Vesicular Arbuscular Mycorrhizal (VAM) fungi- as a major biocontrol agent in modern sustainable agriculture system

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MICROBIOLOGY

Vesicular Arbuscular Mycorrhizal (VAM) Fungi- as a Major Biocontrol Agent in Modern Sustainable Agriculture System[1]

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Abstract—In the present agricultural system, the discriminate use of synthetic chemical fertilizers has predominantly increased throughout the world. Moreover, using excessive use of fertilizers to increase production deteriorates the various soil qualities and pollute water body environment. So using VAM fungi as a biocontrol agent in modern sustainable agriculture, in terms of various parameters like reduction of damage caused by various pathogens, cost effectiveness, energy saving and also as an environment friendly, is a promising perspective in modern agriculture. Also control of plant pathogens in modern agriculture is presently accepted as a key practice in sustainable agriculture because it is based on the management of certain rhizosphere organisms, common components of ecosystems, known to develop antagonistic activities against harmful organisms. *Vesicular Arbuscular mycorrhizal* fungi interact with other microorganisms in the rhizosphere and various other soil constituents. Upon root colonization by VAMF, there occurs profound physiological changes in the host plant. Present agriculture system increasing demand for low-input agriculture and creates greater interest in soil microorganisms which are able to accelerate plant nutrition, health and improve soil quality. The importance of VAM in incresaing food production is far and wide; therefore these can be used in modern sustainable agriculture particulary as biocontrol agent. This review highlights the different interactions of *Vesicular Arbuscular Mycorrhizal Fungi* (VAMF) and the rule of these interactions in the biological control of plant pathogens. But the commercial use of *Vesicular Arbuscular Mycorrhizal fungi* (VAMF) as biocontrol agents is still in its infancy. The main reason is the poor understanding of the mechanisms of the modes of action of VAM fungi in association with the host plants.

Keywords: VAM fungi, Biocontrol, Plant defence, Rhizosphere, Sustainability

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INTRODUCTION

Among the varous microbial groups, arbuscular mycorrhizal (AM) fungi is known to accelerate activities which can improve agricultural developments and hence these microorganisms appears as a current research target with regard to sustainability purposes (Johansson et al., 2004). Mycorrhiza is the mutualistic association between fungi of soil-borne and roots of higher plants (Sieverding, 1991). In this association, the underground portion called mycellium are in contact with the roots of plant and causing no harm to the plant. The term 'mycorrhiza' is actually derived from Greek word which means 'fungus root' (Friberg, 2001). The term was first coined by a German plant pathologist named A.B Frank (1855) to describe the symbiotic association between plant roots and fungi and it is probably the oldest and most widespread plant symbiosis on Earth. Fossil evidence and DNA sequence analysis revealed that their existence back more than 450 million years (Smith and Read 2008). Arbuscular mycorrhiza fungi (AMF) are obligate biotrophs that require the plant host to complete their life cycle. Two types of mycorrhiza are known: ecto and endomycorrhizas. The ectomycorrhizas are characterized by an extracellular fungal growth in the root cortex while as the endomycorrhizas are characterized by forming inter-and intracellular fungal structures, called as vesicles and arbuscles. This characteristic growth gives the endomycorrhiza the alternate name, vesicular arbuscular mycorrhiza and these are the structures where the exchange of nutrients between the partners easily takes place. The extracellular hyphal network spreads widely out of the nutrient depletion zone and accelerates the supply of inorganic nutrients, especially phosphate and nitrate and in return, the fungal heterotroph receives photosynthesized material from the host plant (Smith et al., 2010). Mycorrhizal fungi relationship increased uptake of nutrients, production of growth promoting substances, tolerance to drought, salinity and also regulates the defense mechanism of plants (Hause et al., 2007).

Microbial population in conventional farming systems have been modified because of tillage system and

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indiscriminate use of inorganic fertilizers, herbicides and pesticides (Gianinazzi et al., 2010). The microbial diversity in these systems has been ultimately reduced (Maeder et al., 2002) and the loss of this diversity is still uninvestigated. Large scale use of inorganic fertilizers enormously increased agricultural production regionally and globally but on the other hand, it decreases the soil fertility, soil microbial diversity, run off these fertilizers and ultimately creates water pollution. The functioning of arbuscular mycorrhiza in the field, particularly at ecosystem level attracting increasing attention (Brundrett, 1991) and also due to increased awareness about environmental problems has ultimately led to shift from conventional intensive management to low input for crop production. AMF can play an essential role in such environments.

