorrhizae are being formed by the most of the plants, the involved fungal species having a siphonal structure.

The influence of the mycorrhizae on soil organisms

The modification process of soil properties and of soil microbiota is bidirectional, based on "first to come" rule. The inhibition mechanisms are represented by the competition for the C and energy sources, and also by the production of antibiotics or other inhibitory compounds. If the mycorrhizal species do not find in the environment, in pre-infective phases, beneficial microorganisms, the chances of survival and colonizing a host decrease.

According to ALBERTSEN & al. (2006), associated bacteria play an important role in vesicular-arbuscular fungi development in the organic matter. The process is bidirectional, because the teluric microorganisms respond to the mycorrhizal species extramatrical mycelium growth.

According to RAIESI & GHOLLARATA (2006), the glomaline released by this fungi has negative effects on microbial respiration, this leading to the decrease of organic matter degradation rate from soil.

By secreting mixtures of selective substances, plants will create selective conditions for developing the rhizosphere organisms. The plants are exuding a variety of chemical compounds and anorganic ions, mucilages, also antimicrobial compounds with role in defending the host. Also, the mycorrhizal species mycelium releases some exudates that contain organic compounds that stimulate the development of a hyphospheric microbiota, but in a lower quantity than that produced by the plants [ANDRADE & al. 1997].

In this manner, the host plant and its symbiotic partner mycelium are “selecting” bacteria that are beneficial for their relation [TARKKA & al. 2009].

After this selections, microbial communities will be dominated by some bacterial groups [HRŠELOVÁ & al. 1999; WELSH & al. 2010]. These bacteria stimulate the mycorrhizae development, but are also complementary to the functions of mycorrhizae, as nutrients absorption and biological control of the host plant [FREY-KLETT & al. 2007; cited by TARKKA & al. 2009]. The bacterial diversity in hyphosphere seems to be lower compared to the free soil [GRYNDLER & al. 2000], the gram negative bacteria prevailing [VOSÁTKA, 1996; cited by BAREA & al. 2002].

However, BIANCIOTTO & BONFANTE (2002) observed that there is a big specific diversity in the rhizosphere of mycorrhizal plants compared to the rhizosphere of non-mycorrhizal plants. The mycosphere participates to P recycling process from organic or anorganic compounds [BAREA & al. 2002]. The mycorrhizal associated microorganisms modify, also, the composition of mycorrhizosphere microbiota. In this way, *Streptomyces* Ach505, which colonizes the mycelium of ectomycorrhizal species *Amanita muscaria*, produces auxofuran, an antibiotic that modifies hyphospheric microbiota [RIEDLINGER & al. 2006, cited by HARTMANN & al. 2009].

The *Bulkholderia cepacia* species is frequently present as free in mycorrhizosphere, but it has not been isolated from free soil or from the non-mycorrhizal plants rhizosphere.

Interrelations between the mycorrhizal systems and the soil microbiota

Between soil microbiota, the mycorrhizal species and plants are establishing extremely complex relations, with positive effects [AZCÓN-AGUILAR & BAREA, 1985] or negative effects [LARSEN & al. 2009] over the mycorrhization rate and over these processes efficiency. The root exudates are a valuable nutritive resource for rhizospheric microorganisms, qualitative and quantitative properties of these root exudates are influencing those interrelations established between organisms from this level.

Many soil microorganisms can be considered as being neutral, because they do not bring a benefit nor a loss for the plant host or the mycorrhizal species. However, these organisms influence the soil activity and properties, contributing to organic matter mineralization or can be involved in different physico-chemical processes. Although these organisms do not directly interact with the plants, the processes in which they are involved might have influence over the plant development. The rhizospheric bacteria are bacteria already present in the soil and, as a result of the soil conditions modification (roots development) they find favourable niches to abundantly develop. The rhizospheric microorganisms can have different activities: pathogenic activity, plant protection, antibiotics productions etc.

INTERRELATIONS BETWEEN THE MYCORRHIZAL SYSTEMS AND SOIL ORGANISMS

Many categories of rhizospheric bacteria have the capacity of stimulating the plant development beyond the presence of the mycorrhizal species. For these species, it was used the acronym PGPR (Plant Growth Promoting *Rhizobacteria*) by LINDERMAN [1992, cited by AZCÓN-AGUILAR & BAREA, 1997], including both free and nodulating nitrogen fixing bacteria, soil phosphate solubilising bacteria, as well the bacteria that produce plant growth stimulators or pathogens inhibitors. But when they are both present, the mycorrhizal species and PGPR present complementary functions.

The mechanisms by which some microorganisms can inhibit mycorrhizal development are diverse: they can compete for nutrients [MIRANSARI, 2009] both with mycorrhizal species in preinfective phase, sometimes even in postinfective phase, and with favourable microorganisms. On the other hand, non-favourable microorganisms can directly inhibit the fungi by releasing the antifungal toxins, or indirectly by releasing the phytotoxines, bactericidal or bacteriostatic substances and by modifying the soil properties (pH modification or ratio between different substances in the soil) or they can be pathogenic for fungi and for plants. Other microorganisms are attached to the fungal spores or to the hyphae surfaces [MIRANSARI, 2011], using them as vectors for colonizing the root plants (BIANCOTTO & al. 2000; cited by BAREA & al. 2002).

Bulkholderia, *Ralstonia* and *Pandora* are endobacteria of some vesicular-arbuscular fungi. It has been discovered that these bacteria are constantly present at Gigasporaceae [RUIZ-LOZANO & BONFANTE, 2001; BIANCIOTTO & BONFANTE, 2002] and that fungal species without endosymbiont develop abnormally.

Although there have been made many studies regarding the composition of microbial community from rhizosphere, up to 90% of rhizospheric microorganisms remain unstudied [GOODMAN & al. 1998; cited by BUÉE & al. 2009], as a result of the unrecovery on artificial media. By means of modern techniques, recently developed, this number has been reduced.

FULTHORPE & al. [2008; cited by BUÉE & al. 2009] have analyzed soil samples, by sequencing some nucleic acid molecules, soil samples that have been collected from different biogeographical regions, proving that there are other dominant taxonomical groups of bacteria than previously proposed (through isolation on artificial media). The bacterial communities from rhizosphere fluctuate with root growth, and by that, the densest communities will be found in root hairs regions [BUÉE & al. 2009].

Interrelations between the mycorrhizal systems and the nodulating nitrogen fixing bacteria

Many studies have been focused over the double inoculation of plant with mycorrhizal species and nodulating nitrogen fixing bacteria [AZCÓN-AGUILAR & BAREA, 1997; SIVIERO & al. 2008; GUTIÉRREZ-MICELI & al. 2008; BAREA & al. 2002], because of its applicability in agriculture. These bacteria colonize the roots of some nodules forming plants, and at their level, in different biochemical processes, nitrogenous is synthesized in compounds available by plants using molecular nitrogen. For the plants, this colonization is beneficial, but this involves the reduction of saccharides available for fungi, the effect being the reduction of mycorrhization rate. Nevertheless, a good development of the plants implies an increase of the exudation rate by root plants which lead to a better fungal development. This hypothesis was confirmed by double inoculation, with mycorrhizal species and *Rhizobium* strains [TOBAR & al. 1996; SIVIERO & al. 2008], the authors reported an increase of mycorrhizal units number. TIAN & al. (2003) found a better

development of *Robinia pseudacacia* plantlets by triple inoculation: with endomycorrhizal species, ectomycorrhizal species and *Rhizobium* strains, compared to the double inoculation or simple inoculation.

Interrelations between the mycorrhizal systems and free nitrogen fixing bacteria

The free nitrogen fixing bacteria have positive effects on plants development. One might say that their activity could negatively influence mycorrhiza formation by increasing nitrogenous compounds available for plants meaning the reduction of plant dependency for mycorrhizae, but experimental results obtained by GUTIÉRREZ-MICELI & al. (2008) infirmed this assumption, being noticed positive effects on the mycorrhization rate. The co-inoculation of *Azospirillum* and *Glomus mosseae* made the two species act synergistically, offering nutrients to plants, nutrients which contain same quantity of N and P as by administration of artificial fertilizers. Some strains of *Azospirillum* and *Paenibacillus* have stimulated the vesicular-arbuscular mycelium growth and the mycorrhiza formation [BAREA & al. 2002; BIACIOTTO & BONFANTE, 2002]. However, contradictory results obtained by ZUBEK and colabs. (2009) proved that these processes depend on involved organisms genome.

The *Burkholderia* species are bacteria capable of fixing molecular nitrogen, often isolated from mycorrhizosphere. These bacteria are able to stimulate plant growth and contribute to mineral resources bioavailability [KOELE & al. 2009]. The mycorrhizal species and some bacteria cooperate in soil transformation. These mechanisms imply the roots presence which improve nutrient content in rhizospheric microhabitat and sustain the bacterial inoculum stability [SIVIERO & al. 2008].

The mycorrhizal species increase the surviving rate of these bacteria in rhizosphere, thus *Azotobacter paspali* develops better in *Paspalum notatum* rhizosphere when plants are mycorrhizated [BAREA & al. 1983]. Similarly, nitrogen fixing bacteria isolated from *Drosera villosa* rhizosphere stimulated the rice roots and stalks growth when they were co-inoculated with *Glomus claroideum* [GUTIÉRREZ-MICELI & al. 2008].

Interrelations between the mycorrhizal systems and the mycorrhiza promoting bacteria

Some of bacteria can directly stimulate the mycorrhiza formation by releasing some stimulatory compounds as auxines, gibberellines and cytokinins, substances that influence the root morphology and physiology and contribute to the qualitative and quantitative modification of the root exudates, with direct effects on fungi. These bacteria also produce vitamins and organic acids that stimulate spores germination. Helper bacteria produce hypaphorine type phenolic compounds that increase fungal aggressivity [GARBAYE, 1994, cited by DUPONNOIS & PLENCHETTE, 2003]. However, the effect depends on the inoculum size, if the dose is suboptimal there are not any beneficial effects, if the dose exceeds the optimal values there are negatively effects, possible due to antibiosis effect or resources consumption [FREY-KLETT & al. 1999]. Some fungal species colonize the roots only in extreme habitats by reason of microorganisms competition lack [BOWEN & THEODORU, 1978].

Some authors [VIVAS & al. 2003; MARULANDA & al. 2006] reported positive effects of *Bacillus thuringiensis* inoculation over the mycorrhizal species extra- and

INTERRELATIONS BETWEEN THE MYCORRHIZAL SYSTEMS AND SOIL ORGANISMS

interradicular development, increasing the mycorrhizal intensity and the extramatrical mycelium growing rate. For these bacteria it is used the acronym: MHB – mycorrhizal helper bacteria. Similarly, co-inoculation with *Azospirillum brasilense* or *Bacillus amyloliquefaciens* [OANCEA & al. 2010] as well as coinoculation of *Enterobacter agglomerans* with *Glomus etunicatum* [KIM & al. 1998] led to a better mycorrhizal species development.

In savannas, the mycorrhization rate was high when microclimatic conditions were favorable for rhizospheric bacteria development [LÓPEZ-GUTIÉRREZ & al. 2004]. The inoculation with ectomycorrhizal species success depends on fungal surviving in soil during preinfective phase, and this may be correlated to the helper bacteria presence.

Many studies confirmed the efficacy in stimulating and potentiating of mycorrhization effects of helper bacteria from *Pseudomonas*, *Ralstonia* and *Bacillus* genera: *Pseudomonas fluorescens* [DUNSTAN & al. 1998; BRULÉ & al., 2001; GAMALERO & al. 2004, cited by HAMEEDA & al. 2007], *Pseudomonas putida* [KOZDRÓJ & al. 2007], *Pseudomonas aeruginosa* [KOTHAMASI & al. 2006], *Pseudomonas monteillii* [REDDELL & WARREN, 1986, cited by DUPONNOIS & PLENCHETTE, 2003], *Bacillus subtilis* [DUNSTAN & al. 1998; BRULÉ & al. 2001], *Ralstonia* sp. [KATAOKA & FUTAI, 2009; HRYNKIEWICZ & al. 2010].

Similar effects have been reported in the case of actinomycetes. These organisms stimulated *Amanita muscaria* mycorrhization concomitantly with the inhibition of the pathogen: *Armillaria obscura* and *Heterobasidion annosum* [MAIER & al. 2004], or hyphal growth induction realised by *Streptomyces* strains [SCHREY & al. 2007]. Also, some oxalobacteriaceae stimulated *Glomus mosseae* in vitro growth [MIRANSARI, 2011].

There are some spores associated to the bacteria as *Stenotrophomonas* and *Arthrobacter*, with favourable effects on the spores germination [BHARADWAJ & al. 2008].

Some saprotrophic fungi, as *Trichoderma hartzianum* [IACOMI & al. 2010] can stimulate helper bacteria effects, showing in this manner a multilevel synergistical effect.

There is a strong correlation between rhizospheric microbial species and mycorrhizal ones [DUNSTAN & al. 1998], the helper bacteria beneficial effects over the mycorrhizae being fungi-specific. In the studies realised by PIVATO & al. (2009), *Pseudomonas fluorescens* differently stimulated the development of some *Glomus* species.

Different studies [FRANCO-CORREA & al. 2010; CALVARUSO al. 2007] revealed the fact that many actinomycetes species isolated from mycorrhizosphere had the capacity to solubilise Phosphorus from organic and anorganic soil sources, as well the capacity to produce siderophores or to fix Nitrogen. These bacteria have a more abundantly development in mycorrhizosphere comparing with their development in non-mycorrhizal plants rhizosphere.

ASPARY & al. (2006) showed a high level of dependency between the helper bacteria strains and different mycorrhizal species. These results have been confirmed by other researchers [AZCÓN, 1989]. Some *Bacillus subtilis* strains stimulate *Suillus granulatus* development, but inhibit the development of *Rhizopogon* [KATAOKA & al. 2009]. Also, in a research realised by XIAO & al. (2008), *Bacillus subtilis* significantly decreased *Zea mays* roots colonization frequency by the mycorrhizal species (from 75% at 55.6%), inhibiting spores germination and hyphal growth, contrary to VIVAS & al. (2003) observations.

Interrelations between the mycorrhizal systems and phytopathogens

The mycorrhizal species directly protect the host plant by releasing some compounds toxic to pathogens [ZARNEA, 1994], mechanical protection of the root [ZAMFIRACHE & TOMA, 2000] or by activating host plant defence mechanisms through modulating the salicylic acid and jasmonate metabolism [MIRANSARI, 2011] or flavonoids metabolism [NEHLS & al. 1998], or indirectly by alteration of the microbial community structure due to the induction of the qualitative and quantitative changes of root exudates and also due to the stimulation of some favourable antagonistic microorganisms.

Negative correlations between vesicular-arbuscular fungi and the rhizospheric pathogens have been observed [WEHNER & al. 2010]. There are some variations of soil pathogens inhibiting capacity depending on fungal species.

Some mycorrhizal species [BOWEN & THEODORU, 1978] or the associated helper bacteria [LI & al. 2007; SIASON & al. 2009, cited by WEHNER, 2010] produce antibiotics against phytopathogens like: *Phytophthora cinnamomi*, *Pythium aphanidermatum* or *Gaeumannomyces graminis* var. *tritici*. *Pseudomonas putida* is antagonistic to *Cylindrocarpon destructans*, *Pythium ultimum* & *Rhizoctonia solani* [GU & MAZZOLA, 2003, cited by BUÉE & al. 2009].

According to AZCÓN-AGUILAR & BAREA (1997) the bacteria from *Rhizobacterium* genera can be used as biocontrolling agents. Similarly, *Bacillus subtilis* and *Pseudomonas fluorescens* strains have antagonistic reactions against pathogens, being stimulated by the presence of mycorrhizae [SCHELKLE & PETERSON, 1996; AZCÓN-AGUILAR & BAREA, 1997; NEERAJ & SINGH, 2010].

Some *Streptomyces* strains that colonize Norway Spruce ectomycorrhizae, protect the plant against the attack of *Heterbasidion annosum* [LEHR & al. 2007; cited by HARTMANN & al. 2009]. The bacteria often have the capacity of degrading the toxins produced by phytopathogenic fungi or viral factors of them [COMPANT & al. 2005].

Interrelations between the mycorrhizal systems and saprotrophic fungi

The competition for nutritive resources is the most frequent relation established between mycorrhizal species and soil saprotrophic fungi. In McALLISTER & al. (1994) experiments, the inoculation of *Lactuca sativa* rhizosphere with *Trichoderma koningii* or *Fusarium solani* strains before inoculation with *Glomus mosseae* lead to development inhibition of the last. These effects have not been observed in the case of initial inoculation with *Glomus mosseae*. As mycorrhizal species are colonizing the hosts roots, the relations with saprotrophic fungi are changing, acting often synergistically for making bioavailable some minerals needed by plants. Many telluric species of fungi have strong reactions against phytopathogenic fungi.

AZCÓN-AGUILAR & BAREA (1997) reported synergistical relations between *Glomus* and *Trichoderma* species concerning inhibiting *Fusarium* attacks at tomatoes or *Pythium* attacks at potatoes. By influencing soil microbiota, mycorrhizal species influence, also, the saprotrophic fungal activity, through inhibition processes [TIUNOV & SCHEU, 2005] or through direct or indirect stimulation.

Interrelations between the mycorrhizal systems and protozoans

In the rhizosphere, the protozoans are able to release nutrients with the consumption of the microorganisms. By consuming preferentially some bacteria, the protozoans change the bacterial community structure which leads to modifications in protozoans community, therefore a fast feed-back [RØNN & al. 2002].

The presence of the mycorrhizae can negatively influence protozoans community, indirectly by alteration the soil bacterial community in an unfavourable way for the protozoans or directly by production of some inhibitory compounds [RØNN & al. 2002].

The presence of protozoans has opposite effects to mycorrhizal species, stimulating the root ramification [BONKOWSKI & al. 2001].

Both microbial systems are beneficial and complementary for the plants, because the ectomycorrhizal species increase bioavailability of Phosphorus, and protozoans increase bioavailability of Nitrogen. However, the presence of both categories of organisms leads to an increasing competition for the plant secreted carbohydrates and their numerical reduction [TIMONEN & al. 2004; cited by HERDLER & al. 2008]. Different studies [HERDLER & al. 2008; OLSSON & al. 1996, cited by BONKOWSKI & al. 2001] revealed the fact that double inoculation, with protozoans and with fungi, strongly stimulated the biomass production of plants, concomitantly with the population significantly reduction of both categories of organisms.

Interrelations between the mycorrhizal systems and invertebrates

Although, the direct interactions between mycorrhizal species and the soil fauna are limited, they do exist. Among the soil animals that interact with mycorrhizal species and their host plant, there are different categories of invertebrates such as: insects, nematodes, annelids, mites etc. Many insect species (often larval stages) as well as nematodes, consume or attack both plant roots and mycelium (colemboles), affecting in this way the mycorrhizal symbiosis.

A particularly interesting relation is represented by earthworms. The colonization rate has been better when plants were inoculated with mycorrhizal species in the presence of earthworms from *Pheretina* [ZAREA & al. 2009], their action being beneficial for mycorrhizae through several mechanisms: earthworms can produce phytohormones, and their excrement may contain ten times more propagules than the soil [GANGE, 1993, cited by ZAREA & al. 2009]. Adding earthworms lead to increase the harvest of *Trifolium* by improving the soil chemical properties and by producing the plant regulatory compounds due to microbial activity stimulations by earthworms [QUAGGIOTTI & al. 2004, cited by ZAREA & al. 2009]. The earthworms increase the number of free nitrogen fixing bacteria by qualitative modifications of the soil (modification of porosity and aggregation) and by improving plant water and oxygen uptake. The earthworms, also, stimulate the production of exudates and create microhabitats [ZAREA & al. 2009].

Many species of colenbolas feed with mycorrhizal species, although they prefer saprotrophic fungi [GANGE, 2001; cited by TIUNOV & SCHEU, 2005]. Colembolas feed with mycorrhizal species only when insects population reach high density levels. By feeding with saprotrophic fungal species, colembolas destabilize the soil fungal community, making them more susceptible to be influenced by the mycorrhizal species [TIUNOV & SCHEU, 2005].

Conclusions

Mycorrhiza forming species strongly modify the structure and dimension of rhizospheric microorganisms, either by direct interactions, or indirectly by influencing the release of the root exudates in rhizosphere.

The mycorrhizae exercise, generally, a strong selective pressure on rhizospheric habitats, stimulating the development of mutualistic or comensal microbiota.

The mycorrhizae influence all the relations established between different categories of organisms in rhizospheric microhabitats under late succesional stages, and in young rhizospheric microhabitats the mycorrhizations success depends on the microbial community already established.

The plant benefits from all of mutualistic relations established between mycorrhizal species and the soil organisms, while the fungal partner often competes with different soil organisms for the plant carbohydrates.

The elucidation of the intimate mechanisms that underline the structure of microbial community and the processes that influence the mycorrhizal intensity and rate are premises in the elaboration of the efficient ecological reconstruction strategies or for the sustainable agriculture development.

There are needed some extensive researches concerning signal phase prior to tripartite mutualistic relations development and the involved factors, in order to use and optimize them in the purpose of integrated pest management strategies development.

Acknowledgements

This work was supported by the the European Social Fund in Romania, under the responsibility of the Managing Authority for the Sectoral Operational Programme for Human Resources Development 2007-2013 [grant POSDRU/107/1.5/S/78342]. The first author is also grateful to Prof. univ. dr. Cătălin Tănase for all the advices that he offered.

References

1. AGERER R. 2001. Exploration types of ectomycorrhizae. *Mycorrhiza*, **11**: 107-114.
2. ALBERTSEN A., RAVNSKOV S., GREEN H., JENSEN D. F. & LARSEN J. 2006. Interactions between the external mycelium of the mycorrhizal fungus *glomus intraradices* and other soil microorganism as affected by organic matter. *Soil Biology & Biochemistry*, **38**: 1008-1014.
3. ANDRADE G., MIHARA K. L., LINDERMAN R. G. & BETHLENFALVAY G. J. 1997. Bacteria from rhizosphere and hyphosphere soils of different arbuscular-mycorrhizal fungi. *Plant and Soil*, **192**: 71-79.
4. ASPRAY T. J., FREY-KLETT P., JONES J. E., WHIPPS J. M., GARBAYE J. & BENDING G. D. 2006. Mycorrhization helper bacteria: A case of specificity for altering ectomycorrhiza architecture but not ectomycorrhiza formation. *Mycorrhiza*, **16**: 533-541.
5. AZCÓN R. 1989. Selective interaction between free-living rhizosphere bacteria and vesicular-arbuscular mycorrhizal fungi. *Soil Biology & Biochemistry*, **21**(5): 639-644.
6. AZCÓN-AGUILAR C. & BAREA J. M. 1985. Effect of soil micro-organisms on formation of vesicular-arbuscular mycorrhizae. *Trans Br. Mycol. Soc.*, **84**: 536-537.
7. AZCÓN-AGUILAR C. & BAREA J. M. 1997. Applying mycorrhiza biotechnology to horticulture: significance and potentials. *Scientia Horticulturae*, **68**: 1-24.
8. BAREA J. M., BONIS A. F. & OLIVARES J. 1983. Interactions between *Azospirillum* and VA mycorrhiza and their effects on growth and nutrition of maize and ryegrass. *Soil Biology & Biochemistry*, **15**(6): 700-709.

INTERRELATIONS BETWEEN THE MYCORRHIZAL SYSTEMS AND SOIL ORGANISMS

9. BAREA J. M., AZCÓN R. & AZCÓN-AGUILAR C. 2002. Mycorrhizosphere interactions to improve plant fitness and soil quality. *Antonie van Leeuwenhoek*, **81**: 343-351.
10. BHARADWAJ D. P., LUNDQUIST P. O. & ALSTRÖM S. 2008. Arbuscular mycorrhizal fungal spora associated bacteria affect mycorrhizal colonization, plant growth and potato pathogens. *Soil Biology & Biochemistry*, **40**: 2494-2501.
11. BIANCIOTTO V. & BONFANTE P. 2002. Arbuscular mycorrhizal fungi: a specialised niche for rhizospheric and endocellular bacteria. *Antonie van Leeuwenhoek*, **81**: 365-371.
12. BONKOWSKI M., JENTSCHKE G. & SCHEU S. 2001. Contrasting effects of microbial partners in the rhizosphere interactions between Norway Spruce seedlings (*Picea abies* Karst.), mycorrhiza (*Paxillus involutus* (Batsch) Fr.) and naked amoebae (protozoa). *Applied Soil Ecology*, **18**: 193-204.
13. BOWEN GD. & THEODOROU C. 1978. Interactions between bacteria and ectomycorrhizal fungi. *Soil Biology and Biochemistry*, **11**: 119-126.
14. BRULÉ C., FREY-KLETT P., PIERRAT J. C., COURRIER S., GÉRARD F., LEMOINE M. C., ROUSSELET J. L., SOMMER G. & GARBAYE J. 2001. Survival in the soil of the ectomycorrhizal fungus *Laccaria bicolor* and the effects of a mycorrhiza helper *Pseudomonas fluorescens*. *Soil Biology & Biochemistry*, **33**: 1683-1694.
15. BUÉE M., DE BOERW., MARTIN F., OVERBEEK L. & JURKEVITCH E. 2009. The rhizosphere zoo: An overview of plant-associated communities of microorganisms, including phages, bacteria, archaea, and fungi, and of some of their structuring factors. *Plant Soil*, **321**: 189-212.
16. CALVARUSO C., TURPAULT M. P., LECLERC E. & FREY-KLETT P. 2007. Impact of Ectomycorrhizosphere on the functional diversity of soil bacterial and fungal communities from a forest stand in relation to nutrient mobilization processes. *Microbial Ecology*, **54**: 567-577.
17. COMPANT S., DUFFY B., NOWAK J., CLÉMENT C. & BARKA E. A. 2005. Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Applied and Environmental Microbiology*, **71**(9): 4951-4959.
18. DUCHESNE L. 1989. Protein synthesis in *Pinus resinosa* and the ectomycorrhizal fungus *Paxillus involutus* prior to ectomycorrhiza formation. *Trees*, **3**: 73-77.
19. DUNSTAN W. A., MALAJCZUK M. & DELL B. 1998. Effects of bacteria on mycorrhizal development and growth of container grown *Eucalyptus diversicolor* F. Muell seedlings. *Plant and Soil*, **201**: 241-249.
20. DUPONNOIS R. & PLENCHETTE C. 2003. A mycorrhiza helper bacterium enhances ectomycorrhizal and endomycorrhizal symbiosis of Australian *Acacia* species. *Mycorrhiza*, **13**: 85-91.
21. ENE M., ALEXANDRU M., ŞESAN T. E. 2010. Microscopy and detection by PCR (Polymerase chain reaction): two methods for confirmatory assay on arbuscular mycorrhizal fungi infection, în *Romanian approaches in the frame of European research*, coordonator Tatiana Eugenia ŞESAN. Edit. Universităţii din Bucureşti, 83-93.
22. FODOR E. 2010. Includerea ectomicorizelor în reţeaua sistemului silvic, în *Romanian approaches in the frame of European research*, coordonator Tatiana Eugenia ŞESAN. Edit. Universităţii din Bucureşti, 37-50.
23. FRANCO-CORREA M., QUINTANA A., DUQUE C., SUAREZ C., RODRÍGUEZ M. X. & BAREA J. M. 2010. Evaluation of actinomycete strains for key traits related with plant growth promotion and mycorrhiza helping activities. *Applied Soil Ecology*, **45**: 209-217.
24. FREY-KLETT P., CHURIN J. L., PIERRAT J. C. & GARBAYE J. 1999. Dose effect in the dual inoculation of an ectomycorrhizal fungus on a mycorrhiza helper bacterium in two forest nurseries. *Soil Biology & Biochemistry*, **31**: 1555-1562.
25. GAY G., NORMAND L., MARMEISSE R., SOTTA B. & DEBAUD J. C. 1994. Auxin overproducer mutants of *Hebeloma cylindrosporum* have increased mycorrhizal activity. *New Phytology*, **128**: 645-657.
26. GRYNDLER M., HRŠELOV H. & STRÍTESKÁ D. 2000. Effect of soil bacteria on hyphal growth of the arbuscular mycorrhizal fungus *Glomus claroideus*. *Folia Microbiol.*, **45**(6): 545-551.
27. GUTIÉRREZ-MICELI F. A., MOGUEL-ZAMUDIO B., ABUD-ARCHILA M., GUTIÉRREZ-OLIVA V. F. & DENDOOVEN L. 2008. Sheep manure vermicompost diazotrophic bacteria and mycorrhizae for maize cultivation. *Bioresources Technology*, **99**: 7020-7026.
28. HAMEEDA B., SRIJANA M., RUPELA O. P. & REDDY G. 2007 Effect of bacteria isolated from composts and macrofauna on sorghum growth and mycorrhizal colonization. *World J Microbiol Biotechnol*, **23**: 883-887.
29. HAMPP R., WIESE J., MIKOLAJEWSKI S. & NEHLS U. 1999. Biochemical and molecular aspects of C/N interaction in ectomycorrhizal plants: an update. *Plant and Soil*, **215**: 103-113.
30. HARTMANN A., SCHMID M., TUINEN D. & BERG G. 2009. Plant-driven selection of microbes. *Plant Soil*, **321**: 235-257.

31. HEBE G., HAGER A. & SALZER P. 1999. Initial signalling processes induced by elicitors of ectomycorrhiza-forming fungi in spruce cells can also be triggered by G-protein activating mastoparan and protein phosphatase-inhibiting cantharidin. *Planta*, **207**: 418-425.
32. HERDLER S., KREUZER K., SCHEU S. & BONKOWSKI M. 2008. Interactions between arbuscular mycorrhizal fungi (*Glomus intraradices*, Glomeromycota) and amoeba (*Acanthamoeba castellanii*, Protozoa) in the rhizosphere of rice (*Oryza sativa*). *Soil Biology & Biochemistry*, **40**: 660-668.
33. HRŠELOVÁ H., CHVÁTALOVÁ I., VOSÁTKA M., KLÍR J. & GRYNDLER M. 1999. Correlation of abundance of arbuscular mycorrhizal fungi, bacteria and saprophytic microfungi with soil carbon, nitrogen and phosphorus. *Folia Microbiol.*, **44**(6): 683-687.
34. HRYNKIEWICZ K., CIESIELSKA A., HAUG I. & BAUM C. 2010. Ectomycorrhiza formation and willow growth promotion as affected by associated bacteria: rol of microbial metabolites and use of C sources. *Biol fertil Soils*, **46**: 139-150.
35. IACOMI B., GEAMĂNU I., COȘOVEANU A. 2010. Micorizele arbusculare – diversitate și beneficii în ecosistemele horticole, in ȘESAN T. E. (coord.). *Romanian approaches in the frame of European research*. Edit. Universității din București: 73-82.
36. KATAOKA R. & FUTAI K. 2009. A new mycorrhizal helper bacterium, *Ralstonia species*, in the ectomycorrhizal symbiosis between *Pinus thunbergii* and *Suillus granulatus*. *Biol fertil Soils*, **45**: 315-320.
37. KATAOKA R., TANIGUCHI T. & FUTAI K. 2009. Fungal selectivity of two mycorrhiza helper bacteria on five mycorrhizal fungi associated with *Pinus thunbergii*. *World Journal of Microbiology on Biotechnology*, **25**: 1815-1819.
38. KIM K. Y., JORDAN D. & McDONALD G. A. 1998. Effect of phosphate-solubilizing bacteria and vesicular-arbuscular mycorrhizae on tomato growth and soil microbial activity. *Biol Fertil Soils*, **26**: 79-87.
39. KOELE N., TURPAULT M. P., HILDEBRAND E. E., UROZ S. & FREY-KLETT P. 2009. Interactions between mycorrhizal fungi and mycorrhizosphere bacteria during mineral weathering: Budget analysis and bacterial quantification. *Soil Biology & Biochemistry*, **41**: 1935-1942.
40. KOTHAMASI D., KOTHAMASI S., BHATTACHARYYA A., KUAHD R. C. & BABU C. R. 2006. Arbuscular mycorrhizae and phosphate solubilising bacteria of the rhizosphere of the mangrove ecosystem of Great Nicobar island, India. *Biol Fertil Soils*, **42**: 358-361.
41. KOZDRÓJ J., PIOTROWSKA-SEGET Z. & KRUPA P. 2007. Mycorrhizal fungi and ectomycorrhiza associated bacteria isolated from an industrial desert soil protect pine seedlings against Cd(II) impact. *Ecotoxicology*, **16**: 449-456.
42. LARSEN J., CORNEJO P. & BAREA J. M. 2009. Interactions between the arbuscular mycorrhizal fungus *Glomus intraradices* on the plant growth promoting rhizobacteria *Paenibacillus polymyxa* and *P. maceans* in the mycorrhizosphere of *Cucumis sativus*. *Soil Biology & Biochemistry*, **41**: 286-292.
43. LI B., RAVNSKOV S., XIE G. & LARSEN J. 2007. Biocontrol of *Pythium* damping-off in cucumber by arbuscular mycorrhiza-associated bacteria from the genus *Paenibacillus*. *BioControl*, **52**: 863-875.
44. LÓPEZ-GUTIÉRREZ J. C., TORO M. & LÓPEZ-HERNÁNDEZ D. 2004. Arbuscular mycorrhiza and enzymatic activities in the rhizosphere of *Trachypogon plumosus* Ness. in three acid savana soils. *Agriculture, Ecosystems and Environment*, **103**: 405-411.
45. MAIER A., RIEDLINGER J., FIEDLER H. P. & HAMPP R. 2004. Actinomycetales bacteria from a spruce stand: characterization and effects on growth of root symbiotic and plant parasitic soil fungi in dual culture. *Mycological Progress*, **3**(2): 129-136.
46. MARULANDA A., BAREA J. M. & AZCÓN R. 2006. An indigenous drought-tolerant strain of *Glomus intraradices* associated with a native bacterium improves water transport and root development in *Retama sphaerocarpa*. *Microbial Ecology*, **52**: 670-678.
47. MCALLISTER C. B., GARCÍA-RORNERA I., GODEA A. & OCAMPO J. A. 1994. Interactions between *Trichoderma koningii*, *Fusarium solani* and *Glomus mosseae*: effects on plant growth, arbuscular mycorrhizae and the saprophyte inoculants. *Soil Biology & Biochemistry*, **26**(10): 1363-1367.
48. MEYER A., GROTE R., POLLE A. & BUTTERBECH-BAHL K. 2010. Simulating mycorrhizal contribution to forest C- and N cycling – the MYCOFON model. *Plant and Soil*, **327**: 493-517.
49. MIRANSARI M. 2011. Interactions between arbuscular mycorrhizal fungi and soil bacteria. *Applied Microbial Biotechnology*, **89**: 917-930.
50. MIRANSARI M., BAHRAMI H. A., REJALI F. & MALAKONTI M. J. 2009. Effects of soil compaction and arbuscular mycorrhiza on corn (*Zea mays* L.) nutrient uptake. *Soil & Tillage Research*, **103**: 282-290.

INTERRELATIONS BETWEEN THE MYCORRHIZAL SYSTEMS AND SOIL ORGANISMS

51. NEERAJ & SINGH K. 2010. *Cyamopsis tetragonoloba* (L.) Taub inoculated with arbuscular mycorrhiza and *Pseudomonas fluorescens* and treated with mustard oil cake overcome Macrophomina root-rot losses. *Biol Fertil Soils*, **46**: 237-245.
52. NEHLS U., BÉGUIRISTAIN T., DITENGOU F., LAPEYRIE F. & MARTIN F. 1998. The expression of a symbiosis-regulated gene in eucalypt roots is regulated by auxins and hypaphorine, the triptotaphan betaine of ectomycorrhizal basidiomycete *Pisolithus tinctorius*. *Planta*, **207**: 296-302.
53. OANCEA F., CONSTANTINESCU F., ŞESAN T. E., DINU S., SICUIA O. 2010. Efectele sistemului de agricultură conservativă cu mulci bioactiv asupra agregatelor stabile în apă, a propagulelor micoriziale și a glomalinei dintr-un cernoziom cambic, în volumul *Romanian approaches in the frame of European research*, coordonator Tatiana Eugenia ŞESAN. Edit. Universității din București: 94-106.
54. PIVATO B., OFFRE P., MARCHELLI S., BARBOBAGLIA B., MUOGEL C., LEMANCEAU P. & BERTA G. 2009. Bacterial effects on arbuscular mycorrhizal fungi and mycorrhiza development as influenced by the bacteria, fungi, and host plant. *Mycorrhiza*, **19**: 81-90.
55. RAIESI F. & GHOLLARATA M. 2006. Interactions between phosphorus availability and an AM fungus (*Glomus intraradices*) and their effects on soil microbial respirations, biomass and enzyme activities in a calcareous soil. *Pedobiologia*, **50**: 413-425.
56. REQUENA N., SERRANO E., OCÓN A. & BREUNINGER M. 2007. Plant signal and fungal perception during arbuscular mycorrhiza establishment. *Phytochemistry*, **68**: 33-40.
57. RØNN R., GAVITO M., LARSEN J., JAKOBSEN I., FREDERIKSEN H. & CHRISTENSEN S. 2002. Response of free-living soil protozoa and microorganisms to elevated atmospheric CO₂ and presence of mycorrhiza. *Soil Biology & Biochemistry*, **34**: 923-932.
58. RUIZ-LOZANO J. M. & BONFANTE P. 2001. Intracellular *Burkholderia* strain has no negative effect on the symbiotic efficiency of the arbuscular mycorrhizal fungus *Gigaspora margarita*. *Plant Growth Regulation*, **34**: 347-352.
59. SCHELKLE M. & PETERSON R. L. 1996. Suppression of common root pathogens by helper bacteria and ectomycorrhizal fungi in vitro. *Mycorrhiza*, **6**: 481-485.
60. SCHREY S. D., SALO V., RAUDASKOSKI M., HAMPP R., NEHLS U. & TARKKA M. T. 2007. Interactions with mycorrhiza helper bacterium *Streptomyces* sp. Ach505 modifies organisation of actin cytoskeleton in the ectomycorrhizal fungus *Amanita muscaria* (fly agaric). *Current genetics*, **52**: 77-85.
61. ŞESAN T. E., OANCEA F., TOMA C., MATEI G. M., MATEI S., CHIRA F., FODOR E., MOCAN C., ENE M. & ALEXANDRU M. 2010. Approaches to the study of mycorrhizae in Romania. *Symbiosis*, **52**(2-3): 75-85.
62. SIVIERO M. A., MOTTA A. M., SANTOS LIMA D., BIROLI R. R., HUH S. Y., SANTIONI I. A., MURATE L. S., AANTONIA DE CASTRO C. M., MIYOUCHI M. Y. H., ZABGARO W., NOGUEIRA M. A. & ANDRADE G. 2008. Interaction among N-fixing bacteria and AM fungi in Amazonian legume tree (*Schizolobium amazonicum*). *Applied Soil Ecology*, **39**: 144-152.
63. TALBOT J. M. & TRESEDER K. K. 2009. Control over mycorrhizal uptake of organic nitrogen. *Plant and Soil*, **303**: 87-89.
64. TARKKA M. T., SARNIGUET A. & FREY-KLETT P. 2009. Inter-kingdom encounters: recent advances in molecular bacterium–fungus interactions. *Curr Genet*, **55**: 233-243.
65. TIAN C., HE X., ZHONG Y. & CHEN J. 2003. Effect of inoculation with ecto- and arbuscular mycorrhizae and *Rhizobium* on the growth and nitrogen fixation by black locust, *Robinia pseudoacacia*. *New Forests*, **25**: 125-131.
66. TIMONEN S., SÖDERSTRÖM B. & RAUDASKOSKI M. 1996. Dynamics of cytoskeletal proteins in developing pine ectomycorrhiza. *Mycorrhiza*, **6**: 423-429.
67. TIUNOV A. V. & SCHEU S. 2005. Arbuscular mycorrhiza and Collembola interact in affecting community composition of saprotrophic microfungi. *Oecologia*, **142**: 636-642.
68. TOBAR R. M., AZCÓN-AGUILAR C., SANJUÁN J. & BAREA J. M. 1996. Impact of a genetically modified *Rhizobium* strain with improved nodulation competitiveness on the early stages of arbuscular mycorrhiza formation. *Applied Soil Ecology*, **4**: 15-21.
69. VIVAS A., MARULANDA A., GÓMEZ M., BAREA J. M. & AZCÓN R. 2003. Physiological characteristics (SDH and ALP activities) of arbuscular mycorrhizal colonization as affected by *Bacillus thuringiensis* inoculation under two phosphorus levels. *Soil Biology & Biochemistry*, **35**: 987-996.
70. WEHNER J., ANTUNES P. M., POWELL J. R., MAZUKATOW J. & RILLIG M. C. 2010. Plant pathogen protection by arbuscular mycorrhizae: A role for fungal diversity?. *Pedobiologia*, **53**: 197-201.
71. WELSH A. K., BURKE D. J., HAMERLYNCK E. P. & HAHN D. 2010. Seasonal analyses of arbuscular mycorrhizae, nitrogen-fixing bacteria and growth performance of the salt marsh grass *Spartina patens*. *Plant Soil*, **330**: 251-266.

-
72. XIAO X., CHEN H., CHEN H., WANG J., REN C. & WU L. 2008. Impact of *Bacillus subtilis* JA, a biocontrol strain of fungal plant pathogens, on arbuscular mycorrhiza formation in *Zea mays*. *World J Microbiol Biotechnol*, **24**: 1133-1137.
73. ZAMFIRACHE M.-M. & TOMA C. 2000. *Simbioza în lumea vie*. Iași: Edit. Univ. "Alexandru Ioan Cuza", 186-239.
74. ZAREA M. J., GHALAVAND A., GOLTAPPEH E.M., REJALI F. & ZAMANIYAD M. 2009. Effect of mixed cropping, earthworms (*Phereina* sp.), and arbuscular mycorrhizal fungi (*Glomus mosseae*) on plant yield, mycorrhizal colonozation rate, soil microbial biomass, and nitrogenase. *Pedobiology*, **52**: 223-235.
75. ZARNEA G. 1994. *Tratat de microbiologie generală*. București: Edit. Academiei Române, **5**: 367-391.
76. ZUBEK S., TURNAU K., TSIMILLI-MICHAEL M. & STRASSER R. J. 2009. Response of endangered plant species to inoculation with arbuscular mycorrhizal fungi and soil bacteria. *Mycorrhiza*, **19**: 113-123.