

Mycorrhiza as a biotic factor, influencing the ecosystem stability

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The essence of mycorrhiza as an example of partnership between fungus and plant was considered in the article. The main characteristics of mycorrhiza from the viewpoint of fungus and plant were investigated, which demonstrate mutual benefits for all the participants. The characteristics of mycorrhizal associations through the classification of their types were given. The peculiarities of the associations were determined. The results of field survey as to the location of mycorrhizal associations in natural ecosystems were analyzed. The results confirm the important role of mycorrhizal associations. Modern directions of using mycorrhiza in the economic activities were presented. The advantages of mycorrhiza for plants and fungi were defined and worked out in detail, which enabled to formulate the results of using mycorrhiza in the ecological, social, and economic space.

Key words: mycorrhiza; mycorrhizal association; ecosystem; eco-socio-economic development; partnership

Introduction

At present the population of the world has the tendency to growing, which stipulates the necessity of increasing the volumes of agricultural production under the limited natural conditions. As it is well known, the areas of farmland, suitable for agriculture are not only limited, but also have the dynamics of decreasing because of not responsible attitude of producers to it. In fact, the intensification of agriculture leads to decreasing soil fertility, bio-diversity, and the negative impact on the natural environment. Besides, applying large amounts of mineral fertilizers and raising the level of pesticides led to increasing the acidity and degradation of soils. Such soil conditions are unfavorable for the development of microbial activeness, which is important for agricultural production.

Under favorable conditions, plants and certain microorganisms become interrelated, and these relations, called symbiosis, are useful for all the participants. There are several forms of symbiosis among plants and microorganisms. The most well-known examples of symbiosis are the following: mycorrhizal fungi – plant, bacteria – plants, and actinomycetes – plants. The symbiosis among mycorrhizal fungi and plants is the most widely spread form of symbiosis appearing among plants.

Results

The word “mycorrhiza” is of Latin origin and, first of all, it means the process or association between the root system of fungus and plant. The analysis of the literature during the last decades shows, that the symbioses of fungi and plants and as a result, the formation of mycorrhiza are widely spread and cover on the average 85% of vascular plants on the Earth.

In its modern meaning, mycorrhiza is the association between the plant roots and fungi structurally formed according to the type of mutualistic symbiosis; these organisms exist in mutually dependent and favorable relations in such association (Robertson, Robertson, 1982).

The investigations confirm, that the development of symbiosis between fungi and plants is a complex, many stage process, which includes recognizing, transmitting the signal, interacting between fungus and plant. The formation of mycorrhiza is mutually favorable both for the fungus and plant. Nevertheless, plants can grow and develop without mycorrhizal fungi, while fungi spores are capable only to limited germination and hyphae growth without plants. This proves the fact, that plant signals play the leading role in symbiosis initiation. During the recent years, the research of the signal interaction during mycorrhiza formation has been paid much attention to, but it was impossible to establish completely the nature of plant signals, participating in certain stages of mycorrhiza formation (Robertson, Robertson, 1982).

The phenomenon of mycorrhiza (the symbiotic co-existence of definite kinds of fungi and higher plants) was described by the Polish biologist F.M. Kamenskyi in 1879-1881 (Castellano, Trappe, 1985). For the first time, the term “mycorrhiza” was used by the German biologist A.B. Frank in 1885 for non-pathogenic symbiotic associations between roots and fungi (Bidartondo et al., 2000).

Thus, mycorrhiza represents a symbiotic association, which is necessary for one or both partners, between a fungus (specialized for the life in soils and plants) and the root (or other organ, contacting the substrate) of a living plant, which, first of all, is

responsible for transmitting nutrients (Table 1). Mycorrhizas are found in a special plant organ, where the personal contact takes place owing to the synchronic development of plant fungus.

Table 1. The main characteristics of mycorrhiza

Fungus	Symbiosis	Plant
Is spread in soil	Personal contact between hyphae and plant cells in the structure where the exchange of nutrients takes place	Plants control the mycorrhiza intensity owing to the root growth, digesting old hyphae in plant cells (AM, orchid) or the changed form of root system (ECM)
Is spread in the roots of host plants	Are necessary for one or both partners: the transmitting of mineral substances from fungi to plants; the transferring of metabolites from the plant to fungus	Roots evolved as the environment for mycorrhizal fungi existence
Specialized hyphae (differ from the hyphae, specializing on growing in soil)	Synchronized development of plant fungus, as hyphae only colonize young roots (except orchid mycorrhizas and operational VAM)	Mycorrhiza is usually found in the root, but in some cases, it can be located in stems (for example, some orchids)

Notes: VAM – vesicular-arbuscular mycorrhiza; AM – arbuscular mycorrhiza; ECM – ecto-mycorrhiza.

The source: the author's development

According to our research, to classify mycorrhiza types, the sequential characteristics of their associations are necessary. Such characteristics were fully made by M.C. Brundrett, and they are presented in Table 2.

Table 2. Hierarchical classification scheme for mycorrhizal associations

Category	Definition	Hosts	Fungi
1. Arbuscular mycorrhizas	Associations formed by Glomeromycotan fungi in plants that usually have arbuscules and often have vesicles (also known as vesicular-arbuscular mycorrhizas, AM, VAM)	Plants	Glomeromycota
1.1. Linear VAM	Associations that spread predominantly by longitudinal intercellular hyphae in roots (formerly known as Arum series VAM)	Plants	Glomeromycota
1.2. Coiling VAM	Associations that spread predominantly by intracellular hyphal coils within roots (formerly known as Paris series VAM)	Plants	Glomeromycota
1.2.1. Beaded VAM	Coiling VAM in roots, where interrupted root growth results in short segments divided by constrictions	Woody plants	Glomeromycota
1.2.2. Inner cortex VAM	Coiling VAM with arbuscules in one layer of cells of the root inner cortex	Plants	Glomeromycota
1.2.3. Exploitative VAM	Coiling VAM of myco-heterotrophic plants, usually without arbuscules	Achlorophyllous plants	Glomeromycota
2. Ecto-mycorrhiza (ECM)	Associations with a hyphal mantle enclosing short lateral roots and a Hartig net of labyrinthine hyphae that penetrate between root cells		Higher fungi (asco-, basidio- and zygomycetes)
2.1. Cortical	Hartig net hyphae penetrate between multiple cortex cell layers of short roots	Most are gymnosperm trees	Higher fungi
2.2. Epidermal	Hartig net fungal hyphae are confined to epidermal cells of short roots	Angiosperms (most are trees)	Higher fungi
2.2.1. Transfer cell	Epidermal Hartig net with transfer cells (plant cells with wall ingrowths)	<i>Pisonia</i> (Nyctaginaceae). See Peterson et al. 2004 for others	<i>Tomentella</i> spp. in <i>Pisonia</i> (Chambers et al. 2005)
2.2.2. Monotropoid	Exploitative epidermal ECM of myco-heterotrophic plants in the Ericaceae where individual hyphae penetrate epidermal cells	Ericaceae (Monotropa, Pterospora, Sarcodes)	Basidiomycetes
2.2.3. Arbutoid	ECM of autotrophic plants in the Ericaceae where multiple hyphae penetrate epidermal Hartig net cells	Ericaceae (part only)	Basidiomycetes

3. Orchid	Associations where coils of hyphae (pelotons) penetrate within cells in the plant family Orchidaceae		Most are basidiomycetes in <i>Rhizoctonia</i> alliance
3.1. Orchid Root	Associations within a root cortex	Orchidaceae	
3.2. Orchid Stem	Associations within a stem or rhizome	Orchidaceae	
3.3. Exploitative Orchids	Associations of myco-heterotrophic orchids	Orchidaceae (fully or partially achlorophyllous)	Orchid, ectomycorrhizal, or saprophytic fungi
4. Ericoid	Coils of hyphae within very thin roots (hair roots) of the Ericaceae	Ericaceae (most genera)	Most are Ascomycetes
5. Sub-epidermal	Hyphae in cavities under epidermal cells, only known from an Australian monocot genus	<i>Thysanotus</i> spp. (Laxmaniaceae)	Unknown

Let us consider in more detail the types of mycorrhizal associations, given in Table 2. It will enable us to determine their role in natural eco-systems.

Arbuscular mycorrhizas (Vesicular-Arbuscular Mycorrhizas, VAM or AM) are associations where Glomeromycete fungi produce arbuscules, hyphae, and vesicles within root cortex cells. These associations are defined by the presence of arbuscules. Fungi in roots spread by linear hyphae or coiled hyphae (Figure 1).

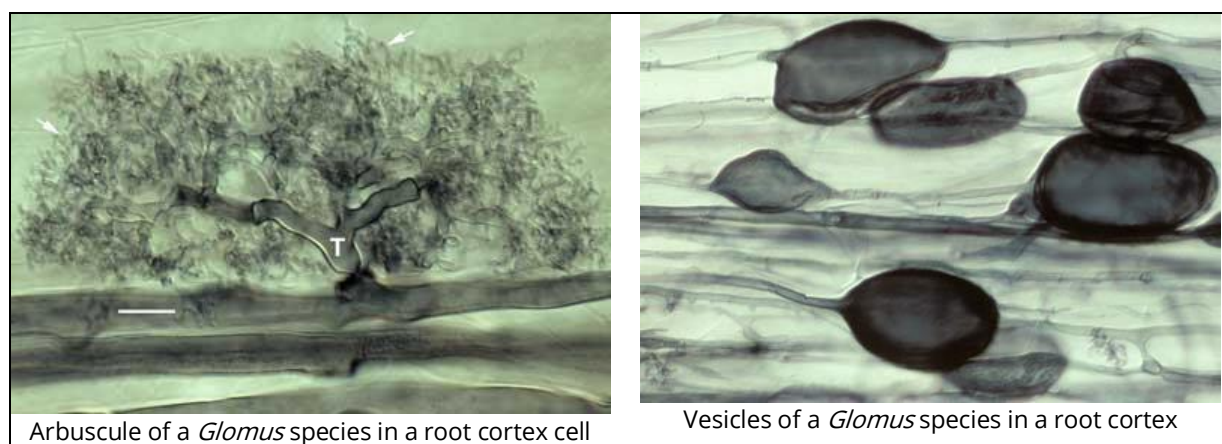


Figure 1. Arbuscular Mycorrhizas (<https://mycorrhizas.info>)

Ectomycorrhizas (ECM) are associations where fungi form a mantle around roots and a Hartig net between root cells. These associations are defined by Hartig net hyphae which grow around cells in the epidermis or cortex of short swollen lateral roots (Figure 2). The former category of ECM is a morphotype (defined by fungi not hosts). Characteristics of this ECM morphotype are summarized by Yu et al. (2001).

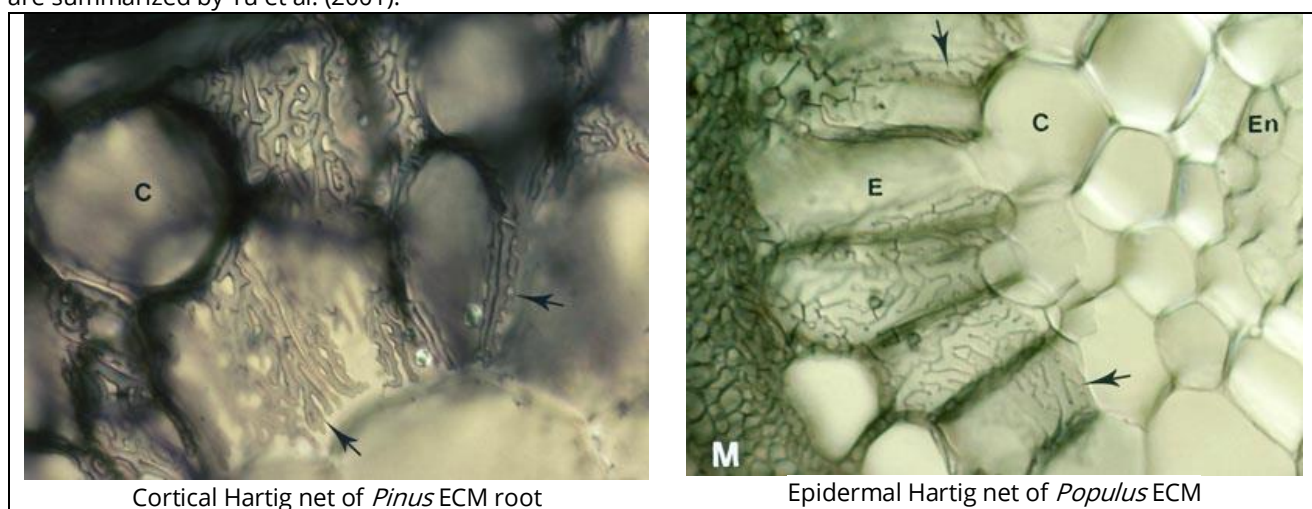


Figure 2. Ectomycorrhizas (<https://mycorrhizas.info>)

Monotropoid mycorrhizas are ECM associations of a few genera of myco-heterotrophic plants in the Ericaceae. These associations are characterised by limited hyphal penetration into epidermal cells (Figure 3). Information on structure of associations and the identity of mycorrhizal fungi in Monotropa, Pterospira, Sarcodes, etc. is provided by Robertson & Robertson (1982), Castellano & Trappe (1985) and Bidartondo et al. (2000).

Arbutoid mycorrhizal associations are variants of ECM found in certain plants in the Ericaceae characterised by hyphal coils in epidermal cells (Figure 4). These mycorrhizal roots are described by Largent et al. (1980), Molina et al. (1992) and Massicotte et al. (1987). *Gaultheria* and *Kalmia* have ericoid mycorrhizas as well as arbutoid associations (Massicotte et al., 2005).

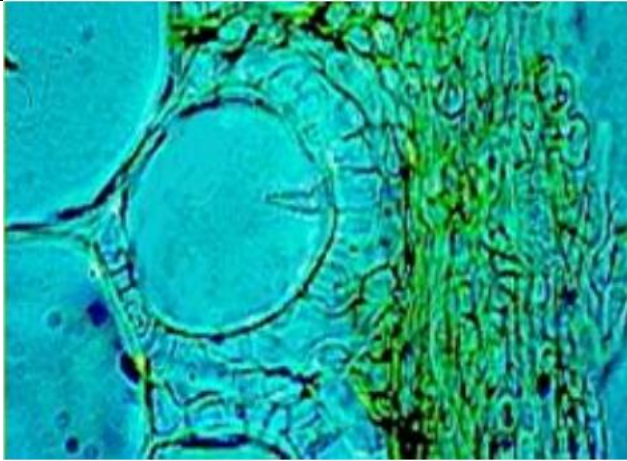


Figure 3. Monotropoid mycorrhizas (<http://www.davidmoore.org.uk/>)

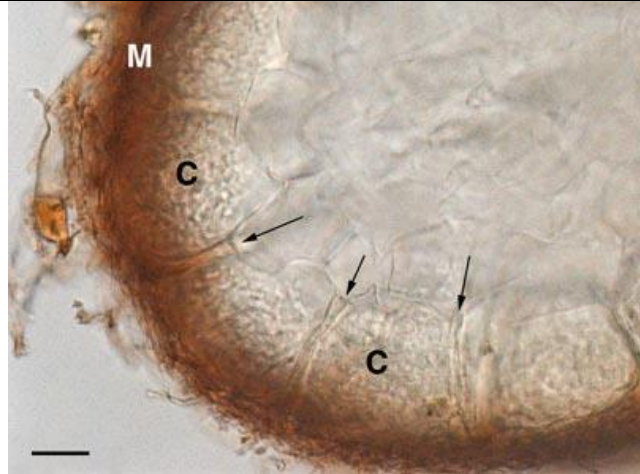
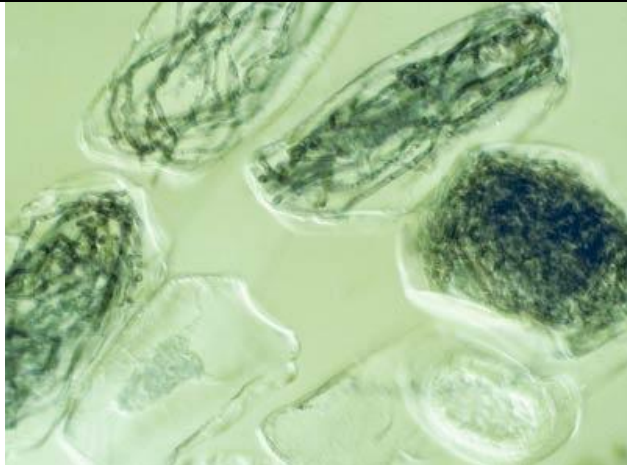
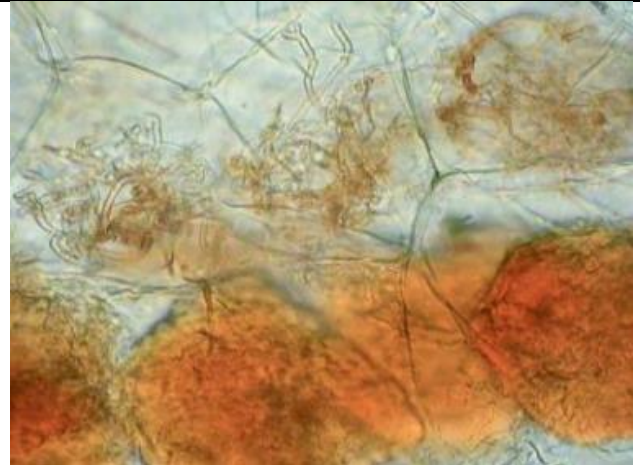


Figure 4. *Arbutus unedo* root with Hartig net (arrows), coils (C) and mantle (M) of stained or unstained hyphae (<https://mycorrhizas.info/>)

Orchid mycorrhizas consist of coils of hyphae within roots or stems of orchidaceous plants (Figure 5). Details of Orchid mycorrhizal associations are not provided here, but Australian Orchids found to have mycorrhizas are listed.



Hyphal coils from orchid mycorrhizas in *Epipactis helleborine* root



Seedlings of *Rhizanthella gardneri* germinated by a mycorrhizal fungus linked to ECM roots of a shrub (*Melaleuca* sp.)

Figure 5. Orchid mycorrhizas (<https://mycorrhizas.info/>)

Ericoid mycorrhizas have hyphal coils in outer cells of the narrow "hair roots" of plants in the family Ericaceae (Figure 6). These associations are not described in detail here, but Australian plants with these mycorrhizas are listed.

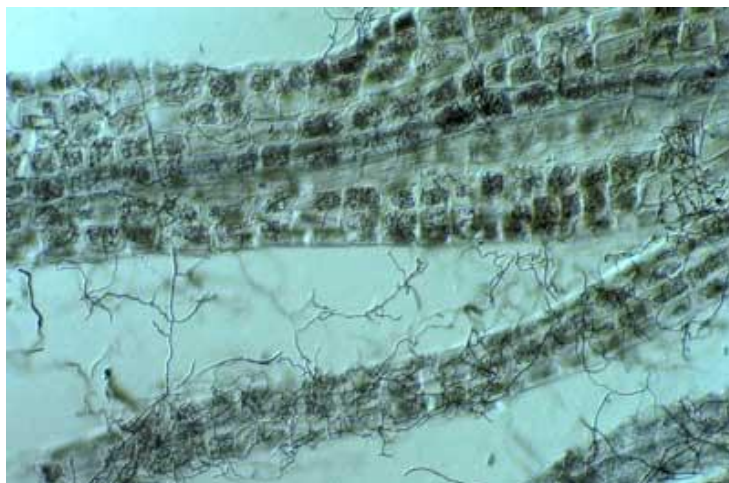


Figure 6. Ericoid mycorrhizas with hyphal coils in hair roots of *Leucopogon verticillatus* (<https://mycorrhizas.info/>)

Field surveys have found that plants with mycorrhizal associations predominate in most natural ecosystems, as summarized in the table below (Table 3).

Table 3. Plants with mycorrhizal associations

Association	Occurrence
Vesicular Arbuscular Mycorrhizal (VAM) Plants	1. Plants with VAM are common in most habitats. 2. It is easier to say where they are not found.
Ectomycorrhizal (ECM) Plants	1. Trees with ECM are dominant in coniferous forests, especially in cold boreal or alpine regions. 2. ECM trees and shrubs common in many broad-leaved forests in temperate or Mediterranean regions. 3. ECM trees also occur in some tropical or subtropical savanna or rain forests habitats.
Nonmycorrhizal (NM) Plants	1. NM plants are most common in disturbed habitats, or sites with extreme environmental or soil conditions. 2. NM plants appear to be more common in Australia than in other continents.

Source: data are from (Brundrett, Abbott, 1991)

Members of the fungus kingdom obtain nutrition from many sources, including decomposition of organic substrates, predation and parasitism, and involvement in mutualistic associations (Kendrick, 1992; Christensen, 1989). Mycorrhizal fungi are a major component of the soil microflora in many ecosystems, but usually have limited saprophytic abilities (Tanesaka et al., 1993; Hobbie et al., 2001). They are considered to have many important roles in natural and managed ecosystems. These fungi are introduced in the Table 4.

Table 4. Mycorrhizal Fungi

Mycorrhiza	Phylum	Families	Anamorphs	Teliomorphs
Arbuscular	Glomeromycota	Glomaceae, Acaulosporaceae, etc.	<i>Glomus</i> , <i>Scutellospora</i> , <i>Acaulospora</i> , etc.	none
Ecto-mycorrhiza (ECM)	Basidiomycota, Ascomycota, Zygomycota	Many families including Amanitaceae, Cortinariaceae, Boletaceae, etc.	Most ECM fungi lack anamorphs, but <i>Cenococcum</i> one example	Many genera including <i>Amanita</i> , <i>Cortinarius</i> , <i>Russula</i> , etc.
Monotropoid ECM	Basidiomycota	Russulaceae, etc.	NA	<i>Russula</i> , <i>Tricholoma</i> , <i>Rhizopogon</i> , etc.
Orchid: not myco-heterotrophic	Basidiomycota (Ascomycete)	<i>Ceratobasidiaceae</i> , <i>Tulasnellaceae</i> , <i>Sebacinaceae</i> (related to Chanterellaceae?) (also many others are reported)	Sterile hyphae: <i>Rhizoctonia</i> alliance: <i>E pulorhiza</i> , <i>Ceratorhiza</i> , <i>Tulasnella</i> , etc. as well as <i>Fusarium</i> , etc.	<i>Ceratobasidium</i> , <i>Thanatophorus</i> , <i>Sebacina</i> , etc.
Orchid: myco-heterotrophic	Basidiomycota	Russulaceae, Telephoraceae, etc.	NA	unrelated clades of ECM, orchid and saprophytic fungi
Ericoid	Ascomycota (Basidiomycota)	Helotiaceae (Sebacinaceae)	NA	<i>Hymenoscyphus</i> , <i>Rhizoscyphus</i> , (<i>Sebacina</i>)

Source: data are from (<https://mycorrhizas.info/>)

Nevertheless, it is necessary to take into account several very important moments at the initial stage for the mycorrhizal partnership to take place:

1. The presence of moisture in the root zone.

The soil temperature not lower than 18 °C.

2. The presence in the soil of soluble phosphates not more than 8%.

3. Soil pH not lower than 5.3.

4. The protection of the fungal preparation or treated plants (planting material) from active ultra-violet irradiation, because ultra-violet rays negatively affect the spores.

After the fungus becomes active owing to the release from the root system and contacts it, the fungus becomes practically invulnerable, and the only condition for its development is the presence of actively functioning root system of the partner. Thus, it should be mentioned, that mycorrhiza plays a considerable role in eco-systems (Table 5):

Table 5. The results of mycorrhizal partnership of plants with fungi

Object	The results of using mycorrhiza
Plants:	
1. Nutrition	1) increasing the area of plant root system contacting with soil by 10-50 times; 2) apart from synthesizing and supplying nutrients (the conversion of non-soluble, difficult for access compounds of phosphorus and other nutrients into the form easy for taking up) mycorrhiza contributes to the dosed plant nutrition; 3) biologically active substances, produced by the fungus are also used by plants together with the nutrients from the soil; 4) owing to mycorrhization, plants are treated as the symbionts of other microorganisms, inhabiting in the soil (for example, nodule bacteria); 5) the reception of amino-sugars is present in plants under the influence of arbuscular mycorrhiza; 6) the utilization of root exudates takes place; 7) the release of biologically active wastes is improved; 8) the selective action on rhizosphere microorganisms is executed; 9) the mechanical protection of root system is provided (case in ectomycorrhizal); 10) stimulating plant to protective substances synthesis.
2. Development	1) the concentration of phyto-hormones considerably increases, which leads to the activization of plant growth; 2) the plants develop more quickly, form more flowers in the primordium, which results in harvest increase; 3) the inhibiting of competing plants, not participating in mycorrhizal association takes place.
3. Resistance against unfavorable conditions and diseases	1) plants endure unfavorable natural conditions - drought, frosts, abundant rainfall easier; 2) forming mycorrhiza with the root of the host plant, the fungus protects it from diseases, such as phytophthora, fusariose; 3) owing to the ability to split inorganic and organic compounds, the fungus clears the living space of the plant from salinization or leaching; 4) the roots with mycorrhiza are resistant against the impact of soil pathogens. The fungus induces the synthesis of protective phenols-flavonides in plant cells; 5) mycorrhization contributes to creating additional mycorrhizal associations with nodule and other soil bacteria, other fungi-symbionts and other plants, which grow in the zone of the system functioning. This system was named the unified mycorrhizal network – CMN. The CMN distributes carbon inside the eco-system, conducts nutrition and redistribution of nitrogen, phosphorus, and water among plants-partners, strengthens transpiration and increases drought resistance; 6) mycorrhized plants become more resistant against drought, because fungi are adapted to lower values of free moisture in the environment, than plants, and owing the developed mycelium they are able to absorb moisture from deeper soil layers and also from micro-particles, where the root system itself cannot penetrate; 7) mycorrhized plants are more resistant against the raised level of heavy metals in the soil.
Soil:	
1. Aggregate state	1) making the soil fluffy, forming a lot of hollows and niches, which make the soil air absorbing and moisture-retentive; 2) the network of roots and hyphae permeate the aggregates, assisting in accumulating glycoprotein-glomatin in the soil, 60% of which consists of carbon. Glomatin presupposes agglutinating the soil crumbs and raises their hydrophobia (water-repellent qualities); 3) releasing glomalin in the soil (the substance performing the function of glue and agglutinating the finest soil particles into bigger ones and then agglutinating the bigger particles together), which structurizes the soil.
2. Fertility	1) hyphae – is the environment, rich in organic substance for the development of soil fauna, the vital activities of which also enrich the soil with organic matter and raise soil fertility; 2) mycorrhizal fungi contribute to preserving carbon in the soil by changing the quality of soil organic substance; 3) mycorrhizas influence soil microbial populations; 4) hyphae in the soil play an important role in passing nutrients, helping to avoid losses, particularly in cases, when roots are not active.
3. Fungi	1) supplying the products of assimilation; 2) providing with organic substances after plant dies; 3) supporting the water balance of fungus during dry period.

The source: the author's research

1. The plant-partner obtains selective advantages in competitive struggle:

- inhibiting the development of non-partner kinds;
- lowering the intra-species competition owing to the redistribution of substances;
- raising the viability and easier metabolism.

2. The integral role of mycorrhizas:

- redistribution of nutrients: from one species to others; from died plants to living; from grown plants to plantlets.

3. Lowering the competition among the plants and raising the community stability.

4. Renovating the balanced plant groups, which improve land reclamation and nature protection.

At present, mycorrhiza is mainly used for:

1. Individual plots of land – growing ecologically safe agricultural products for personal needs and selling the surplus to the population, creating or renovating high soil fertility.
 2. Farms – cultivating grain crops, vegetables, and legumes. Using mycorrhiza enables to decrease the amount of watering and receive ecologically safe products, the price of which on the market is higher, than of ordinary products.
 3. Hydroponics – mycorrhiza increases the area of plant root nutrition by hundreds of times, grown by hydroponics method.
 4. Domestic and professional floriculture – using mycorrhiza for looking after tender, exotic, and rare plants.
 5. Farms for producing transplants – receiving plant material with well developed, proliferative root system, without using chemicals.
 6. Young orchards – for taking away stress after replanting on the permanent place, decreasing the period of transplants' adaptation, quicker growth, and increment.
 7. Glasshouses – growing vegetables or flowers for selling.
 8. Landscape design – creating closed eco-system on the territory of the client, which is based on the creation of favorable conditions for plants (correct nutrition and protection against diseases) together with simultaneous soil fertility restoration.
- Thus, the peculiarities of mycorrhizas, given above, the influence of mycorrhizal partnership on the soil and plants, and the directions of using enable us to consider the results of using mycorrhiza for the general ecological, social, and economic space (Table 6), taking into the account the experience of its using in many spheres of activities.

Table 6. The results of using mycorrhiza for ecological, social, and economic space

Direction	The results of using mycorrhiza
Ecology	1) restoring balanced plant groupings, which contributes to land reclamation and nature protection; 2) forest restoration, fight against withering, receiving high quality transplants; 3) strengthening of dams and fortification constructions; 4) restoration of polluted territories in places of ecological disasters; 5) restoration of agricultural lands; 6) rejuvenating of fruit trees and bushes; 7) decreasing or complete refusing from the use of chemical means for plant protection and chemical fertilizers; 8) receiving ecologically safe products; 9) fungal variety is a bio-indicator of the environment quality; 10) fungi, adapted to the local soil conditions, are necessary for agriculture, horticulture and forestry.
Society	1) decreasing the negative impact of chemical means for plant protection and fertilizers on all the participants of the process of cultivating, harvesting, and processing products; 2) raising the quality of food products, affecting the absorption of micro-elements and polluting substances; 3) decreasing the level of the population diseases; 4) these fungi are used as medicines and natural dyes; 5) beautifying of squares, lawns, flower-beds, parks, football fields, sports grounds, etc.
Economics	1) decreasing financial spending on the system of plant protection and fertilizers; 2) increasing yields; 3) the cost of ecologically safe products is higher; 4) spreading the markets of selling both in the country and abroad; 5) raising the profitability of producer's activities; 6) raising the image of producer.

The source: the author's research.

Conclusions

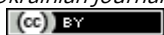
Thus, mycorrhiza formation is a mutually beneficial process both for the plant and fungus. Moreover, fungi get the access to the products of plant photosynthesis, in their turn, fungal hyphae proliferate in the soil, which enables a mycorrhized plant to increase the volume of soil, accessible to it. The plant on the roots of which mycorrhiza appeared, are more adaptable to the environment, they are more protected against unfavorable ecological conditions, including drought, low temperatures, salinity, soil pollution, and wind. Besides, the symbiosis of mycorrhiza forming fungi and plants contributes to plant resistance against pathogens and diseases. Thus, further studying of the structure and functions of mycorrhiza will enable to use the received knowledge not only in agriculture and forestry, but also in various spheres of human activities.

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