VAM FUNGI AS A BIOLOGICAL CONTROL AGENT

The AM fungi association compete with the pathogens of plant to get nutrients and space, by producing antibiotics or by inducing resistance in the host plants, and these microbes have been used for biocontrol of pathogens (Berg et al., 2007). It has been suggested that AM fungi increase host tolerance of pathogen attack by compensating for the loss of root biomass or function caused by pathogens including nematodes and fungi (Cordier et al., 1998). Early research work showed that changes in the soil microorganisms population induced by mycorrhiza formation may lead to the stimulation of special components of the resident microbiota and that can be antagonistic to root pathogens. Various mechanisms involved in the AMF-mediated biocontrol and the mechanisms include direct effect of AMF on the pathogen, competition for space or nutrients, or indirect, plant-mediated, effects. The latter indirect plant-mediated effects can further be divided into plant tolerance; plant defence resistance induced by AMF and also alleviate plant exudation leading to altered rhizosphere interactions. The different mechanisms cannot be considered as completely independent from each other and the biocontrol results come from the combination of these different mechanisms (Vierheilig et al., 2008; Cameron et al., 2013). The relative significance of a particulat mechanism can vary depending on the specific AMF-pathogen-plant interaction.

In recent years, much progress has been made, especially in the domains of induced systemic resistance as well as on the role of the rhizosphere in biological control (Pieterse et al., 2014). The main conclusions that can be drawn are: (1) AMF associations can reduce the damage caused by various plant pathogens which are soil-borne (2) the capability of the AM associations so for tested for enhancing resistance or tolerance in roots are not same for the different AM fungi (3) protection is not effective for all pathogens, and (4) protection is changed particularly by soil and other environmental conditions. Thus the interactions between different AM fungi and plant pathogens will vary with the host plant as well as the culture system.The interactions between AM fungi and plant parasitic nematodes of various plants were studied by various scientists and they reported that root colonization by AM fungi increases tolerance of the host to Meloidogyne species, such as that of peanut to Meloidogyne Arenaria (Carling et al., 1996); banana to M incognita (Jaizme et al., 1997) and Prunus root stocks toM. javanica (Calvet et al., 2001).

MECHANISMS BY WHICH AMF ACTS AS A BIOCONTROL AGENT

In recent experimental studies, it has been observed that the inoculated AM plants receive protection from pathogens as compared to their non-mycorrhizal counterparts. (Filion et al., 2003). How AM fungi protects the plants from the infection of various pathohgens, various mechanisms have been proposed to explain its protection capability (Whipps, 2004; Dalpe, 2005). AM fungal taxa vary both in the expression of traits and in their ability to protect host plants against pathogens associated (Maherali and Klironomos 2007; Sikes et al., 2009). Most studies carried out by various scientists reported that interactions between AM fungi and plant parasitic nematodes increases the root colonization and hence increases tolerance of the host to *Meloidogyne* species. Mechanisms that could account for the protective (biocontrol) activity ascribed to AM fungi include improvement of plant nutrition status, altered root architecture, competition for nutrients and space, induction of systemic resistance, Changes in microbial community in the rhizospheric zone, activation of plant defence mechanisms.

ENHANCED NUTRIENT UPTAKE OF THE HOST PLANT

It is well known that AM fungi can increase the nutrient uptake of their host plants. Arbuscular mycorrhizal association with the host plant increases the uptake of water and most essential mineral nutrients for their host plant, such as phosphate and nitrogen (Parniske, 2008; Baum et al., 2015). But probably also micro-elements such as zinc and in return, AM fungi receives photosynthetic carbon from their host (Smith and Smith, 2011a). The plants that took up vast amounts of nutrients through their AM fungal association have the potential to tolerate against various pathogenic infections (Karagiannidis et al., 2002) and also it is not clear whether this increased tolerance was a direct consequence of improved nutrition. In other research studies, not involving the AM symbiosis, enhancement in nutrient uptake did not result in improved pathogen tolerance.

Higher uptake of phosphate has been recently proposed as a main mechanism for the AMF-mediated biocontrol and the addition of phosphate to non-mycorrhizal plants did not result in a similar reduction of pathogen infection (Bodker et al., 1998). The research findings of Fritz et al (2006) showed that tomato plants infected by *Rhizophagus irregularis* expressed very less symptoms which were caused by *A. solani* than non-mycorrhizal plants, while no enhancement was observed regarding phosphate uptake. Hence, there is not always a positive correlation between enhanced phosphate uptake and promotion of plant growth in mycorrhizal plants, as in some cases suppression of plant growth resulted as a consequence of AMF colonization, even when phosphate transport from the AMF to the host plant was taking place (Smith and Smith, 2011b). Cotton field plants infected with a semi-endoparasitic nematode *Rotylenchulus reniformis* have the potential to tolerate higher PPN (Plant-parasitic nematodes) population densities in their roots (Pettigrew et al., 2005).

