Applications of Mycorrhizal Symbiosis to the Ecosystem

Subjects: Microbiology

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Mycorrhizal fungi exhibit the exceptional feature of dwelling partly inside as well as outside the plant roots. The term mycorrhizae comes from the Greek word 'mykes' and 'rhiza', meaning 'fungus' and 'root' respectively, which was first applied to the association of trees with fungal symbionts. Mycorrhizal fungi, which are members of Glomeromycota, are common on the landscape and associate with over 80% of plants in a diversity of managed (agricultural) and unmanaged (natural) ecosystems. Mycorrhization benefits plants by up-regulating the catalytic activities of soil enzymes (such as phosphatases, dehydrogenase, nitrogenase, etc.), assisting in the breakdown of complex organic compounds of soil, and positively influencing other microbes present in the rhizosphere for improved nutrients uptake. Activation of these mechanisms, in turn, provides the ability to withstand drought stress, alleviate salinity, helps with micronutrient absorption and better water absorption, and defense systems in the plants. Owing to these benefits, mycorrhizae have gained a lot of consideration towards multidisciplinary research and have huge applications in agriculture as bio-fertilizers, in fuel production due to the increased plant biomass, and in soil rehabilitation, phytoextraction, and phytoremediation, etc.

Keywords: ecosystems. ; Mycorrhizae ; soil

1. Positive Impacts on Plant Growth and Nutritional Requirements

The most prominent assistance provided by symbiotic association of plant-mycorrhizae is to improve growth through the sustainable and enhanced supply of micronutrients. The most evident nutrients involved in this phenomenon is Phosphorous (P) which has additional benefits such as carbon assimilation, regulated enzymatic activities, water retention, and improved soil quality which leads to a positive impact on plant growth [1][2]. AMF are associated with the regulated flow of water and nutrients in exchange of carbohydrates from the host [2]. The mycorrhizal association modifies the morphology of the host roots and improves water-mineral uptake from the rhizosphere [3][4][5]. These associations show varying colonization patterns and capacities depending upon the plant species [6]. AM symbiosis also regulate rhizospheric enzymes such as urease, glucosidases, dehydrogenase, nitrogenase, phosphatase, catalase, peroxidase and soil polyphenol oxidases to provide better soil antioxidant activities [7][8][9][10].

Rhizospheric enzymes improve soil aggregation by hydrolysis and the activation of non-available organic matter in soil, the transfer of nutrients within or between the plants, stabilizing mycorrhizal products like hydrophobins, polysaccharides, glomalin related soil proteins and other extracellular composites, and chelating toxic substances in the rhizosphere [10]. Increased phosphatase activities by mycorrhizal association amplifies levels of phosphorus release from the soil organic matter, hence enhanced translocation of nutrients from the soil to the host plant. In addition, the pattern of intra-radical and extra-radical hyphal structures influence the phosphorus metabolisms among AM species [11]. Conclusively, most of the plants in the natural environment depend on mycorrhizal associations for their nourishment, and these associations have been reported for the transport of about 50% of fixed N and 90% of P into the plant [12][13].

