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Arbuscular mycorrhiza in sustainable agriculture: Prospective and challenges*

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At a time in which global food demand is exponentially increasing with concomitant shrinkage in the availability of farmable lands, microbes furnish a key role in sustainably optimizing agricultural processes. One such significant group of microbes that is extremely instrumental in sustainable agriculture is Arbuscular Mycorrhizal Fungi (AMF). This group of fungi thrives in soil and is crucial to the multitudinous biological functions of plants. My interest in Plant-AMF interactions would not have had the spirit it has without the inevitable support of my supervisor, Late Prof. K.G. Mukerji, whose wisdom, passion for science, and authoritative guidance have been immeasurably valuable in my growth as a person and blossoming scientific temperament in me over all these years. My greatest degree of appreciation goes out to him for exposing me to the realms of this promising group of beneficial fungi that serve as agro-ecosystem engineers by fostering crop growth, securing nutrients, and even fending off pests and pathogens. The natural benefits of these microbes are a powerful complement to existing plant and soil treatments. I place on record my sincere gratitude to the honorable members of the Mycological Society of India (MSI) for entrusting me and putting me at the forefront. I appreciate the very foundation and vision of MSI that has the endeavor to bring together the mycologists of the country and with the broad objective of promoting the growth of mycology in India with wider perspectives. It is with great pleasure and humility that I express my deep sense of gratitude for having been able to serve this society over the years and pledge to continue to do so to the best of my ability. We, as a society, can go long in cultivating the interest of young researchers in mycology and its application and in realizing the long chased vision of sustainable agriculture.

INTRODUCTION

The crisis on food security has been looming large owing to the mushrooming population and rising income of the developing countries. In the last five decades, increasing food requirement has compelled doubling the productivity of grain yields (FAO, 2017). This has been accomplished by the employment of pesticides and chemical fertilizers, breeding of high-yielding crop cultivars, and intensive irrigation. Nevertheless, exhaustive use of agricultural fertilizers has inadvertently resulted in depletion of natural resources and severe environmental damage, with agriculture fertilizers alone accounting for more nitrogen and phosphorus released into the environment than all the natural processes in combination (Tilman *et al.,* 2001). Therefore, prolonged usage of fertilizers at existing rates is untenable. For that purpose, modern agriculture must aim to accomplish two separate objectives concurrently: (i) to satiate the nutritional requirements of a swelling human population and (ii) to reduce the deleterious effect of modern agricultural practices on the environment (Duhamel and Vandenkoorn-huyse, 2013). Interestingly, Goal 2 of the 2030 Agenda for Sustainable Development of the United Nations: 'End hunger, achieve food security and improved nutrition and promote sustainable agriculture' entail these two points. Genetic engineering offers prospects to the above goals; however, commercialization of genetically modified plants still faces several roadblocks, such as intellectual property issues, public acceptance, and risk assessment. Further, there are serious marketing and economic challenges to overcome. Globally, there is increasing interest in microbial fertilizers and more cognizance of the benefits of rhizosphere microorganisms (Alori *et al.,* 2017). Scientists, worldwide, are enthused to screen soil residing microorganisms for their plant growth-enhancing abilities. These beneficial rhizosphere microbes have exposed a market of "bio-fertilizers" for novel fertilizers globally.

All the major crop plants that feed the human populations worldwide form symbiosis with fungal species belonging to the Phylum *Glomeromycota*, named AMF. These are obligate symbionts that trade photosynthetic products of host plants with water and mineral nutrients from the soil (Smith and Read, 2008). Besides sugars, lipids also are transferred to the fungi from plants (Jiang *et al.,* 2017; Luginbuehl *et al.,* 2017). The fungus subsists as spores and extraradical hyphae in the rhizosphere. The hyphae of AMF exclusively colonize root cortical cells and form arbuscules, hyphae, and vesicles. The exchange of carbohydrates and other mineral nutrients takes place inside the cortical cells bearing intracellular arbuscules and across the interface between the two symbionts. As a result, AMF can improve the restraint on plant growth

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resulting from an inadequate supply of nutrients (Nouri *et al.,* 2014).

ARBUSCULAR MYCORRHIZAL FUNGI AS BIOFERTILIZERS

Arbuscular mycorrhizal fungi have the potential to significantly improve plants' acquisition of mineral nutrients, essentially in nutrient-deficit environments (Giri *et al.,* 2000). Besides, it is also established that plants own a symbiotic pathway for Pi uptake (Smith and Smith, 2011). The AMF mycelia that emanate from the root significantly enhance the approach of roots to a larger soil volume and facilitate the acquisition of mineral nutrients that are otherwise not attainable by the roots (Smith *et al.,* 2000). Moreover, fungal hyphae are relatively thin as compared with roots and hence can penetrate smaller pores (Allen, 2011). The last stage of the symbiotic mineral nutrient transfer takes place at the apoplastic space (PAS), which is created as a result of the plant-derived membrane called the periarbuscular membrane (PAM). Mineral nutrients from the PAS are captured by plant transporters positioned in PAM and allocate to the cortical cells (Javot *et al.,* 2011; Bapaume and Reinhardt, 2012). In addition to the plant Pi transporters (Harrison *et al.,* 2002; Walder *et al.,* 2015), the presence of mycorrhiza-inducible ammonium transporters on PAM have also been documented (Gomez *et al.,* 2009; Koegel *et al.,* 2013). On top of Pi and N uptake, AM symbiosis expands the nutritional status of sulfur in host plants, thereby affecting the expression profile of plant sulfate transporters (Giovannetti *et al.,* 2014). Extraradical hyphae also significantly surge the uptake of immobile micronutrients such as Zn and Cu and other soil-derived mineral cations such as Ca^{2+}, Fe^{3+}, K^{+}, and Mg^{2+} (Clark and Zeto, 2000; Smith and Read, 2008).

ARBUSCULAR MYCORRHIZAL FUNGI AS AGROECOSYSTEM ENGINEERS

Arbuscular mycorrhizal fungi influence wider communities and the local environment, both above- and below-ground owing to their ability to transport organic carbon and mineral nutrients (van der Heijden *et al.,* 1998). Thus, they have been labeled as 'agroecosystem engineers' (Cameron, 2010). AMF promote many facets of plant life, especially improved mineral nutrition, enhanced growth, greater stress tolerance, and boosted disease resistance (Giri *et al.,* 2000*,* 2003, 2005; Kapoor *et al.,* 2000, 2002a,b*,* 2004; Evelin *et al.,* 2012, 2013; Evelin and Kapoor, 2014; Mandal *et al.,* 2015; Sharma *et al.,* 2017; Thokchom *et al.,* 2020). This manifold assistance of AMF transforms into significant ecological services. The correct management of these services furnished by AM fungi will have marked footprints on conservation and utilization of natural resources with a net profit to human existence (Gianinazzi *et al.,* 2010)

A noteworthy ecosystem service provided by AMF is up-gradation of soil health through mitigation of soil erosion and/or by improving soil structure. Soil structure is crucial to soil health and several subsequent ecosystem services are essential in safeguarding sustainability in crop yield and agroecosystem (Bardgett and van der Putten, 2014). The extraradical hyphae of AMF have been demonstrated to clasp soil particles and aggregate together (Mardhiah *et al.,* 2016). The proteinaceous secretions (glomalin) by AMF serve as soil glue and signify a substantial proportion of soil organic matter (Simpson *et al.,* 2004; Treseder and Turner, 2007). The abundance of AMF in the soil prevents the leaching of mineral nutrients (van der Heijden, 1998; Bender *et al.,* 2015), thereby enhancing soil nutrient content and reducing the risk of ground water contamination. AMF also improve soil's capacity to hold water (Rillig and Mummey, 2006) and concomitant soil resilience to erosion by wind and water (Ortiz *et al.,* 2015).

Several studies have revealed the implications between mycorrhizal plants and disease-causing microorganisms and pests (Hao *et al.,* 2012; Philippot *et al.,* 2013). Colonisation by AMF induces immense alterations in plant metabolism, including signaling pathways mediated by jasmonate and salicylic acid that constitute strategic mechanisms of plant defense, leading to the local and systemic immune response of plants (Cameron *et al.,* 2013). The establishment of the symbiosis in roots has a systemic priming effect. It affects anticipatory re-allocation of defense compounds so that expression of defense response genes is more rapid and robust than in non-inoculated plants, when challenged by a pathogen/pest (Jung *et al.,* 2012; Song *et al.,* 2015). Such benefits conferred by these plant biostimulants will eventually plunge the usage of fungal pesticides, which is a crucial requisite in sustainable farming approaches (Gabriel *et al.,* 2013).

Exhaustive compilation of data points out that AMF manipulate the growth of other soil organisms via common mycelial networks (CMNs). AMF facilitate communication among conspecific plants enabling the transfer of signals via CMN from pest-infested plants to uninfested plants (Babikova *et al.,* 2013), provoking plant defense activation prior to the attack on the plant, that may restrain the spread of the infestation and consequent loss in yield (Babikova *et al.,* 2013). However, the identity of signaling compound(s) as well as the duration and space over which they stay effective remains obscure. Further, the multispecies hyphal networks and signaling between neighboring hetero-specific plants, such as weeds, may curb the magnitude to which the mycorrhiza-mediated interplant signaling can be exploited in crop fields.

Mycorrhizal fungal biomass serves as the principal carbon sink globally, since significant amount of CO_2 fixed via photosynthesis (>20%) is maneuvered towards fungal biomass synthesis (Vosátka *et al.,* 2012). Carbon allocation from the plant is one of the important factors in controlling the degree to which AMF are valuable to a host plant. Information on concurrent evaluation of C, P, and N exchange within the symbiosis is deficient in literature. An enriched CO_2 atmosphere has been demonstrated to shrink the carbon-for-nutrient exchange efficacy between the symbionts (Field *et al.,* 2015). However, this relationship remains unclear in agricultural crop plants. With IPCC (Intergovernmental Panel on Climate Change) predictions on surge in atmospheric CO_2 concentrations, understanding the response of mycorrhizal symbiosis especially with respect to crop plants, under a CO_2-

rich atmosphere is vital. In arrangement with suitable crop models for diverse climate projections, it ought to be high precedence to ascertain if AMF have the capability to alleviate future environmental perturbations and their impact upon global crop production. Both above- and below-ground plants' characters that deliver functional plasticity to AM in response to unpredictable environmental conditions should be identified, thus, providing them with resilience to change in climatic conditions while retaining yield. The simultaneous investigation should be carried out to ascertain plant attributes in diverse crop genotypes, thriving in divergent soil types and using varied land management techniques, for optimum symbiotic functioning under varying environmental conditions. These identified attributes may thenceforth be merged into commercial crop breeding programs.

Utilization of the potential of AMF to improve phytoremediation has been testified (Bhargava *et al.,* 2012; Meier *et al.,* 2012). There are numerous reports on the ability of AMF to curtail heavy metals' translocation to the above-ground parts of the plant so as to ensure the safety of food crops (Sharma *et al.,* 2017). On the contrary, several other fungi can boost phytoextraction of heavy metals and consequently aid in contaminated soils' remediation. Thus, in this aspect, it is imperative that AMF inoculants are carefully selected so as to preclude undesirable or opposite effects. Lately, AMF have been recounted to fortify the nutritional quality of food crops with an improved profile of particular mineral nutrients such as zinc, iron, and magnesium (Albrechtova *et al.,* 2012).

In view of sustainable agriculture, the potential of other beneficial soil microbes should be thoroughly explored and harnessed, either discretely or in conjunction with AMF. Co-inoculation or synergistic introduction of AMF with other beneficial microorganisms (such as plant growth-promoting rhizobacteria or other endophytes) offers enormous benefits to crop production (Albrechtova *et al.,* 2012), and therefore are more desirable. For instance, co-inoculation of AMF with rhizobacteria (Babalola, 2010) and/or *Trichoderma* species relatively improve plant development more than single inoculation.

In a nut shell, besides the application as biofertilizers, novel findings on AMF that could add to the maintenance of agricultural sustainability embrace their roles in regulating soil erosion, improving phytoremediation, and eradication of other organisms that may be harmful to crops through the common mycelial network.

CHALLENGES AND FUTURE PROSPECTIVES

Deeper insights into plant-fungus interactions: Since time immemorial, the presence of symbiotic association has been documented and hence it can be considered as a conserved phenomenon. It is essential to decoding the molecular dialog between plants and fungus, the mechanisms and important genes from the plants and the fungus that control the interaction. Though the genes that facilitate the symbiotic association between both the symbionts are conserved, a dearth of knowledge on their biochemical functions has made understanding their functions a perplexing problem. What makes plant interactions with AMF distinctive from that with pathogenic fungi is another main query that needs to be addressed. In this context, a global outlook of the plant-mycorrhizal interaction is required to understand the molecular mechanisms of this interaction. The ongoing research on this front should be combined with state-of-art technological approaches and comprehended by incorporating diverse omics data to expand the dimensions of our understanding of this promiscuous symbiotic association (Kumar, 2016; Zipfel and Oldroyd, 2017).

The response of plants to AMF colonization can differ vividly between and within species (Klironomos, 2003; Hoeksema *et al.,* 2010), ranging from amplified plant nutrient assimilation and growth to negative or neutral responses where the fungal symbiont offers slight or no reckonable benefits (Ellouze *et al.,* 2016; Sawers *et al.,* 2017; Watts-Williams *et al.,* 2019). These disparities in the responses are the outcome of differences in the genotypes of plant and AMF and environmental conditions as well. The fungal characteristics that contribute to specificity in the outcomes comprise dissimilarities in the physiology, functional traits, genetic variability, and molecular features *viz.* signaling molecules and fungal effectors. Furthermore, the AMF species can differ in their P uptake proficiencies that may also add to the specificity in the outcome as the plant P uptake pathway is repressed in the symbiotic association. Thus, various AMF ecotypes should be evaluated for identifying the most effective strain for a particular plant genotype-based on the requirement of the active ingredient. To what extent the responses of plants differ when the interacting fungi are phylogenetically closely related is a subject that necessitates further research.

We need to identify basic metabolic pathways that govern the interaction with rhizosphere for upholding sustainable agriculture, and have a strong understanding of the contributions of AMF to these pathways. Keeping in mind the intricacy of the interaction, it is crucial to use statistical and other mathematical tools such as structural equation modeling, which can relate the influence of mycorrhiza in all the identified pathways.

Challenges in application of AMF in sustainable agriculture: Studies for several decades have resolved the physiological and molecular mechanisms supporting the functioning of a single plant-AMF species association in unsophisticated experimental systems, substantiating beneficial effects of AMF inoculation on growth and tolerance of plants to a/biotic stresses. Majority of these studies have been carried out under controlled environmental conditions in the laboratory, greenhouse or pots that remotely simulate natural conditions. Therefore, there is a need for experiments performed on plants grown in agricultural fields under natural conditions to be conducted in a commercially viable way. Understanding roles of AMF in the complexities of agroecosystems pose a considerable challenge to completely unlock the potential benefits of AMF (Babikova *et al.,* 2013). To date, only a few studies document the effect of AMF at the field, landscape, or ecosystem levels.

One of the biggest challenges is the economical production of a large amount of viable AMF inoculum necessary for extensive open-field. Unlike other plant growth-promoting microorganisms, AMF cannot be grown in pure culture and necessitate host plant for growth and completion of the lifecycle. Therefore, it is obligatory to have a propagation phase with the host plant that compels approaches that are quite different and require time and space. While AMF inoculation in plant propagation/cultivation systems via transplantation can be carried out with relatively more ease, since less quantity of inoculum is required, bulk production of AMF inoculum continues to be economically exorbitant, labor-intensive, and technically unreasonable. Another challenge in the use of AMF in agriculture is the absence of a rapid method to ascertain as well as quantify AMF colonization in the host roots.

The deficiencies and conflict in datasets from pot-based experiments or field trials have ensured no strong agreement on the application of AMF in sustainable agriculture. The variability in response to AMF inoculation generates a lack of confidence in its overall competence by the agricultural community. It is paramount to distinguish unambiguously between variability in response from uncertainty (Leifheit *et al.,* 2014); often supposed as being synonymous by both stakeholders and scientists. This emphasizes the exigent demand for more meticulous site-specific investigations (Rillig *et al.,* 2019). Accurate site-specific information delivery can seize this variability (Rillig *et al.,* 2016).

While most of the studies entail the use of single-isolate in improving plant performance, it is important to assess inoculation with numerous AMF species and/or isolates, resembling agricultural ecosystems that harbor diverse AMF in individual plants. This should also be accompanied by wholesale field trials at diverse agrological locations. It will also assist in evaluating functional complementarities and synergism among different combinations of AMF species/ isolates in mixtures, leading to detection of the best AMF combinations for further application. Besides, the efficacy/ synergism of AMF isolates should be evaluated in combination with other useful microorganisms *viz.* plant growth-promoting bacteria and fungi (*Trichoderma* spp) (Lingua *et al.,* 2013; Colla *et al.,* 2015; Rouphael *et al.,* 2015).

The diversity of AMF in agricultural soils has been ruined by conservative agricultural practices such as tillage, overutilization of fertilizers, crop rotations, and long fallow periods (Helgason *et al.,* 1998). These practices disrupt the development of extraradical hyphal networks thereby creating long periods where AMF have limited access to host plants and consequently to C supply (Helgason *et al.,* 1998). On the other hand, owing to competition with well-adapted indigenous microbial communities, laboratory-raised AMF isolates or commercially available strains exhibit limitations in their perseverance and establishment (Loján *et al.,* 2017). Thus, the selection of native AMF isolates could give more fruitful results. Once the biodiversity of AMF is reinstated and well established in agriculture fields, it is important to adopt agronomic practices that are AMF-friendly so that the biodiverse mycorrhizal hyphal network remains unchanged and infective in the future.

It is worth noting that much of the knowledge gained so far on AMF-crop interactions is based on the agroecosystems of the temperate regions. There exist a considerable dearth of knowledge regarding the interaction in the tropics in developing nations, where food insecurity symbolizes a huge challenge (Ceballos *et al.,* 2013; Rodriguez and Sanders, 2015). The soils in tropical vis-à-vis temperate agroecosystems are characterized by relatively low nutrient availability. The tropical soils have high phosphate-fixing abilities hence show low phosphate bioavailability. Thus, the introduction of AMF in tropical agricultural soils would have an immense possibility in increasing crop production and decreasing the use of chemical fertilizers.

In conclusion, to utilize mycorrhizal technology for a greener future, the research should aim at ascertaining the mechanism of the interaction in natural conditions of the agroecosystem. At an ecosystem scale, multiple interconnected plants and fungal partners share dynamic milieus. Investigating such complex ecosystems will help in understanding the novel ecological mechanisms and exploit them to benefit crop production. As discussed before, AMF inoculation may not be constructive in all agricultural setups as mycorrhizal effects are highly context-dependent. To rule out uncertainties, a site-specific case-by-case assessment is required. Global diversity and abundance of AMF in agricultural soils should be repeatedly monitored and conserved and could be amended by the reintroduction of AMF spores and propagules through inoculation and favorable adjustment of management practices. (Lekberg and Koide, 2005). Efforts need to be invested to harness AMF diversity and efficiency to fortify crop health by the employment of suitable inocula. Application of synthetic biology should be promoted to develop customized AMF inoculum with better symbiotic efficiency and the ability to improve plant welfare. Isolation of native and adaptive ecotypes of AMF from ecologically disturbed soil can offer a prospective tool for the successful restoration of the vitiated ecosystem. Further, it is imperative to identify plant traits allied with AMF responsiveness, functionality, and climate resilience (cold/drought tolerance), and incorporate these in modern crop cultivars via crop breeding efforts.

REFERENCES

Albrechtova, J., Latr, A., Nedorost, L. *et al.* 2012. Dual inoculation with mycorrhizal and saprotrophic fungi applicable in sustainable cultivation improves the yield and nutritive value of onion. *Sci World J.* 2012. doi:10.1100/2012/374091.

Allen, M.F. 2011. Linking water and nutrients through the vadose zone: a fungal interface between the soil and plant systems. **3**: 155-163; doi: 10.3724/SP.J.1227. 2011.00155.

Alori, E.T., Glick, B.R. and Babalola, O.O. 2017. Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *Front. Microbiol.* **8**: 971-983; doi: 10.3389/fmicb.2017.00971.

Babalola, O.O. 2010. Beneficial bacteria of agricultural importance. *Biotechnol. Lett.* **32:** 1559-1570; doi: 10.1007/s10529-010-0347-0.

Babikova, Z., Gilbert, L., Bruce, T.J. *et al.* 2013. Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecol. Lett.* **16**: 835-843; doi: org/ 10.1111/ele.12115

Bapaume, L. and Reinhardt, D. 2012. How membranes shape plant symbioses: signaling and transport in nodulation and arbuscular mycorrhiza. *Plant Traffic Transp.* **3**: 223-236; doi: 10.3389/fpls.2012.00223

Bardgett, R.D. andvan der Putten, W.H. 2014. Below ground biodiversity and ecosystem functioning. *Nature* **515**: 505-511; doi:10.1038/nature13855

Bender, S.F., Conen, F. and Van der Heijden, M.G. 2015. Mycorrhizal effects on nutrient cycling, nutrient leaching and N_2O production in experimental grassland. *Soil Biol. Biochem.* **80**: 283-292; doi: 10.1016/j.soilbio.2014.10.016

Bhargava, A., Carmona, F.F., Bhargava, M. *et al.* 2012. Approaches for enhanced phytoextraction of heavy metals. *J. Environ. Manag.* **105**: 103-120; doi:10. 1016/j.jenvman.2012.04.002

Cameron, D.D. 2010. Arbuscular mycorrhizal fungi as (agro) ecosystem engineers. *Plant Soil* **333**: 1-5; doi: 10. 1007/s11104-010-0361-y

Cameron, D.D., Neal, A.L., van Wees, S.C. *et al.* 2013. Mycorrhiza-induced resistance: more than the sum of its parts? *Trends Plant Sci.* **18**: 539-545; doi: 10. 1016/j.tplants.2013.06.004

Ceballos, I., Ruiz, M., Fernández, C. *et al.* 2013. The *in vitro* mass-produced model mycorrhizal fungus, *Rhizophagus irregularis*, significantly increases yields of the globally important food security crop cassava. *PLoS One* **8**: *e*70633; doi: 10.1371/ journal.pone.0070633

Clark, R.Á. and Zeto, S.K. 2000. Mineral acquisition by arbuscular mycorrhizal plants. *J. Plant Nutr.* **23**: 867-902; doi: 10.1080/01904160009382068

Colla, G., Rouphael, Y., Bonini, P. *et al.* 2015. Coating seeds with endophytic fungi enhances growth, nutrient uptake, yield and grain quality of winter wheat. *Int. J. Plant Prod.* **9**: 171-90.

Duhamel, M. and Vandenkoornhuyse, P. 2013. Sustainable agriculture: possible trajectories from mutualistic symbiosis and plant neodomestication. *Trends Plant Sci.***18**: 597-600; doi: 10.1016/j.tplants.2013.08.010

Ellouze, W., Hamel, C., DePauw, R.M. *et al.* 2016. Potential to breed for mycorrhizal association in durum wheat. *Can. J. Microbiol.* **62**: 263-271; doi: 10.1139/ cjm-2014-0598

Evelin, H., Giri, B. and Kapoor, R. 2012. Contribution of *Glomus intraradices* inoculation on nutrient acquisition and mitigation of ionic imbalance in NaCl stressed *Trigonella foenum-graecum*. *Mycorrhiza* **22**: 203-217; doi: 10.1007/s00572-011-0392-0

Evelin, H., Giri, B. and Kapoor, R. 2013. Ultrastructural evidence for AMF mediated salt stress mitigation in *Trigonella foenum-graecum*. *Mycorrhiza* **23**: 71-86; doi: 10.1007/s00572-012-0449-8

Evelin, H. and Kapoor, R. 2014. Arbuscular mycorrhizal symbiosis modulates antioxidant response in salt stressed *Trigonella foenum-graecum* plants. *Mycorrhiza* **24**:197-208; doi: 10.1007/s00572-013-0529-4

FAO (Food and Agriculture Organization of the United Nations). 2017. The Future of Food and Agriculture: Trends and Challenges. www.fao.org/3/i6583e/ i6583e.pdf.

Field, K. J., Pressel, S., Duckett, J.G. *et al.* 2015. Symbiotic options for the conquest of land. *Trends Ecol. Evol.* **30**: 477-486; doi: 10.1016/j.tree.2015.05.007

Gabriel, D., Sait, S.M., Kunin, W.E. *et al.* 2013. Food production vs. biodiversity: comparing organic and conventional agriculture. *J. Appl. Ecol.* **50**: 355-364; doi: 10.1111/1365-2664.12035

Gianinazzi, S., Gollotte, A., Binet, M.N. *et al.* 2010. Agro-ecology: the key role of arbuscular mycorrhizas in ecosystem services. *Mycorrhiza* **20**: 519-530; doi: 10.1007/s00572-010-0333-3

Giovannetti, M., Tolosano, M., Volpe, V. *et al.* 2014. Identification and functional characterization of a sulfate transporter induced by both sulfur starvation and mycorrhiza formation in *Lotus japonicus. New Phytol.* **204**: 609-619; doi: 10.1111/nph.12949.

Giri, B., Kapoor, R. and Mukerji, K.G. 2000. *Sesbania aegyptiaca* seedling response to VA mycorrhization in rehabilitation of two ecologically diverse soils. *Phytomorphology* **50**: 327-332.

Giri, B., Kapoor, R. and Mukerji, K.G. 2003. Influence of arbuscular mycorrhizal fungi and salinity on growth, biomass and mineral nutrition of *Acacia auriculiformis*. *Biol. Fert. Soils* **38:** 170-175; doi: 10.1007/s00374-003-0636-z.

Giri, B., Kapoor, R. and Mukerji, K. G. 2005. Effect of arbuscular mycorrhiza *Glomus fasciculatum* and *G. macrocarpum* on the growth and nutrient content of *Cassia siamea* in semi-arid Indian waste land soil. *New For.* **29:** 63-73; doi: 10.1007/s11056-004-4689-0.

Gomez, S.K., Javot, H., Deewatthanawong, P. *et al.* 2009. *Medicago truncatula* and *Glomus intraradices* gene expression in cortical cells harboring arbuscules in the arbuscular mycorrhizal symbiosis. *BMC Plant*

Biol. **9:** 10-19; doi: 10.1186/1471-2229-9-10.

Hao, Z., Fayolle, L., van Tuinen, D. *et al.* 2012. Local and systemic mycorrhiza-induced protection against the ectoparasitic nematode *Xiphinema index* involves priming of defense gene responses in grapevine. *J. Exp. Bot.* **63**: 3657-3672; doi:10.1093/jxb/ers046.

Harrison, M. J., Dewbre, G. R. and Liu, J. 2002. A phosphate transporter from *Medicago truncatula* involved in the acquisition of phosphate released by arbuscular mycorrhizal fungi. *Plant Cell* **14**: 2413-2429; doi: 10.1105/tpc.004861.

Helgason, T., Daniell, T.J., Husband, R. *et al.* 1998. Ploughing up the wood-wide web? *Nature* **394**: 431-431; doi: 10.1038/28764.

Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A. *et al.* 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecol. Lett.* **13**: 394-407; doi: 10.1111/j.1461-0248. 2009.01430.x

Javot, H., Penmetsa, R.V., Breuillin, F. *et al.* 2011. *Medicago truncatula* mtpt4 mutants reveal a role for nitrogen in the regulation of arbuscule degeneration in arbuscular mycorrhizal symbiosis. *Plant J.* **68**: 954-965; doi: 10.1111/j.1365-313X.2011.04746.x

Jiang, Y., Wang, W., Xie, Q. *et al.* 2017. Plants transfer lipids to sustain colonization by mutualistic mycorrhizal and parasitic fungi. *Science* **356**: 1172-1175.

Jung, S.C., Martinez-Medina, A., Lopez-Raez, J.A. *et al.* 2012. Mycorrhiza-induced resistance and priming of plant defenses. *J. Chem. Ecol.* **38**: 651-664; doi: 10.1126/science.aam9970.

Kapoor, R., Giri, B. and Mukerji, K.G. 2000. Effect of mycorrhization on growth and essential oil yield in *Anethum graveolens* L. *Indian J. Plant Physiol.* **6**: 77-80.

Kapoor, R., Giri, B. and Mukerji, K.G. 2002a. Mycorrhization of coriander to enhance the concentration and quality of oil in seeds. *J. Sci. Food Agric.* **82**: 1-4 ; doi: 10.1002/jsfa.1039.