ALTERED ROOT ARCHITECTURE

In most research studies it has been suggested that AM fungal colonization changes root architecture of the host plant (Gutjahr and Paszkowski, 2013) Apart from an increased nutrient status, mycorrhizal plants often show increased root growth and branching (Gamalero et al., 2010). The research findings of Atkinson et al. 1994 demonstrated that colonization by AM induces significant changes in root morphology, as well as in the meristematic and nuclear activities of root cells. This might affect rhizosphere interactions and particularly pathogen-infection development. The responses showed by root morphology resulting from AMF colonization seem to depend on characteristics of plant, with tap root system appearing to gain more benefit from AMF than fibrous root system in terms of gained biomass and nutrient acquisition (Yang et al., 2014). Although a solid correlation could not have been found, how increased root branching system in mycorrhizal plants have implications on pathogen infection. Positive synergistic effects could result from an enhancement in root vigour, because of higher nutrient uptake capacity and might even counterbalance the suppressed root growth caused by various root pathogens. The negative impact of migratory endoparasitic nematodes *Radopholus similis* and *P. coffeae* on root branching in banana plant was counterbalanced by the increase in root branching due to colonization by the AMF *Funneliformis mosseae* (Elsen et al., 2003).

COMPETITION FOR HOST NUTRIENTS, SPACE AND INFECTION/COLONIZATION SITES

Competition for host nutrients or for space and infection sites do occur between micro-organisms having same physiological requirements in an ecological niche, especially where resources such as carbon might be limited (Vos et al., 2014). Nutrient competition, especially on carbon competition, has been proposed as a main mechanism of the AMF-mediated biocontrol (Jung et al., 2012). When AM fungi have primary access to photosynthates of the host plant, the demand for higher carbon inhibits pathogen growth. Pathogen biocontrol activity of AM symbiosis by competition for carbon compounds is a generalized mechanism because of little or no evidence for pathogen biocontrol activity of AM symbiosis. The transfer of carbon from the total assimilated carbon of the host plant to the AMF is nearly to range from 4 to 20% (Hammer et al., 2011) and hence thus seems plausible that AMF compete with pathogens for carbon resource. Competition for the available space implies that a higher degree of colonization of the AMF with the host root leads to a higher level of AMF-mediated biocontrol activity (Vierheilig et al., 2008).

Competition could be direct for root space (root tissues) by AM fungi, soil-borne fungal pathogens and plant parasitic nematodes if colonisation is occurring at the same time (Smith, 1988). A mature AMF colonization which is distinguished by the presence of arbuscules and seems to be a prerequisite for biocontrol (Pozo and Azcon, 2007). The process of reproduction of *Meloidogyne incognita* was reduced when the symbiotic relationship was well established prior to inoculation by *M. incognita* (Dos Anjos et al. 2010). However, a biocontrol activity was observed when coffee plants were co-inoculating with AMF together with M. Eexigua (Alban et al., 2013). The number of infection sites on a particular root system will determine the extent of pathogen ingress. Vigo et al. 200 found that the number of infection sites was reduced within mycorrhizal root systems and thus suggesting that the number of infection sites was important for subsequent pathogen infection.

CHANGES IN THE INTERACTION OF RHIZOSPHERIC MICROBES

The changes induced by AM in the population of soil microorganisms populations may lead to stimulation of those ccomponents by microbiota, which are antagonistic to root pathogens. The research findings of Meyer and Linderman (1986) showed that AM establishment can alter both the total population and specific functional groups of rhizospheric microorganisms and they also found that in the cultures of *Phytophthora cinnamomi*, the number of sporangia and zoospores were reduced by applying extracts of rhizospheric soil from AM plants. Changes due to the influence AM fungi on mycorrhizosphere microbial communities may lead to directly to the reduction of population of fungal pathogens (Larsen et al. 2003). Various factors like altered exudation patterns, putative direct AM fungal effects, different root size and architecture, altered physiology may contribute changes in the community of microbes which are mostly quantitative and qualitative caused by AM fungi (Toljander et al. 2007). It has been reported that there are differences in root exudate quantity and quality between mycorrhizal and non-mycorrhizal plants on the basis of various compounds like sugars, organic acids and amino acids (Hage-Ahmed et al., 2013). Changes in root exudation can also causes a change in the diversity of microbes in the rhizosphere, and hence affect plant-pathogen interactions (Lioussanne, 2010).

ACTIVATION OF PLANT DEFENCE MECHANISMS

Response to AM colonization by the activation of specific plant defence mechanisms is the basis mechanism for the protective action of AM fungi. Various research findings revealed that AM symbiosis involves several genes and numerous protein products to activate plant defence mechanism. Using modern molecular biology techniques and immunological and histochemical analyses will probably provide more information about the defence mechanisms.

The early stages of the interaction between AM and plant, the plant host responses to the interaction by activating defense-related responses and that are subsequently suppressed (Garcia-Garrido, 2002; Liu et al., 2003). Before entering the plant roots, the fungus partner activate the plant's immune system as a biotrophic pathogen (Guimil et al., 2005; Paszkowski, 2006). The transient increase of endogenous salicylic acid (S A) in the roots of a plant occurs in quick fashion in response to AM colonization which is observed by the accumulation of special defensive compounds like reactive oxygen species, specific isoforms of hydrolytic enzymes, and also the activation of the phenylpropanoid pathway (Roman et al., 2011). During early colonization of plant roots particulary by *Glomus intraradices*, increases the amount of various essential enzymes of phenylpropanoid pathway (Phenylalanine ammonium-lyase (PAL) and chalcone isomerase enzyme specific for flavonoid/isoflavonoid biosynthesis, but their concentration decreased sharply to levels at or below those in uninoculated controls (Volpin et al. 1994, 1995). Hence these research findings revealed that AM fungi initiate a host defence response which is subsequently suppressed.

CONCLUSION

There are various proposed mechanisms for the bioprotection action of VAM fungi in sustainable agriculture system, but is suggested that effective bioprotection is a result of all the mechanisms discussed above, whether working separately and/or together. The challenge for developing more sustainable production systems in the future includes gaining a better understanding of the mechanisms involved and the plant pathogen and fungal and environmental factors that together dictate the scale and timing of their expression. The identification of defense regulatory elements that may operate in priming of plant defenses in mycorrhizal plants may have important practical implications regarding the effectiveness of AMF in the biological control and integrated management of pests and diseases. Thus far, few research about AMF-mediated biocontrol involved "omics" tools and systems biology approaches but this will increase over time and will provide more detailed insights in the complex mechanisms underlying AMF-mediated biocontrol. These insights might in turn lead to the effective application of AMF in the agriculture field.

REFERENCES

1. Alban, R., Guerrero, R., and Toro, M., Interactions between a root-knot nematode (*Meloidogyne exigua*) and arbuscular mycorrhizae in coffee plant development (*Coffea arabica*), *Am. J. Plant Sci.,* 2013, vol. 4, pp. 19–23.
2. Atkinson, S., Berta, G., and Hooker, J.E., Impact of mycorrhizal colonisation on root architecture, root longevity and the formation of growth regulators, in *Impact of Arbuscular Mycorrhizas on Sustainable Agriculture and Natural Ecosystems,* Gianinazzi, S. and Schuepp, H., Eds., Basel: ALS, Birkhauser Verlag, 1994, pp. 47–60.
3. Baum, C., El-Tohamy, W., and Gruda, N., Increasing the productivity and product quality of vegetable crops using arbuscular mycorrhizal fungi: A review, *Sci. Hortic. (Amsterdam),* 2015, vol. 187, pp. 131–141.
4. Elsen, A., Beeterens, R., Swennen, R., and Waele, D., Effects of an arbuscular mycorrhizal fungus and two plant-parasitic nematodes on Musa genotypes differing in root morphology, *Biol. Fertil. Soils,* 2003, vol. 38, pp. 367–376.
5. Berg, G., Grosch, R., and Scherwinski, K., Risk assessment for microbial antagonists: Are there effects on non-target organisms?, *Gesunde Pflanzen,* 2007, vol. 59, pp. 107–117.
6. Bodker, L., Kjoller, R., and Rosendahl, S., Effect of phosphate and the arbuscular mycorrhizal fungus *Glomus intraradices* on disease severity of root rot of peas (*Pisum sativum*) caused by *Aphanomyces euteiches, Mycorrhiza,* 1998, vol. 8, pp. 169–174.
7. Brundrett, M., Mycorrhizas in natural ecosystem, in *Advances in Ecological Research,* Macfayden, B.M. and Fitter, A.H., Eds., London: Academic Press, 1991, pp. 171–173.

8. Calvet, C., Pinochet, J., Hernández-Dorrego, A., Estaún, V., and Camprubi, A., Field micro plot performance of the peach-almond hybrid GF-677 after inoculation with arbuscular mycorrhizal fungi in a replant soil infested with root-knot nematodes, *Mycorrhiza,* 2001, vol. 10, pp. 295–300.

9. Cameron, D., Neal, A., van Wees, S., and Ton, J., Mycorrhiza-induced resistance: More than the sum of its parts?, *Trends Plant Sci.,* 2013, vol. 18, pp. 539–545.

10. Carling, D.E., Roncadori, R.W., and Hussey, R.S., