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THE RELATION BETWEEN MUTUALISTIC MYCORRHIZA AND ENDOPHYTIC PLANT-FUNGUS ASSOCIATIONS AND THEIR EFFECT ON HOST PLANTS

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Aim. A review of the literature to establish the mechanisms of the main mutualistic interactions that are important for the potential application of symbiotic fungi as biofertilizers, bioprotectors and bioregulators for more sustainable and so-called greening agriculture, soil restoration and understanding the role of microsymbionts in natural ecosystems.

Methods. Comparative analysis of scientific literature. **Results.** Root mycorrhization is a potent factor of plant growth intensification, metabolic processes activation and macro-organism development improvement. Mycorrhiza formation is notable for angiosperms and gymnosperms, yet many representatives of bryophytes, ferns, and mosses also reveal (other) close symbiotic relations with fungi. Mycorrhizal fungi account for about 10 % of identified fungal species, including essentially all of the Glomeromycota and substantial fractions of the Ascomycota and Basidiomycota. Depending on the fungal structures and microsymbiont position in tissues or cells of the macrosymbiont, arbuscular, ericoid, arbutoid, monotropoid, orchid mycorrhiza and so-called ectendomycorrhiza, and ectomycorrhiza are distinguished. This review gives an overview of the signalling interaction between partners and the bidirectional mechanism of nutrient exchange or other mutual benefits. **Conclusions.** Microscopic saprophytic fungi, capable of penetrating plant roots and playing a critical role in plant adaptation to abiotic and biotic stressors, are of special interest in mutualistic symbioses. In addition, while forming mutualistic symbioses with plants, the saprophytic fungi promote biomass increase and enhance the food traits of plants. The type of interaction depends on both micro- and macrosymbiot; it may in some cases and for some organisms fluctuate from mutualistic, commensalistic to antagonistic, even parasitic interactions, demonstrating different stages of mutualism evolution and co-habitation and/or evolution of plants and fungi. A better understanding of the diverse roles of symbiotic microorganisms in ecosystems will improve the ways of their application in agriculture.

Key words: bidirectional symbiosis, mycorrhiza, endophytism, signalling interaction, metabolites.

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MUTUALISTIC FUNGI – PLANTS ROOTS INTERACTIONS

The mutualistic interactions between fungi and the plant root system, resulting in the formation of their close interaction, is a common natural phenomenon (Lanfranco et al, 2016). The research of such interac-

tions is of both fundamental theoretical and practical value since most terrestrial plants form close interactions with one or several species of fungi (van der Heijden et al, 2015). Moreover, the application of fungal symbionts is significant practical implications for agriculture, horticulture, forestry, and ecosystem management (Bago et al, 2000; Genre et al, 2020; Rimington et al, 2020). Thus, a significant aspect of applied microbiology is the study of symbiotic microorganisms,

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Main types of plant-fungal interactions

Fungal partner	Plant partner
<i>Endomycorrhiza</i>	
<i>Arbuscular mycorrhiza</i>	
<p>Division Glomeromycota, class Glomeromycetes, which more than 325 species (CICG, 2023) (Helgason and Fitter, 2005; Redecker and Raab, 2006)</p>	<p>Magnoliopsida: all herbs, a significant number of woody plants of the tropics and subtropics, some woody plants of the temperate zone (Jones and Hendrix, 1987; Tawaraya et al, 2003; Wang and Qiu, 2006; da Silva, 2020. Gymnosperma (Read et al, 2000), sporophytes and gametophytes of some ferns (Cooper, 1976; Lüttge, 2020), such as <i>Mankyua chejuense</i> (Oh et al, 2021), <i>Angiopteris lygodiiifolia</i> and <i>Osmunda japonica</i> (Ogura-Tsujita et al, 2013), <i>Botrychium virginianum</i> (Kovács et al, 2007), <i>Salvinia molesta</i>, <i>Christella parasitica</i> and <i>Adiantum lunulatum</i> (Muthukumar & Prabha, 2013). Sporophytes and gametophytes of some Bryophyta (mosses) (Winther and Friedman, 2007; Vigneron et al, 2018.), such as <i>Anthoceros punctatus</i> (Schüßler, 2000), <i>Rhizophagus intraradices</i> and <i>Dominikia aurea</i> (Valdés et al, 2023), <i>Symphyogyna circinata</i>, <i>S. hymenophyllum</i> and <i>S. rubritincta</i> (Cottet & Messuti, 2019)</p>
<i>Ericoid mycorrhiza</i>	
<p>Some fungi of the phylum Ascomycota, which belong to orders Leotiales, Onygenales and Hypocreales (Xiao and Berch, 1995; Hambleton et al, 1998, Monreal et al, 1999) and some Basidiomycota (Kolarik & Vohnik, 2018; Sietiö et al, 2018). The most studied of them is <i>Hyaloscypha hepaticicola</i> (Fehrer et al, 2019)</p>	<p>Some representatives of the order Ericales, subfamily Ericoideae (the main representatives of the ecosystems in wastelands and swamps) (Peterson and Massicotte, 2004), tribe Epacrideae, genus <i>Epacris</i> – about 40 species of deciduous shrubs) and subfamily <i>Vaccinoideae</i> (represented by shrubs, trees, and lianas) (Luteyn, 2002; Van Geel et al, 2020; Pacheco Flores de Valgaz et al, 2022. For example, <i>Calluna vulgaris</i> and <i>Vaccinium myrtillus</i> (Bougoure et al, 2007)</p>
<i>Arbutoid mycorrhiza</i>	
<p>Some representatives of the phylum Basidiomycota (Molina and Trappe, 1992; Molina et al, 1997; Peterson and Massicotte, 2004; For example, <i>Sebacina</i> (Sebacinales) (Kühdorf et al, 2014), <i>Cortinarius</i> (Kühdorf et al, 2016), <i>Leotia cf. lubrica</i> (Kühdorf et al, 2015), <i>Tuber borchii</i> (Lancellotti et al, 2014) <i>T. melanosporum</i> and <i>T. aestivum</i> (Ori et al, 2020), <i>Lactarius deliciosus</i> (Gomes et al, 2016), <i>Pisolithus arhizus</i> (Gomes et al, 2013), ect</p>	<p>20 species of perennial evergreen herbaceous plants with creeping roots) (Cullings, 1994; Selosse et al, 2007). For example, <i>Arctostaphylos uva-ursi</i> and <i>Arbutus menziesii</i> (Molina et al, 1997), <i>Arbutus unedo</i> (Lancellotti et al, 2014; Gomes et al, 2013, 2016; Ori et al, 2020), <i>Comarostaphylis arbutoides</i> (Kühdorf et al, 2014; 2015).</p>
<i>Monotropoid mycorrhiza</i>	
<p>Some representatives of the division Basidiomycota, which are notable for specialization regarding the macrosymbionts. Some representatives of the family Russulaceae (Bidartondo and Bruns, 2001; Yokoyama et al, 2005; Lambers and Oliveira, 2019). Some representatives of species <i>Tricholoma</i>, <i>Rhizopogon</i>, <i>Hydnellum</i> and <i>Gautieria</i> (Bruns and Read, 2000; Bidartondo and Bruns, 2001; Yokoyama et al, 2005; Bidartondo and Bruns, 2005; Lee & Eom, 2014; Natesan et al, 2023)</p>	<p>The representatives of Ericales of the subfamily Monotropoideae, which belong to ten genera: <i>Allotropia</i> (Massicotte et al, 2010), <i>Monotropa</i> (Massicotte et al, 2005; Lee & Eom, 2014), <i>Monotropastrum</i> (Imamura & Kurogi, 2003), <i>Pleuricospora</i> (Massicotte et al, 2010), <i>Pterospora</i> (Massicotte et al, 2005), <i>Sarcodes</i> (Salazar-Magallón et al, 2021), etc (Leake, 1994; Leake, 2005). All plants are heterotrophs without chlorophyll (Leake, 1994; Harley & Harley, 1987)</p>

Fungal partner	Plant partner
<i>Orchid mycorrhiza</i>	
The representatives of the division Basidiomycota, which belong to the order Cantharellales (<i>Ceratorhiza</i> , <i>Ceratomyces</i> , <i>Tulasnella</i> and anamorphous forms of the genus <i>Epulorhiza</i>), as well as the genus <i>Sebacina</i> and anamorphous forms of the genus <i>Rhizoctonia</i> (Zelmer et al, 1996; Sathiyadash et al, 2020; Freestone et al, 2021; Zhang et al, 2022)	Herbs and woody (lianas) forms of the family Orchidaceae (Peterson and Massicotte, 2004; Lambers and Oliveira, 2019; Sathiyadash et al, 2020; Freestone et al, 2021), including some species of <i>Rhizanthella</i> (Warcup, 1985; Bougoure et al, 2009), which stay underground until blossoming and completely dependent on mycorrhiza-forming fungi due to the absence of their own reserves to support their viability (Smith and Read, 2008; Howard et al, 2022)
<i>Ectendomycorrhiza</i>	
A limited number of fungi of the division Ascomycota (Yu et al, 2001). For example, <i>Wilcoxina micolae</i> and <i>W. rehmi</i> (Egger, 1991; Egger, 1996), <i>Sphaerosporella brunnea</i> (Pezizales) and two species of <i>Leotiales</i> (<i>Cadophora finlandica</i> and <i>Chloridium paucisporum</i>) (Yu et al, 2001; Peterson et al, 2008), <i>Terfezia boudieri</i> (Turgeman et al, 2016), <i>T. claveryi</i> and <i>Tirmania nivea</i> (Marqués-Gálvez et al, 2021)	Coniferous plants, which belong to two genera <i>Pinus</i> and <i>Larix</i> , (Yu et al, 2001; Peterson and Massicotte, 2004) and family Cistaceae, such as <i>Helianthemum almeriense</i> (Marqués-Gálvez et al, 2021) and <i>H. sessiliflorum</i> (Turgeman et al, 2016)
<i>Ectomycorrhiza</i>	
The representative of the divisions of Basidiomycota, Ascomycota, which covers 7,000–10,000 fungal species and some species of <i>Endogone</i> from the Zygomycota (Bruns et al, 2002; Mayor et al, 2009; Rudawska and Leski, 2021).	Almost all the plants, are represented by trees and shrubs of the families Acaraceae, Betulaceae, Bignoniaceae, Caprifoliaceae, Casuarinaceae, Cistaceae, Cupressaceae, Dipterocarpaceae, Elaeagnaceae, Epacridaceae, Ericaceae, Fabaceae (Caesalpinioideae), Gnetaceae, Juglandaceae, Myricaceae, Myrtaceae, Nyctaginaceae, Oleaceae, Pinaceae, Platanaceae, Polygalaceae, Rhamnaceae, Rosaceae, Salicaceae, Sapindaceae, Sapotaceae, Sterculiaceae, Stylidiaceae, Thymeliaceae, Tiliaceae, Ulmaceae, Vitaceae and sometimes the grassy forms of the families Cyperaceae, Goodenaceae, Polygonaceae (Harley and Smith, 1983; Taylor and Alexander, 2005; Mayor et al, 2009; Rudawska and Leski, 2021).
<i>Endophytic associations</i>	
<i>Acremonium</i> (Khan et al, 2021), <i>Alternaria</i> (Wang et al, 2014), <i>Aspergillus</i> (El-Hawary et al, 2020), <i>Chaetomium</i> (Kopilov et al, 2020; Kopylov et al, 2021), <i>Claviceps</i> (Panaccione et al, 2014), <i>Collectotrichum</i> (Wang et al, 2016), <i>Cryptococcus</i> (Deng et al, 2012), <i>Curvularia</i> (Priyadharsini & Muthukumar, 2017), <i>Fusarium</i> (Toghueo, 2020), <i>Geomyces</i> (Katsuramoto et al, 2023), <i>Glomus</i> (Orchard et al, 2016), <i>Leptospora</i> (Pereira, 2008), <i>Microdochium</i> (Matušinsky et al, 2022), <i>Neotyphodium</i> , <i>Paecilomyces</i> , <i>Penicillium</i> (Nischitha & Shivanna, 2022), <i>Plectosphaerella</i> (Patyka et al, 2022; Tsekhmister & Kyslynska, 2022); <i>Phaeoconiella</i> (Whiting et al, 2001), <i>Piriformospora</i> (Mohd et al, 2017), <i>Rhizoctonia</i> (Otero et al, 2002), <i>Rhizopus</i> (Ismail et al, 2020), <i>Rhodotorula</i> (Firrincieli et al, 2015), <i>Talaromyces</i> (Palem et al, 2015), <i>Trichoderma</i> (Ming et al, 2013), <i>Wallemia</i> (Wang et al, 2016), <i>Xylaria</i> (Zheng et al, 2018) ect	Cotton (<i>Gossypium hirsutum</i>) (Jin et al, 2021), peas (<i>Cajanus cajan</i>) (Zhao et al, 2012), corn (<i>Zea mays</i>) (Terna et al, 2022), barley (<i>Hordeum vulgare</i>) (Deshmukh et al, 2006), tomato (<i>Lycopersicon esculentum</i>) (Sinno et al, 2020), millet (<i>Eleusine coracana</i>) (Nandhini et al, 2018), wheat (<i>Triticum aestivum</i>) (Larran et al, 2007; Colla et al, 2015; Ofek-Lalzar et al, 2016), rapeseed (<i>Brassica chinensis</i>) (Deng et al, 2012), rice (<i>Oryza sativa</i>) (Wang et al, 2016), soybeans (<i>Glycine max</i>) (Pereira, 2008; Fernandes et al, 2015), sunflower (<i>Helianthus annuus</i>) (Ismail et al, 2020), chile (<i>Capsicum annuum</i>) (Suman et al, 2016; Verma et al, 2017), buckwheat (<i>Fagopyrum esculentum</i>) (Kopylov et al, 2021) and many others agricultural crops (Kopilov et al, 2020) and another plants (Suryanarayanan et al, 2018).

their taxonomic diversity, genetics, ecologic niches, metabolic products, their place in the microbiome and their application as plant growth and development stimulants.

A special place among the large number of microorganisms inhabiting the rhizosphere is occupied by mycorrhizal fungi, which is connected with their close interaction with the root system of plants. According to some estimates, about 250,000 plant species are capable of forming mycorrhiza (Smith and Read 2008; Singh et al, 2022). Among them, 80 % vascular plants, the remaining a larger number of gametophytes of bryophytes and ferny plants, and some representatives of ferny sporophytes (Wang and Qiu 2006; Ferrari et al, 2020).

Mycorrhiza formation is an ecological process in which macro- and microsymbionts are in mutually beneficial and interdependent partnership, ensuring highly efficient adaptation of plants to unfavorable ecologic factors: nutrition deficiency, attack of phytopathogens and phytophages and abiotic stresses (Rodriguez et al., 2009; Delaux and Schornack, 2021). The mycorrhiza is formed by the fungal mycelium and plant root system, which may incur morphological and anatomic changes, acquiring specific traits, such as vesicles, arbuscules, pelotons, etc. due to the symbiosis (Petersen et al, 2004; Smith and Read, 2008; Ren et al, 2021; Khaliq et al, 2022). The functioning of mycorrhiza is based on establishing specific trophic relations between symbionts, due to which the absorption activity of plants increases, and fungi, in their turn, obtain access to photosynthesis products and other metabolites of plants (Petersen et al, 2004; Hagh-Doust et al, 2022).

Along with mycorrhizal symbiosis, significant attention of researchers is directed to another little-studied process, namely, endophytic soil saprotrophic fungi in plant roots (Spatafora, 2007). Unlike mycorrhizal fungi, endophytes do not form specific structures and are active only under certain conditions (Baron and Rigobelo, 2021). Metabolic and growth processes are activated in plants infected with endophytic fungi (Poveda et al, 2021), the immune status increases, resistance to stress factors increases (Poveda et al, 2020; Cui et al, 2021).

The micro- and macroorganisms, capable of forming mutualistic symbioses and endophytic associations and types of plant-fungal interactions, are presented in **Table**.

THE SIGNALING INTERACTION BETWEEN MACRO- AND MICROSymbionTS OF FUNGUS-PLANT FORMATION

Endomycorrhiza. The endophytic mycorrhiza, which has been studied the most, is the arbuscular mycorrhiza (AM). It is notable for ecosystems with significant biodiversity, which gives the opportunity for many symbiont plants (Smith and Read 2008). The remarkable changes in the root cells and unique physiology of development of arbuscular mycorrhiza suggest the presence of specific regulatory pathways which lead to the expression of specific genes responsible for symbiotic interactions of plants and mycorrhizal fungi (Franken and Requena, 2001, Hause and Fester, 2004; Bahadur et al, 2019).

In the development of mycelium of species of the important arbuscular mycorrhizal genus *Rhizophagus* in the epidermis and cortex of the plant root, there is a modification of the cellular wall, the induction of the synthesis of phytoalexins, the accumulation of callose and effector proteins that stimulate symbiotic biotrophy, short-circuiting the plant's defence mechanisms, and defense proteins (peroxidases and lytic enzymes) (Smith and Read, 2008; Sędziewska Toro and Brachmann, 2016)

Root excretions of plants-macrosymbionts stimulate the germination of the spores of *Rhizophagus*, the formation of primary hyphae, infecting the root, and the formation of special fungal attachment structures – appressoria (Gianinazzi-Pearson, 1996; Scervino et al, 2007).

The introduction of high phosphorus concentrations into the root zone of plants has a negative impact on the reaction of fungal hyphae (Tawaraya et al, 1994). The flavonoids are characterized by a stable stimulatory effect on the growth and branching of germ tubes of *Gigaspora margarita* and some species of the genus *Glomus*, which results in enhancing the degree of root colonization by fungi. Regardless of the stimulatory properties, the flavonoids do not play a key role in mycorrhiza formation (Buee et al, 2000, Akiyama et al, 2005).

It is known that after germination, the pre-symbiotic growth and branching of mycelium are stimulated by the signals, coming from the roots of a vast number of host plants (Buee et al, 2000). The branching factor (BF) was isolated from *Lotus japonicum* and identified as strigolactone (Akiyama et al, 2005). This substance was previously known as a stimulator for germinat-

ing the seeds of Intracellular parasites *Striga* and *Oribanthe*. Other natural and synthetic analogs of strigolactones stimulate the branching of the germ tubes in *Gigaspora margarita* under very low concentrations (Smith and Read 2008; Fiorilli et al, 2021; Campos-López et al, 2022).

Strigolactones are sesquiterpene lactones, which are formed in the plant roots and are excreted into the root zone. Under the deficiency of mineral nutrition elements (for instance, nitrogen and phosphorus), the synthesis of strigolactones in the root system increases sharply. Enhanced branching of hyphae to the formation of a large pre-symbiotic hyphal network which increases the probability of contact between the fungal structures and plants for the beginning of colonization (Buee et al, 2000, Akiyama et al, 2005; Fiorilli et al, 2019; Ho-Plágaro and García-Garrid).

The contact between the fungus and the root occurs when hyphae stick to the surface of the latter, and in 2–3 days, swollen appressoria are formed. The stimulus to the appressoria formation is related to the metabolites such as fatty acids of the cell walls of the rhizodermis and is absent in many plants, incompatible with fungi (Nagahashi and Douds, 1997; Deising et al, 2000; Gadkar et al, 2001).

The penetration of arbuscular mycorrhizal fungi via the plant cell wall occurs due to the decrease in the hyphae diameter, the formation of a small loose knot, and its further increase in volume while entering the apoplast. The changes in the membrane structure in the course of fungal hyphae penetration into the intercellular space demonstrate a possible role of fungal enzymes – pectinases (García-Romera et al, 1991), which was biochemically confirmed by detecting them in the spores and free mycelium (García-Garrido et al, 2000). The signalling interaction between macro- and micro-symbionts on different stages of endomycorrhiza formation, using the AM example, is schematically presented in **Figure 1**.

The increase in the physiological activity was found in the hyphal knots, formed by *Glomus intraradices* in *Asphodelus fistulos* due to the increase in the activity of succinate dehydrogenase (SDG) and acid phosphatase (APA) and alkaline phosphatase (ALP) (Hart and Reader, 2002, van Aarle et al, 2005).

Ergosterol was suggested as a quantitative marker of endomycorrhizal colonization, but the symbionts of arbuscular mycorrhiza do not exhibit any differences regarding this trait which limits the application of this substance as a marker in the field conditions (Olsson et al, 2003).

During the formation of symbiotic structures, there are considerable changes in the fungal metabolism of carbon which is related to the high capability of micro-symbiont to acquire hexoses. The plants supply the arbuscular mycorrhiza with sucrose, where it gets hydrolyzed under the impact of plant enzymes, thus supporting the pool of hexoses available for transportation. Some data demonstrate the increase in the level of gene expression for invertase and sucrose-synthetase in arbuscular mycorrhizal roots (Smith and Smith, 1990; Wipf et al, 2019), but their expression is not directly linked to the volume of the pool of carbohydrates. A quick transformation of sucrose into hexoses (within a plant) and hexoses into lipids and trehaloses (in fungal structures) maintains the gradient of concentrations which promotes the diffusion of carbohydrates via the contact zone (Harrison, 1996). The increase in the expression of plant transporter genes of hexoses in arbuscular mycorrhizal roots may be a mechanism to control the outflow of carbon to the fungal symbiont (the export of carbohydrates from the plant cells and the reverse absorption of hexoses from the interphase apoplast) (Jakobsen and Rosendahl, 1990; Bravo et al, 2017; Martino and Crawford, 2021).

It was demonstrated in many field experiments that 5–8 % of carbon in the plants was used in the breathing process of free arbuscular mycorrhizal mycelium in soil (Heinemeyer et al., 2006). It was later determined by the method of labelled ^{13}C that the outlays of carbon for free mycelium, associated with *Plantago lanceolata* of the fungus of the genus *Glomus* were considerably smaller than the total amount of the plant photosynthesis products (Mensah et al, 2015). A high amount of carbon, used by arbuscular mycorrhizal fungi to maintain the symbiotic interaction, was put into action to enhance plant growth. However, the outlays were balanced via an increase in photosynthesis activity or a decrease in root growth. It is noteworthy that different species of fungi used different amounts of plant photosynthesis products (Smith and Read, 2008; Zhang et al, 2018).

The research on the distribution of photosynthesis products was conducted along with the study of ^{32}P transportation to the plant via fungal mycelium. The species *Scutellopora calospora* was the least effective and *Glomus caledonium* – the most effective symbiont in the ratio between ^{14}C , absorbed by hyphae, and translocated ^{32}P , which is explained by the diversity of colonization types, the difference in symbiotic functions on the level of transportation velocity via contact zones or the difference in metabolic activity. The rate of phosphorus consumption per one unit of hyphae length

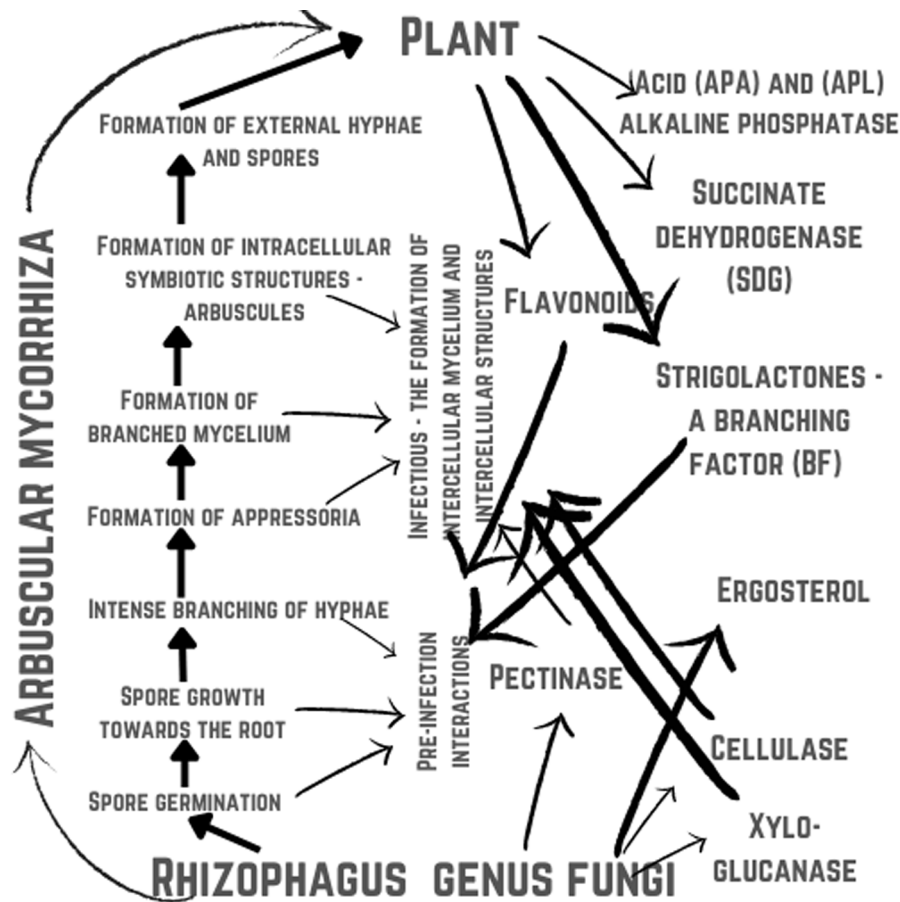


Fig. 1. The signalling interaction between macro- and microsymbionts on different stages of endomycorrhiza formation

within one species of fungi was insignificant, but the total amount of phosphorus, getting transported to the plant, varied considerably both on the intraspecies and interspecies levels (Bücking and Shachar-Hill, 2005; Vries et al, 2021).

The hydrolysis of polyphosphates and their transportation to the plant occurred under the complex effect of exopolyphosphates, endopolyphosphates, and non-specific acid phosphatases. Two enzymes of exopolyphosphate type with different pH optima, specificity to the substrate, and different lengths of the chains were found in AM of fungi. The genes of these enzymes were expressed in the internal and external mycelia, which could be related to the differences in the length of polyphosphate chains. The role of alkaline phosphatases in the hydrolysis of polyphosphates is yet to be studied, but both its activity and SDG activity are used as markers of cytochemical activity of arbuscular mycorrhiza fungi, associated with the plant (Benedetto et al, 2005; Etesami et al, 2021).

The transportation of phosphorus from the fungus to the plant occurred with a velocity that exceeded that

of a regular outflow considerably, which indicated the presence of specific mechanisms of enhanced P outflow from the fungal partner and thus the inhibited re-absorption from the apoplast. The mobilization of phosphorus reserves (polyphosphates) occurred due to their release from the vacuole pool and translocation into the interphase apoplast. The outflow of phosphorus from the intraradical fungal structures was enhanced after the introduction of glucose and desoxyglucose from the outside. A low expression of arbuscular mycorrhizal fungal highly affine transporter of phosphorus (GvPT) in intraradical structures prevented the reverse absorption by the fungus. However, GmosPT was expressed within the roots on a stable low level which demonstrated the ability of a fungal partner to regulate the amount of phosphorus, available for the plant, via re-absorption of phosphorus which was coming into the apoplast (Benedetto et al, 2005, Nagy et al, 2006).

There are known transporters of phosphorus in plants, which express only into arbuscular mycorrhizal roots (AM-specific) or increase the expression during the colonization considerably (AM-induced). Such trans-

porters were found in dicotyledon *Solonom tubersum*, *S. lycopersicon*, *Medicago truncatula*, *Lotus japonicas* and *Populus*, and monocotyledon *Oryza sativa*, *Triticum aestivum*, *Hordeum vulgare*, and *Zea mays*. A wide distribution of P transporters means that such transporters can be present in all potential AM plants (Maeda et al, 2006; Wang et al, 2020; Santander et al, 2021).

Sometimes there was a decrease in direct phosphorus absorption by rhizoderma of the roots and root hairs which was conditioned by the decrease in the amount of phosphorus in the rhizosphere or a decrease in the expression of transporters in the root cells. For instance, genes MtPtl from *Medicago truncatula*, HvPtl1 and HvPtl2 from *Hordeum vulgare* were sometimes subject to decreased regulation during the colonization by arbuscular mycorrhiza fungi. The expression of these genes depended on the amount of phosphorus so the increase in the concentration of this element in arbuscular mycorrhizal plants caused the decrease in their expression. On the contrary, the immediate action of the signals of the fungal partner played a considerable role in the transportation of phosphorus. Both mechanisms may be in action at the same time (Smith and Read 2008; Li et al, 2018; Cui et al, 2019).

Arbuscular mycorrhizal fungi influence the consumption of other macro- and microelements of plant nutrition. Their hyphae and roots are capable of absorbing ammonium and nitrates (Hodge 2001; Bhandana et al, 2021). The increased absorption of copper was confirmed in many pairs of symbiotics, though the volume of transportation from the fungal symbiont to the plant symbiont remained low (Manjunath and Habte, 1988; Tang et al, 2021). The presence of arbuscular mycorrhiza under deficient conditions promoted the increase in zinc absorption; there are also some data about the intoxication of mycorrhizal plants in soils with high content of this element (Jansa et al, 2003; Watts-Williams and Cavagnaro, 2018; Saboor et al, 2021).

Ectendomycorrhizal associations. Ectendomycorrhizal associations are often present in nurseries of coniferous trees (Terhonen et al., 2019). The specificities of ectendomycorrhiza are the colonization of short roots, the development of a thin mantle, the Hartig net, and intracellular hyphae. On the early stages of mantle formation, the hyphae surround root hairs and get incorporated into mucus on the surface of the roots. Usually, the extraradical hyphae are only a few. Later the Hartig net develops as a single layer between epidermal and cork cells, and its hyphae are spirally wound in the direction of cellulose fibrils around the cellular wall.

They penetrate through the cellular wall via pores and enter the apoplast using the appressoria. The intracellular hyphae form complexes in rhizodermal and cork cells (Stefani et al, 2010; Lamarche et al, 2011). Both branched hyphae of the Hartig net and intracellular hyphae often contain Woronin bodies, remarkable for Ascomycota fungi. Fungal hyphae preserve their activity near the initials of side roots and colonize young roots while passing through bark (Stefani et al, 2010; Mattoo and Nonzom, 2021).

It is known that fungi, forming ectendomycorrhiza, can destroy complex carbohydrates, and the formed monosaccharides are transferred to young roots (Phillips, 2017). However, the degree of distribution of extraradical hyphae in soil has not been studied in detail, and there is no experimental evidence of their involvement in transporting nutrients to the roots.

The fungi *Wilcoxina mikolae* and *W. rehmsii* are capable of synthesizing siderophore ferricrocin (Yu et al, 2001; Peterson, 2012). Thus, there is an opinion that the formation of ectendomycorrhiza protects plants from the toxic effect of excessive iron concentrations. However, most issues regarding the ecological role of ectendomycorrhizal fungi are yet to be studied.

Ectomycorrhiza. The formation of ectomycorrhiza is accompanied by many morphological changes in both partners. A “case” of densely interwoven hyphae is formed around the root of the fungus, the system of hyphae in the cortex tissues is the Hartig net. As for the plant, many side roots are formed, and there is a reduction of root hairs which ensures tight contact between hyphae walls and plant cells (Smith and Read, 2008).

Some studies demonstrate the synthesis of hydrophobins (small size, moderate number of hydrophobic proteins, rich in cysteines). While accumulating in the cellular walls, hydrophobins supply them with hydrophobic properties required for various interactions (Ball et al, 2019).

It is known that hormones, including cytokinins and heteroauxin, make an impact on hyphae growth and branching. There are changes in the morphology of hyphae around the host plant root and their growth is enhanced. The ectomycorrhiza eucalyptus was found to have plant metabolites (flavonoid rutin and cytokinin, zeatin), which change the character of hyphae branching considerably (Gay and Debaud, 1987, Lagrange et al, 2001).

Under the effect of zeatin, there is a stimulated accumulation of metabolites in the hyphae of the fungus *Pisolithus microcarpus* (Beguiristain et al, 1995; Hill

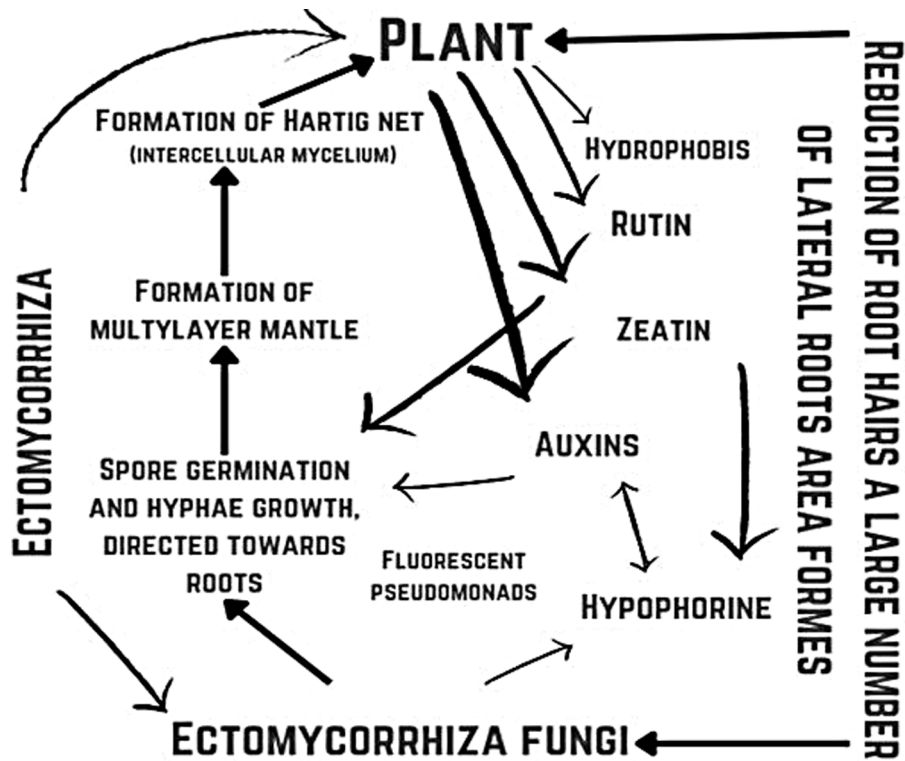


Fig. 2. The signalling interaction between macro- and microsymbionts on different stages of ectomycorrhiza formation

et al, 2021). One of them, hypaphorine (a tryptophan derivative) is formed by the fungus in large amounts during the ectomycorrhizal symbiosis development (Beguiristain and Lapeyrie, 1997). The antagonism between the endogenous indolyl-3-acetic acid of the plant and hypaphorine, excreted by the fungal partner, regulates the process of symbiosis formation (Ditengou et al, 2000).

The signalling interaction between macro- and microsymbionts on different stages of endomycorrhiza formation is schematically presented in **Figure 2**.

Most ectomycorrhizal symbionts are characterized by a limited ability to use oligosaccharides as growth substrates. However, the ability of fungi to the decomposition of cellulose and pectin may be related to their penetration into the plant root tissues, where the formation of enzymes should be localized and causes the softening of the cellular wall during the symbiosis formation (Lindeberg and Lindeberg, 1977; Drijber and McPherson, 2021).

Ectomycorrhiza is notable for the dependence between the activity of photosynthesis and the uptake of phosphorus to the plant. For instance, colonized plants absorb three times more phosphorus from the soil during the same period in the initial stages of plant vegetation. At the same time, in later stages of plant

development, the difference between P absorption in ectomycorrhizal and non-mycorrhizal plants is much less significant. Therefore, the benefit in the form of phosphorus uptake on the early stages of plant growth is maximal under minimal outlays required for the formation and maintenance of fungal structures (Jones et al, 1991; Moreira et al, 2022).

The transportation of phosphorus through the contact zone in ectomycorrhiza is regulated by the concentration of orthophosphate in the cytoplasm of the Hartig net and the intensity of its inflow into the interphase apoplast. A considerable dependence between phosphorus inflow to ectomycorrhiza and the transportation from the fungal symbiont to the plant was found. However, sometimes in mycorrhiza, formed by *Suillus bovinus*, the increased inflow of phosphorus to the roots of *Pinus sylvestris* did not affect the transportation of this element via ectomycorrhizal contact zone, and in case of mycorrhiza *Pisolithus tinctorius* we found the dependence on the number of absorbed substances. It should be noted that due to the formed ectomycorrhizal symbiosis, the degree of free mycelium development and the ability of some fungal species to absorb phosphorus from poorly soluble organic sources are higher as compared with the arbuscular mycorrhiza symbiosis. Also, the hyphae both get distributed beyond the

zone of nutrient depletion and continue developing further (George and Marschner, 1996; Kafle et al, 2019).

Most species of ectomycorrhizal fungi consume ammonium, nitrates, and some simple nitrogen-containing organic substances, which have their differences both on intraspecies and interspecies levels (Smith and Read, 2008). The molecular research using *Hebolema* spp. demonstrated that N-dependent expression of genes of nitrogen importers is regulated by the nitrogen content inside hyphae (Benjdia et al, 2006).

Ectomycorrhizal fungi are capable of ensuring the resistance of the macrosymbiont to drought, and moisture deficit causes serious changes in the colonization degree, the structure of fungal grouping, and their physiological activity (Bell and Adams, 2004; Kumar and Dubey, 2022).

In most vegetative aggregations, mycorrhiza fungi colonize many plants and may transfer nutrients between them. Only some plants benefit from endophytic symbiosis, which gets considerable competitive traits as a result (Harman and Uphoff, 2019).

Endophytic associations of fungi and plants. Saprophytic soil fungi are also capable of forming endophytic associations with plant roots. No formation of specific mycorrhizal structures was noted, yet the disease signs were absent too. Therefore, endophytes are microorganisms, inhibiting the internal environment of plants, at least at some stage of their life cycle, not exhibiting any harmful effects on the plant (van der Heijden et al, 2015; Kopilov et al, 2020; Kopylov et al, 2021; Peng et al, 2022).

Endophytic fungi colonize the tissues of leaves, stems, and roots of plants. The latter are often mistaken for mycorrhiza fungi, yet endophytes differ from mycorrhiza-forming fungi by their taxonomic position and specificities of functioning (Arnold and Lutzoni, 2007, Rodriguez and Redman, 2008; Lynch, 2014). Contrary to mycorrhiza-forming fungi, they do not form specific structures and can exist in the macrosymbiont organism for a long time, exhibiting their activity only under some conditions (Spatafora, 2007).

Most endophytic fungi belong to the division of Ascomycota, and some to the division of Basidiomycota (Rana et al, 2020 a). Many fungi, which belong to different genera, are mentioned as endophytes of most crops (Table) (Verma et al, 2017, Rana et al, 2020 b,c). There are only fragmentary data about the localization of endophytic microorganisms inside the plant roots: intercellular mycelium, mycelium in the major vessels

of secondary tissues, intercellular septate mycelium with some points of penetration into cells (Rana et al, 2019; Sujatha et al, 2020).

Endophytic fungi can stimulate plant growth actively or passively. Firstly, fungi can produce growth-regulating substances or induce the formation of phytohormones by plants, stimulating the accumulation of underground and aboveground biomass by the macrosymbiont. Secondly, the microsymbiont can increase the number of mineral nutrition elements (phosphorus, potassium, and zinc), which come to the plant (Yadav et al, 2022). In addition, the formation of the endophytic association activates the photosynthesis processes of the plant (Selim et al, 2012).

Endophytic fungi play a significant role in defensive processes, inducing the immune system of the macroorganism, as a result, the resistance of plants to phytopathogenic diseases increases, and the resistance to abiotic (drought, low temperatures, and salt stress) and biotic stress factors is formed (Verma, 2017).

In response to the phytopathogen effect, endophytic fungi use various mechanisms of plant protection: competition between the endophyte and pathogen on the same resources (exclusion of the competition niche); direct antagonism of pathogens via antibiosis, parasitism, or predation; changing hormonal levels of plants (auxins, gibberellins, abscisic acid, and ethylene); producing siderophores and ACC deaminase; supplying vitamins, necessary for plants (Bae et al, 2009).

The soil-saprotrophic fungus *C. cochliodes* 3250 can actively grow in root zone of such crops as wheat, barley, rye, triticale, corn, sunflower, soybeans and form fruit bodies on their roots. Also there is an increased activity of succinate dehydrogenase (SDH) in the roots of treated plants: wheat (by 1.2 times), barley (by 3.2 times), rye (by 3.5 times), triticale (3.4 times), corn (3.2 times), sunflower (1.6 times), soybeans (2.9 times) and buckwheat (1.5 times) (Kopylov et al, 2021).

C. cochliodes 3250 forms sporocarpson surface of root fibrils, penetrates directly into rhizodermis cells and forms endophytic association with common buckwheat, having an influence upon plants. It has been discovered that pre-sowing treatment of buckwheat by *C. cochliodes* 3250 activates the basic physiological responses of plants typical for the formation of symbiosis: growth of the total (by 145 %) and active working (by 7 %) root surfaces; increased plants length (by 27 %), increased leaf area (by 11 %) and chloro-

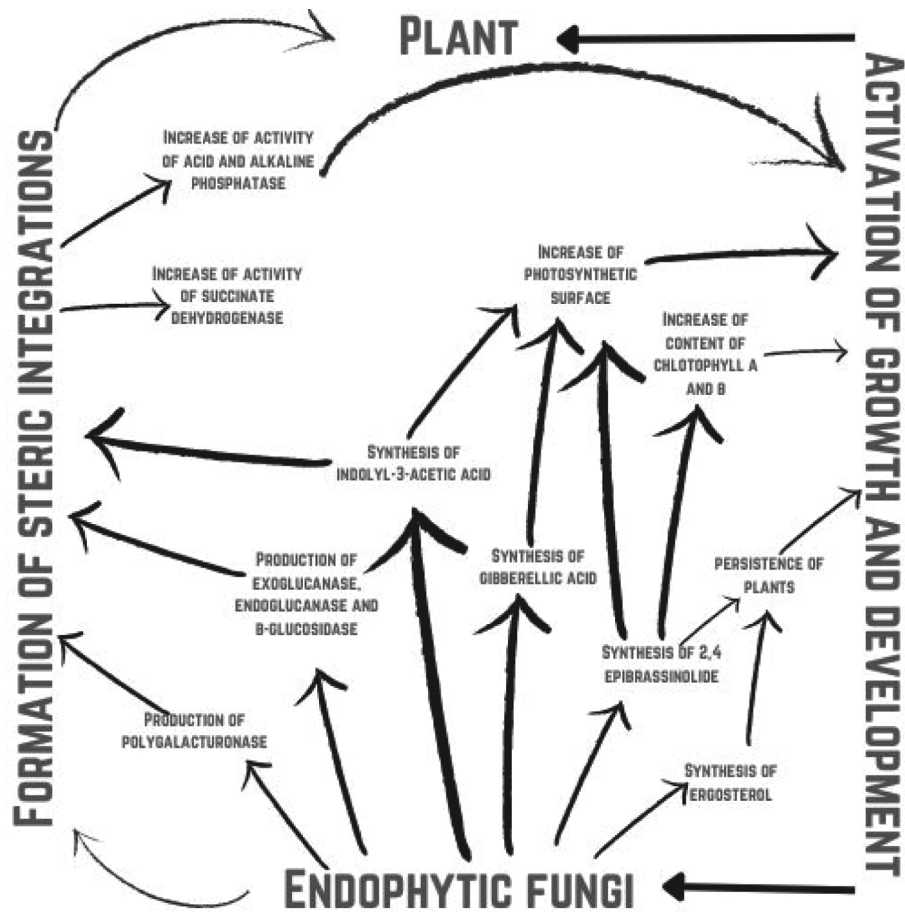


Fig. 3. The functional relationship between micro- and macrosymbionts of the endophytic association between endophytic fungi and plants

phyll a and b content increase (by 17 %). That fungus increases the activity of acid (326 %) and alkaline (391 %) phosphatase in the roots of buckwheat during the entire vegetation period meaning the formed symbiosis is effective (Kopilov et al, 2020).

C. cochliodes 3250 can produce 2,4-epibrassinolide (45.71 µg/g of dry weight and 0.011 µg/ml of culture liquid), being crucial for plants' resistance to pathogens, and ergosterol (17.88 µg/ml of culture liquid). Beyond that, the fungus can synthesize phytohormonal substances: indolyl-3-acetic acid (24.6 µg/g of dry weight, 8.7 µg/ml of culture liquid) and gibberellic acid (301.5 µg/g of dry weight, 56.4 µg/ml of culture liquid). Synthesized indolyl-3-acetic acid and ergosterol synthesized can serve as the main mediator molecules in the process of formation of *C. cochliodes* 3250 symbiotic systems with plants (Dragovoz et al, 2017). Exogluconase activity in the fungus culture liquid was 0.67 units/ml on the 9th day of cultivation, meaning that *C. cochliodes* 3250 can degrade the cellulose crystalline state. Endogluconases ensure hydrolysis of

amorphous cellulose to cellobiose (exogluconase activity of *C. cochliodes* 3250 was 0.52 units/ml on the 9th day). β-glucosidase completes the breakdown of cellulose and provides hydrolysis of cellobiose to glucose (β-glucosidase activity of *C. cochliodes* 3250 was 1.02 unit/ml in the 12th day). Polygalacturonic activity of the culture liquid of *C. cochliodes* 3250 predetermines the process of depolymerization of the adherent layer of pectin between the adjacent walls of plant cells. The highest polygalacturonase activity was recorded on the 9th day of cultivation of micromycete and was 2.95 units/ml. (Yovenko, 2016).

When used seeds pre-sowing treatment this fungus by *C. cochliodes* 3250 it was found in buckwheat rhizosphere, rhizoplane, and histosphere. It means that the fungus can do well in the culture zone of crops (Kopylov et al, 2021). Micromycetes in the buckwheat rhizosphere increased the number of diazotrophs of *Azospirillum* and *Azotobacter*; the number of all studied ecologically trophic groups of diazotrophs in the rhizoplane, improving the activity of fixation of mole-

cular nitrogen in the rhizosphere (1.3 times) and in the rhizoplane (11.3 times) (Kopylov and Yovenko, 2016).

The field study has found that pre-sowing treatment of buckwheat seed by *C. cochliodes* 3250 initiated plant growth. The photosynthetic surface area of plants treated by fungus increased by 28.6 % if compared to the control group. A more effective photosynthetic device improved the plant tops. The field study has found that in the case of pre-sowing treatment of buckwheat seed by the fungus the blooming period starts 5–7 days earlier. It has been recorded that plant leaves have the highest content of photosynthetic when approaching reproductive development. *C. cochliodes* 3250 increases the content of chlorophyll a by 17.9 % and chlorophyll b by 21.5 % during blooming period of plants (Kyslynska, 2017). If we talk about formation of the effective associative system: *C. cochliodes* 3250 – the content of phosphorus in vegetative organs of buckwheat plants increased by 13.9 %, improved the similarity and consistency of plants, increased the number of inflorescences and grains, and improved plant growth (Kopylov et al, 2020). Based on the three-year field studies it has been found that the increase of yield in the case of pre-sowing inoculation by *C. cochliodes* 3250 it is 22.0 % (Kyslynska, Khalep, 2019).

The details of endophytic interaction on the example of endophytic saprotrophic fungus with plants are presented in **Figure 3**.

It was found that the application of endophytic fungi in agriculture plays an important role in preserving the biodiversity of the aggregations, the decrease in the degree of soil degradation, which is caused by excessive use of insecticides (Bae et al, 2009, Guo et al, 2008). Thus, the mutual association of plants and fungi is formed in a wide range of terrestrial media and plays an important role in mineral nutrition and resistance of plants to abiotic and biotic stress factors. A micromycete affects a plant, improving the growth and development of the macroorganism, which demonstrates the formation of effective endophytic association (Eid et al, 2019; Durairajan et al, 2020; Gupta et al, 2022). The main integral efficiency index for the impact of endophytic fungi is an increase in the yield (Gupta et al, 2020; Elango et al, 2020; Sible et al, 2021; Attia et al, 2022).

CONCLUSIONS

A high number of mutualistic interaction types was formed due to the mutual co-evolution of micro- and macropartners. Depending on the colonization type and interaction role, the association between plants and microorganisms is classified into such types: mycorrhizal,

pathogenic, epiphytial, saprotrophic, and endophytic. Mycorrhiza-forming fungi and endophytic microorganisms are capable of penetrating internal tissues, forming associative systems with macroorganisms, and have a positive effect on plants. The endophytic association is a balanced dynamic system between the virulence of the micropartner and the defensive factors of the macropartner. When this balance is disrupted, some endophytic species may change their ecologic strategies into pathogenic or saprotrophic ones. This is exactly why the mutualistic symbiosis between a plant and a fungus should be considered only as a dynamic equilibrium between these organisms.

Within one type of endophytic microorganisms, both specific (forming associative systems with only one species or variety of plants) and general (capable of forming symbiotic relationships with a wide range of macropartners) are distinguished. Similar selectivity is found for macrosymbionts. The character of mutualistic symbiosis is considerably affected by genetic factors in the organism of each partner, characterized by considerable variability, and manifests different effects in the symbiotic system functioning. Thus, the type of interaction depends on both partners; it may fluctuate from mutualistic to antagonistic, and in some cases, parasitic interactions, demonstrating different stages of mutualism evolution and co-evolution of plants and fungi.

Usually, the specificities of the interaction between endophytic fungi and plants are compared with mycorrhizal fungi, sometimes with rhizosphere bacteria, stimulating plant growth (PGP). However, endophytic microorganisms deserve special attention of researchers due to their considerable role in stimulating the growth and survivability of plants in stress conditions. The main advantage of endophytes, among other biocontrol agents, is their ability to colonize the internal tissues of plants.

Only a deep understanding of the formation mechanism for endophytic associations with plants will facilitate their maximal efficient application in agriculture, which is most relevant for the improvement of plant growth and enhancing the yield of crops.

Considering the above, it is relevant to study and compare the mechanisms of interaction of classical mycorrhizal fungi and endophytic fungi with plants. In addition, the search for endophytic saprotrophic fungi, which are able to penetrate the roots of plants, form endophytic associations and have a positive effect on the macropartner.

Взаємозв'язки між формуванням мікоризи та ендоефітних рослинно-грибних асоціацій, їхній вплив на рослини

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Мета. Огляд літератури для встановлення механізмів основних мутуалістичних взаємодій, важливих для потенційного застосування симбіотичних грибів як біодобрих, біопротекторів і біорегуляторів, з метою екологізації сільського господарства, відновлення родючості ґрунтів та розуміння ролі мікосимбіонтів у природних екосистемах. **Методи.** Порівняльний аналіз наукової літератури. **Результати.** Мікоризація коренів є потужним фактором інтенсифікації росту рослин, активації метаболічних процесів і покращення розвитку макроорганізму. Формування мікоризи притаманне більшою мірою покритонасінним і голонасінним, однак у багатьох представників мохоподібних, папоротей та плаунів також виявлено тісні симбіотичні зв'язки з грибами. Гриби, що утворюють мікоризу, відносяться до відділів Glomeromycota, Ascomycota та Basidiomycota. Залежно від грибних структур та особливостей розміщення мікосимбіонтів у тканинах або клітинах макроорганізму розрізняють арбускулярну мікоризу, ерикоїдну, арбутоїдну мікоризу, монотрофодну мікоризу, мікоризу орхідних, ектендомікоризу, ектомікоризу. Сигнальна взаємодія між партнерами та механізм двонаправленого обміну поживними речовинами або інша взаємовигода охарактеризовані в даній оглядовій статті. **Висновки.** Мікроскопічні сапротрофні гриби, здатні проникати в коріння рослин і відігравати важливу роль у пристосуванні рослин до абіотичних і біотичних стресорів, представляють особливий інтерес у мутуалістичних симбіозах. Крім того, утворюючи з рослинами мутуалістичний симбіоз, сапротрофні гриби сприяють збільшенню біомаси та посиленню харчових властивостей рослин. Тип взаємодії залежить як від мікро-, так і від макросимбіота; у деяких випадках і для деяких організмів він може коливатися від мутуалістичних, коменсалістських до антагоністичних, навіть паразитичних взаємодій, демонструючи різні етапи еволюції мутуалізму та спільного проживання та/або еволюції

рослин і грибів. Краще розуміння різноманітних ролей симбіотичних мікроорганізмів в екосистемах покращить способи їх застосування в сільському господарстві.

Ключові слова: двонаправлений симбіоз, мікориза, ендоефіт, сигнальна взаємодія, метаболіти.

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