Kapoor, R., Giri, B. and Mukerji, K.G. 2002b. *Glomus macrocarpum*: a potential bioinoculant to improve essential oil quality and concentration in dill (*Anethum graveolens* L.) and carum (*Trachyspermum ammi* (Linn.) Sprague). *World J. Microbiol. Biotechnol.* **18**: 459-463; doi: 10.1023/A:1015522100497.

Kapoor, R., Giri, B. and Mukerji, K.G. 2004. Improved growth and essential oil yield and quality in *Foeniculum vulgare* Mill. on mycorrhizal inoculation supplemented with P-fertilizer. *Bioresour. Technol.* **93**: 309-311; doi: 10.1016/ j.biortech. 2003.10.028.

Klironomos, J.N. 2003.Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* **84**: 2292-2301. doi: 10.1890/02-0413.

Koegel, S., Ait Lahmidi, N., Arnould, C. *et al.* 2013. The family of ammonium transporters (AMT) in *Sorghum bicolor*: two AMT members are induced locally, but not systemically in roots colonized by arbuscular mycorrhizal fungi. *New Phytol.* **198**: 853-865; doi: 10.1111/nph.12199

Kumar, V.V. 2016. Plant Growth-Promoting Microorganisms: Interaction with Plants and Soil. In: *Plant, Soil and Microbes*. Springer, Cham. pp. 1-16.

Leifheit, E.F., Veresoglou, S.D. and Lehmann, A. 2014. Multiple factors influence the role of arbuscular mycorrhizal fungi in soil aggregation- a meta-analysis. *Plant Soil* **374**: 523-537; doi: 10.1007/s11104-013-1899-2.

Lekberg, Y. and Koide, R.T. 2005. Is plant performance limited by abundance of arbuscular mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003. *New Phytol.* **168**: 189-204; doi: 10.1111/j.1469-8137.2005.01490.x

Lingua, G., Bona, E., Manassero, P. *et al.* 2013. Arbuscular mycorrhizal fungi and plant growth-promoting pseudomonads increases anthocyanin concentration in strawberry fruits (*Fragaria* x *Ananassa* var. *selva*) in conditions of reduced fertilization. *Int. J. Mol. Sci.***14**: 16207-16225.

Loján, P., Senés-Guerrero, C., Suárez, J.P. *et al.* 2017. Potato field-inoculation in Ecuador with *Rhizophagus irregularis:* no impact on growth performance and associated arbuscular mycorrhizal fungal communities. *Symbiosis* **73**: 45-56; doi: 10.1007/s 13199-016-0471-2

Luginbuehl, L.H., Menard, G.N., Kurup, S. *et al.* 2017. Fatty acids in arbuscular mycorrhizal fungi are synthesized by the host plant. *Science* **356**: 1175-1178; doi: 10.1126/science.aan0081

Mandal, S., Upadhyay, S., Singh, V. P. *et al.* 2015. Enhanced production of steviol glycosides in mycorrhizal plants: a concerted effect of arbuscular mycorrhizal symbiosis on transcription of biosynthetic genes. *Plant Physiol. Biochem.* **89**: 100-106; doi: 10.1016/ j.plaphy.2015.02.010.

Mardhiah, U., Caruso, T., Gurnell, A. *et al.* 2016. Arbuscular mycorrhizal fungal hyphae reduce soil erosion by surface water flow in a greenhouse experiment. Appl. *Soil Ecol.* **99**: 137-140; doi: 10.1016/ j.apsoil. 2015.11.027.

Meier, S., Borie, F., Bolan, N. *et al.* 2012. Phytoremediation of metal-polluted soils by arbuscular mycorrhizal fungi. *Crit. Rev. Env. Sci. Tec.* **42**: 741-775; doi: 10.1080/10643389.2010.528518.

Nouri, E., Breuillin-Sessoms, F., Feller, U. *et al.* 2014. Phosphorus and nitrogen regulate arbuscular mycorrhizal symbiosis in *Petunia hybrida*. *PloS One.* **9**: e90841; doi:10.1371/journal.pone. 0090841

Ortiz, N., Armada, E., Duque, E. *et al.* 2015. Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: effectiveness of autochthonous or allochthonous strains. *J. Plant Physiol.* **174**: 87-96; doi: 10.1016/j.jplph.2014.08.019.

Philippot, L., Raaijmakers, J.M., Lemanceau, P. *et al.* 2013. Going back to the roots: the microbial ecology of the rhizosphere. *Nat. Rev. Microbiol.* **11**: 789-799; doi: 10.1038/nrmicro3109.

Rillig, M.C., Aguilar-Trigueros, C.A., Camenzind, T. *et al.* 2019. Why farmers should manage the arbuscular mycorrhizal symbiosis. *New Phytol.* **222**: 1171-1175; doi: 10.1111/nph.15602.

Rillig, M.C., Mummey, D.L., Ramsey, P.W. *et al.* 2006. Phylogeny of arbuscular mycorrhizal fungi predicts community composition of symbiosis-associated bacteria. *FEMS Microbiol. Ecol.* **57**: 389-395; doi: 10.1111/j.1574-6941.2006.00129.x.

Rillig, M.C., Sosa-Hernandez, M.A., Roy, J. *et al.* 2016. Towards an integrated mycorrhizal technology: harnessing mycorrhizae for sustainable intensification in agriculture. *Front. Plant Sci.* **7**: 1625-1639; doi: 10.3389/fpls.2016.01625.

Rodriguez, A. and Sanders, I.R. 2015. The role of community and population ecology in applying mycorrhizal fungi for improved food security. *The ISME Journal* **9**: 1053-1061; doi: 10.1038/ismej.2014.207.

Rouphael, Y., Franken, P., Schneider, C. *et al.* 2015. Arbuscular mycorrhizal fungi act as biostimulants in horticultural crops. *Sci. Hortic.* **196**: 91-108; doi: 10.1016/j.scienta.2015.09.002.

Sawers, R.J., Svane, S.F., Quan, C. *et al.* 2017. Phosphorus acquisition efficiency in arbuscular mycorrhizal maize is correlated with the abundance of root-external hyphae and the accumulation of transcripts encoding PHT1 phosphate transporters. *New Phytol.* **214**: 632-643; doi.org/10.1111/nph. 14403.

Sharma, S., Anand, G., Singh, N. *et al.* 2017. Arbuscular mycorrhiza augments arsenic tolerance in wheat (*Triticum aestivum* L.) by strengthening antioxidant defense system and thiol metabolism. *Front. Plant Sci.* **8**: 906-921; doi: 10.3389/fpls.2017.00906.

Simpson, R.T., Frey, S.D., Six, J. *et al.* 2004. Preferential accumulation of microbial carbon in aggregate structures of no-tillage soils. *Soil Sci. Soc. Am. J.* **68**: 1249-1255; doi: 10.2136/sssaj2004.1249.

Smith, A.H., Lingas, E.O. and Rahman, M. 2000. Contamination of drinking-water by arsenic in Bangladesh: a public health emergency. *Bull. World Health Organ.* **78**: 1093-1103; doi: abbs.who.int/iris/ handle/10665/57459.

Smith, S.E. and Read, D.J. 2008. *Mycorrhizal Symbiosis.* San Diego, CA, Academic Press.

Smith, S.E. and Smith, F.A. 2011. Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. *Ann. Rev. Plant Biol.* **62**: 227-250; doi: 10.1146/annurev-arplant-042110-103846.

Song, Y., Chen, D., Lu, K. *et al.* 2015. Enhanced tomato disease resistance primed by arbuscular mycorrhizal fungus. *Front. Plant Sci.* **6**: 786-804; doi: 10.3389/fpls.2015.00786.

Thokchom, S. D., Gupta, S. and Kapoor, R. 2020. Arbuscular mycorrhiza augments essential oil composition and antioxidant properties of *Ocimum tenuiflorum* L. A popular green tea additive. *Ind. Crop Prod.* **153**: 112-418; doi: 10.1016/j.indcrop.2020.112418.

Tilman, D., Fargione, J., Wolff, B. *et al.* 2001. Forecasting agriculturally driven global environmental change. *Science* **292**: 281-284; doi: 10.1126/science. 1057544.

Treseder, K.K. and Turner, K.M. 2007. Glomalin in ecosystems. *Soil Sci. Soc. Am. J.* **71**: 1257-1266; doi: 10.2136/sssaj2006.0377.

van der Heijden, M.G., Boller, T., Wiemken, A. *et al.* 1998. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* **79**: 2082-2091; doi: 10.1890/0012-9658 (1998)079[2082:DAMFSA] 2.0.CO;2.

Vosátka, M., Látr, A., Gianinazzi, S. *et al.* 2012. Development of arbuscular mycorrhizal bio-technology and industry: current achievements and bottlenecks. *Symbiosis* **58**: 29-37; doi: 10.1007/s13199-012-0208-9.

Walder, F., Brulé, D., Koegel, S. *et al.* 2015. Plant phosphorus acquisition in a common mycorrhizal network: regulation of phosphate transporter genes of the Pht1 family in sorghum and flax. *New Phytol.* **205**: 1632-1645; doi: 10.1111/nph.13292.

Watts-Williams, S.J., Emmett, B.D., Levesque-Tremblay, V. *et al.* 2019. Diverse *Sorghum bicolor* accessions show marked variation in growth and transcriptional responses to arbuscular mycorrhizal fungi. *Plant Cell Environ.* **42**: 1758-1774; doi: 10.1111/pce. 13509.

Zipfel, C. and Oldroyd, G.E. 2017. Plant signalling in symbiosis and immunity. *Nature* **543**: 328-336; doi: 10.1038/nature22009.