2. AMF and Mineral Nutrition

Mycorrhizal symbiosis has gained significant attention with regards to agricultural sustainability due to its characteristic properties of mineral nutrients uptake, utilization, translocation, and how it acts as a biocontrol instrument to the plants. As mentioned in previous sections, they exhibit a critical mediator between the roots and soil, where the soil nutrients acquired by fungal partners get moved to the plant partner in exchange for the photosynthetic carbon produce. Mycelial extensions on the roots' surface help plants to capture nutrients more efficiently by increasing the surface area, and hence maximum the absorption of soil minerals [14]. The mycorrhizal association triggers the transfer of minerals such as phosphate, ammonium, nitrate, zinc, copper, potassium, sulfur, etc. with the help of various transporters (**Table 1**) [15][16]. Phosphate transporters (PTs) present in the mycorrhizal fungi due to their high affinity have been extensively studied for their functional and molecular characteristics imparting nutritional benefits towards plant development [13][17]. AM associations have also been reported to promote P uptake cascade in plants, by triggering expression of some phosphate transporters in many plant species such as in *M. truncatula* (MtPT4), *A. sinicus* (AsPT1) and *O. sativa* (OsPT11) [18][19][20]. In this way, phosphate accumulated via mycelial absorption (an active process) is accessible to the plants. These transporter proteins are considered to be indicators of mycorrhizal symbiosis embedded on periarbuscular membranes (PAM) (**Figure 1**) [21]. Other plant transporter genes for micro and macronutrients like ammonium (AMs), sulfur (SULTF), zinc (ZIPs), nitrate (NPF), potassium (KTs) etc. have also been identified in mycorrhized plants. These transport systems are coupled with a positive impact on arbuscular development as well as a regulatory response to the plant homeostasis [18][22]. In addition, potassium (K^+) plays a significant role in plant physiological processes and a symbiotic association with fungus not only increases the potassium supply, but also provide resistance against drought stress to the plant. Potassium accessibility in soil, however, is of concern due to their high mineral adsorption characteristics. Although, these (K^+) transporters are associated with myc-symbiosis, their significant physiological involvements have been less explored [22]. Moreover, myc-inoculation into the agricultural sites could soon possibly be an effective method for improved crop productivity, nutritional flow, and regulation of symbiotic associations [12].

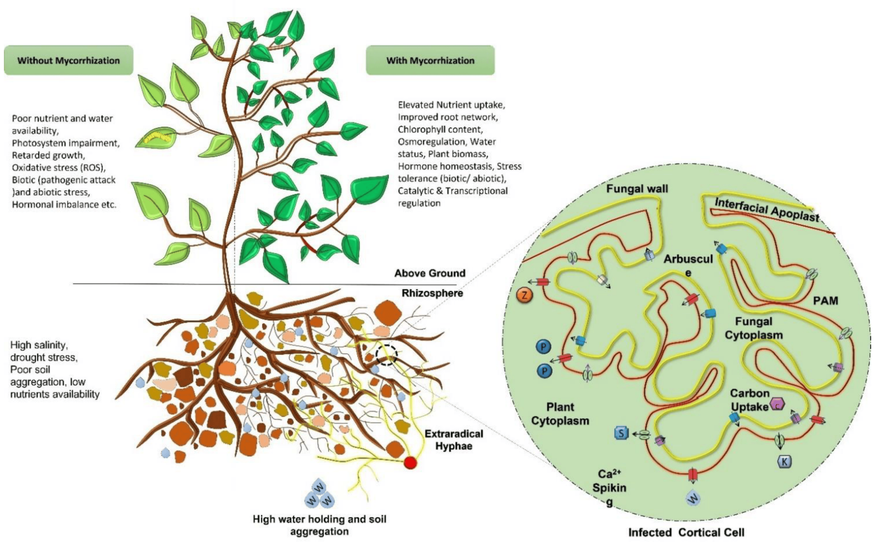

Figure 1. The effect of mycorrhizal associations on plant growth and restoration of soil: alleviated nutrient supply, poor root network and impaired plant growth without mycorrhizal exposure (**left**), and rhizospheric extraradical hyphae extension deep into inaccessible soils (soil aggregation), elevation in nutrient uptake (ionic exchange by arbuscule formation through IFA) and improve plant growth (**right**).

Table 1. Regulation of mineral nutrition via transporters in mycorrhizae associated plants.

Sr. No.	Mineral	Mycorrhizal sp.	Plant sp.	Host Plant Transporters	Effect of Mycorrhizal Symbiosis	Reference
1.	Phosphate	*Claroideoglomus etunicatum*	*Camellia sinensis*	CsPT1 & CsPT4	AMF up-regulated root CsPT1 expression, while down-regulated the CsPT4 expression. AMF inoculation significantly promoted P acquisition capacity of tea plants, especially in roots through improving root growth and enhancing soil acid phosphatase activity and root CsPT1 expression.	[23]
		Rhizophagus irregularis	*Zea mays*	ZmPht1;6 & ZmPht1;11	AMF improved plant growth and Pi assimilation, AMF colonization strongly improved the nutritional status of the plants and increased the internal P concentration. ZmPht1;6 over expression at a high level in AMF-colonized roots. While less expressed ZmPht1;11 also stimulated by AMF colonization.	[24]

Sr. No.	Mineral	Mycorrhizal sp.	Plant sp.	Host Plant Transporters	Effect of Mycorrhizal Symbiosis	Reference
2.		*Gigaspora margarita or Funnelliformis mosseae*	*Lotus japonicus*	LjPT4	LjPT4 affects proper arbuscule formation on the fungal side and for improved Pi uptake on the plant side.	[25]
3.	Sulfur	*Rhizophagus irregularis*	*Zea mays*	ZmSULTR1.2a, ZmSULTR2.1, ZmSULTR3.5	Upregulation of ZmSULTR1.2a & ZmSULTR2.1 in sulfur deprived conditions while downregulation of ZmSULTR3.5 in mycorrhized plants.	[26]
4.	Copper	*Rhizophagus irregularis*	*Medicago truncatula*	MtCOPT2	Preferential expression of MtCOPT2 during mycorrhizal symbiosis.	[27]
	Nitrate	*Rhizophagus irregularis*	*Oryza sativa, Zea mays, Sorghum bicolor, Medicago truncatula*	OsNPF4.5, ZmNPF4.5, SbNPF4.5, MtNPF4.5	Myc-symbiosis resulted in efficient up-regulation of OsNPF4.5, ZmNPF4.5 and SbNPF4.5, while slight induction of MtNPF4.5.	[28]
		Rhizophagus irregularis	*Oryza sativa*	OsNPF genes: NPF2.2/ PTR2, NPF1.3, NPF6.4 and NPF4.12	Enhanced expression of nitrate transporter genes in mycorrhizal roots in nutrient dependent manner.	[29]
5.	Ammonium	*Rhizophagus irregularis*	*Oryza sativa*	OsAM1, OsAM10, OsAM20, OsAM25	Significant upregulation in roots via AMF symbiosis.	[29]
		Rhizophagus irregularis	*Oryza sativa*	OsAMT3.1	Up-regulation of OsAMT3.1 in rice mycorrhizal roots	[28]
6.	Zinc	*Rhizophagus irregularis*	*Medicago truncatula*	MtZIP5, MtZIP2	AMF symbiosis caused higher expression of MtZIP5 in poor rhizospheric Zn condition and reduction in MtZIP2 at elevated soil Zn concentration.	[30]
		Rhizophagus irregularis/mock-inoculated	*Hordeum vulgare*	HvZIP3, HvZIP7, HvZIP8, HvZIP10, HvZI13	Out of five transporters, HvZI13 found most significantly upregulated, HvZI3 & 8 upregulated also in Zn deficient conditions, while HvZI7 & 10 downregulated.	[31]
7.	Potassium	*Rhizophagus irregularis*	*Lycium barbarum Solanum lycopersicum*	LbKT1, LbSKOR SlHAK10	Regulated expression of LbKT1 and LbSKOR for varying water & potassium availability	[32][33]

3. AMF as Bio-Fertilizer

Generally, bio-fertilizers are substances which include microbial population and when applied to the soil, result in improved plant growth by promoting mineral nutrition uptake, water supply, protection against biotic/abiotic stresses, and soil quality. In particular, the fungal microorganisms (due to thin hyphal structures) have emerged as extremely proficient networks with the capabilities of nutrient acquisition from soil inaccessible to the plant roots [34]. Hence, mycorrhizal symbiosis is promising in alleviating limitations related to nutrient uptake [12]. It is also a very interesting fact that the plants invest almost a hundred times of the energy (in C form) required to produce a root than a single hypha which further travels beyond the exhausted nutritional regions of the soil for sustainable nutrient supply. These inferences support the cost-effective nature of the mycorrhizal symbiosis [35]. Mycorrhizal symbiosis is propitious for improved soil texture and other physicochemical properties that result in aggregate formation (in dry or wet conditions), improved soil catalytic performances, proper aeration because of hyphal entanglement, balanced soil pH, etc. Fungal hyphae penetrating deep into the soil form a mesh-like hold upon soil particles and result in micro and macroaggregates formation [36]. Glomalin, the fungal exudate is associated with the formation of these aggregates and helps to hold the soil matrix [35]. These aggregates ultimately provide: (a) protection against soil erosion through heavy wind and water flow, (b) porous texture to the soil, (c) carbon fixation by protecting the organic matter decay by other microbial populations and (d) soil moisture regulation [36][37]. In a recent study, it has been indicated that Glomalin related proteins (product of AMF) help in the restoration of eroded lands by increased soil aggregation and organic carbon sequestration [38]. A variety of mycorrhizal biofertilizers are available on the market (such as Rootplus, Vamstar, Myko-win, Rutmy, Farrata, VAM, Mycoxol, etc.) and have been used widely in agriculture for higher crop yield, production, and soil fertility.

4. Mitigation of Biotic & Abiotic Stress

Harsh environmental conditions (abiotic stress) and pathogenic attack (biotic stress) are the major intimidations to global agricultural produce. Negative consequences of these stresses can impede plant growth, nutritional inequities, physiological ailments, ionic toxicity, and cause hormonal imbalance. To overcome the negative consequences, plant adopt several physiological, morphological, structural, and biochemical modifications to alleviate stress [39][40]. A mutualistic association with soil microorganisms promises a stress-tolerant approach towards improved plant defense [41]. From previous reports, it appears that myc-plants exhibit more efficiency in growing under stress conditions [42][43][44]. Reports are available describing stress resistance via: (a) regulated ionic uptake for improved osmoregulation (P↑, N↑, Mn, K↑, Na↓, etc.), (b) up-regulated photosynthetic performance, (c) alleviated oxidative stress, (d) enhanced soil catalytic (mainly phosphatases) activities (for improved availability of mineral elements), (e) the dilution effect on harmful salts/minerals, (f) hormonal balancing, (g) regulation of plant-fungus aquaporin and mineral transporter genes, and (h) elevated water status (Figure. 3) [40][45][46][47]. Different mitigation responses for various biotic/abiotic stresses have been listed (**Table 2**). However, the mitigation mechanisms for various stress conditions have been debatable and, depending upon the associated myc-plant species, mitigation responses may vary.

Table 2. Influence of different mycorrhizal sp. on soil restoration by phytoremediation of toxic metals.

Pollutant	Mycorrhizal Species	Plant Species	Possible Mechanism	Literature Cited
Chromium (Cr)	*Rhizophagus irregularis*	*Daucuscarota*	**Reduced translocation, and immobilization of Cr^{6+} through EPS (extracellular polymers) production. distribution of Cr in roots**	[48]
	Rhizophagus irregularis	*bermudagrass [Cynodondactylon (Linn.)*	**Cr absorption and immobilization by AM roots, Reduction of Cr^{6+} to Cr^{3+} within fungal structures, inhibited Cr flow from roots to shoots,**	[49]
	Rhizophagus irregularis	*Taraxacum platypecidum*	**Cr absorption and immobilization by AM roots, inhibit Cr translocation from roots to shoots, promoted plant growth**	[49]
	Glomus deserticola	*Prosopisjuli flora-velutina*	**Accumulation of Cr in vascular tissue and decreased the translocation of Cr into shoots**	[50]
Zinc (Zn)	*Glomus mosseae & G. intraradices*	*Vetiver grass*	**Increased P uptake by the plant and improved overall growth (*G. intraradices* showed more rehabilitation capacity)**	[51]
	Glomu smosseae	*Trifolium pratense*	**Zn accumulation in roots which decreases in shoots as the Zn conc. rises to its maximum, improved P sustenance**	[52]
	Glomus deserticola	*Eucalyptus globulus*	**Increased root to shoot metal accumulation, high metabolic activity, symbiotic effect of saprophytic fungal sp. on mycoremediation process**	[53]
Lead (Pb)	*Glomus mosseae& G. intraradices*	*Vetiver grass*	**Increased P uptake by the plant and improved overall growth (*G. mosseae* showed more rehabilitation capacity)**	[51]

Pollutant	Mycorrhizal Species	Plant Species	Possible Mechanism	Literature Cited
Aluminium	*Glomus mosseae and G. deserticola*	*Eucalyptus globulus*	Promoted overall growth, mineral nutrition, chlorophyll production and enzymatic performances (which further increased due to synergistic effect of *G. deserticola* and *T. koningii*), enhanced Pb accumulation	[54]
	Pisolithus sp.	*Schinusmolle*	Phytoextraction or phytostbilization, Glomalin production supported chelation, rise in photochemical efficacy	[55]
	R. irregularis	*Zea mays*	Increased accumulation of total phytochelating content in shoots	[56]
Copper (Cu)	*Funneliformis mosseae; R. intraradices*	*Capsicum annuum*	Cu Higher total dry weight and the leaf	[57]
	Arbascular Mycorrhizal Fungi (AMF)	*Elsholtzia splendens*	Increase in germination rate and the germination index of the seeds as well as the fresh weights of hypocotyl and radicle	[58]
	Claroideoglomus claroideum	*Oenothera picensis*	Protect plant from metal toxicity, enhance both plant establishment and nutrition	[59]
	R. irregularis	*Phragmites australis*	Stress tolerance via up-regulating photo systems membrane complexes, improved plant growth.	[60]
	Rhizoglomus clarum	*Canavalia ensiformis*	Alleviated amounts of Cu due to phytoextraction in addition to earthworms	[61]
	Rhizophagus clarus	*Canavalia ensiformis*	Alleviated amounts of Cu due to phytoextraction & phytostabilization in addition to bovine	[62]
	Claroideo glomu sclaroideum and	*Oenothera picensis*	Cu chelation with AM-secreted glomalin protein	[63]
Mercury (Hg)	*Glomussp.,Gigaspora* sp. &*Skutelespora* sp.	*Cyperus kyllingia, Lindernia crustacea, Paspalum conjugatum*	P. conjugatum resulted maximum phytoextraction, while C.kyllingia exhibited maximum (Hg) tolerance	[64]
	Native AM fungal morphotypes	*Axonopus compressus, and Erato polymnioides*	A. compressus ensued phythoextracting; Eratopolymnioides–Hg phytostabilization	[65]
	AMF	*Lolium perenne*	Decreased shoot:root (St:Rt) (Hg conc.), increased metal assimilation in roots	[66]
Nickel (Ni)	*Funneliformis mosseae (also named as Glomus mosseae)*	*Festuca arundinacea*	Enhance expression of ABC transporters and metallothione induced metal intoxication, decreased metal translocation	[67]
	Acaulospora sp. (indigenous)	*Canavalia ensiformis*		[68]

Pollutant	Mycorrhizal Species	Plant Species	Possible Mechanism	Literature Cited
Arsenic (As)	*AMF mix*	*Lens culinaris*	Alleviated uptake by roots and shoots as an effect of mycorrhizal association	[69]
	Rhizophagus intraradices (formerly named G. intraradices)	*Plantago lanceolata*	Down-regulating phosphate/arsenate transporters could assist plants to enhance the As tolerance	[70]
	Rhizoglomus intraradices & Glomus etunicatum	*Triticum aestivum*	Regulated P/As ratio, enhanced antioxidant production, holding As into non-toxic forms via increased production of biopolymers	[4]
	Rhizoglomus intraradices	*Robiniapseudoacacia*	Induced changes in root morphology, increased shoot-root dry weights, controlled phyto-hormone concentration etc.	[4]
	Acaulospora scrobiculata	*Anadenantheraperegrina*	Promoted P uptake lead to higher growth rates, As concentrations in the roots and shoots.	[5]
	Funelliformis mosseae and Piriformos poraindica	*T. aestivum*	Biomass uplift, imposed catalytic activities for G-SH transferase, catalase, peroxidase etc., and antioxidant genes upregulation	[71]
Cadmium (Cd)	*Glomus intraradices*	*Zea mays*	Mycorrhizae in association with biochar resulted alleviation in Cd accumulation in plant and restricted mobilization, soil rehabiliation	[72]
	Glomus monosporum, G. clarum, Gigaspora nigra, and Acaulospora laevis	*Trigonella foenum-graecum*	Decreased St: Rt Cd ratio, enhanced antioxidant activities	[73]
	Rhizophagus irregularis	*Phragmites australis*	Immobilization of Cd in roots, increased mineral uptake (Mn& P mainly) to survive Cd-toxicity	[74]
	Glomus intraradices, Glomus mosseae, Glomus claroideum, and Glomus geosporum	*Nicotiana tabacum*	Phyto stabilization of lead via immobilization in extraradical mycelial network	[75]
	Glomusmosseae	*Cajanus ajan*	Diminished oxidative disturbances (free radicle formation), high non-protein thiols (-SH) production and high antioxidant activities	[76]
	Claroideoglomus etunicatum	*Sorghum bicolor*	Increased the glomalin content for improved soil, Cd stabilization in mycorrhizal roots &phytoextraction (by shoots), high nutrient uptake	[77]

5. Potential Applications in Phytoremediation

Heavy metal accumulation (Pb, Cd, Hg, Al, Cu, Zn, Cr, etc.) in soil due to natural or human activities has been a serious and persistent environmental threat [51][53][55][66][78]. Owing to their non-degradable nature, these toxic substances pollute the natural resources and the food chains which ultimately reflects adverse effects on the atmospheric, aquatic as well as terrestrial ecosystems. Various chemical and physical remediation techniques are there to overcome the negative effects of heavy metals, while bio-remediation techniques have proved to be more promising in terms of cost-effectiveness and maintaining the soil fertility (by preventing serious soil degradation) [21][22][79]. Some of these heavy metals can be excreted from the body, while others accumulate successively depending upon the exposure, dosage, route, etc. and exhibit chronic behavior [78]. Ubiquitous distribution and abundance of Pb has been one of the hazardous effects on the environment, imposing serious harm to plant growth [54]. Some plant species survive in the presence of heavy metals in the soil, which specifies the presence of some expanded mechanistic approach to adapt in such polluted environments, also called phytoremediation. These plants are designated as hyper-accumulators due to this promising characteristic of accumulating high amounts of heavy metals within the tissue [80][81]. Plants involved in detoxification of soil pollutants usually show sluggish growth, taking a longer time in soil cleaning. While, in combination of mycorrhizal symbiosis plants exhibit a high growth rate, increased biomass, phytochemical activities, and therefore, eradication of soil pollutants at a high rate [82]. However, heavy metals as soil contaminants also hamper colonization and spore formation of mycorrhizal fungi due to increment in root exudate production that limits the supply of carbon sources to the fungal symbionts [83][84]. Mycorrhizal association improves phytoremediation efficiencies. The plant species undergo biological modifications such as increased upward translocation of essential minerals (Zn/Cu) and holding harmful metals (Pb/Cd) in the roots to protect the plant which allows them to survive in extreme abiotic stress [85]. There have been some mechanistic behaviors signifying the removal of toxic substances: metal ion immobilization within mycorrhizal structures; blocking the metal uptake by conversion into non-toxic or ineffective complexes in rhizosphere via chelation, bonding with other biomolecules and precipitation; segregation inside the mycorrhizal vacuole or arbuscules; cytosolic accumulation using biopolymers; stimulating or enhancing antioxidant activities to prevent cellular damage; use of membrane transporters towards or against the concentration gradient for metal translocation; metal ions diffusion to an alleviated response; enhancing nutrient flow to the host; increasing enzymatic efficiencies of soil; stimulating root exudation and up-regulating rhizospheric activities [55][75][77][86]. Further, the impact of mycorrhizal association with hyper-accumulating plant species on phytoremediation efficiencies is depicted (**Table 2**).

6. Enhanced Biological Produce and Agricultural Profitability

Myc-association plays a vital role in managing sustainable plant growth, in addition to improved responses to changing and stressful environmental conditions. As evidenced, the applications of different mycorrhizal species such as *G. coronatum*, *G. mosseae*, *G. decipiens* have been reported for their increased biological yield (cobs per plant, grains, in maize) [6]. Also, these associations have shown enhanced nutritive values through the production of organic (sugars, amino acids) and secondary metabolites (flavonoids, carotenoids, phytochemicals, and volatile organic complexes) [7][12][32][87]. They are responsible for the enhanced C and N fixation, soil fertility, and texture, high food storage, thus a cost-effective approach for the farmers [88]. Another significant factor is the quality yield production, which has been also reported to be enhanced and accompanied by myc-fungi inoculation [12][33][89]. Based on the reported facts, soil microbiota directly influences agricultural profitability [1].

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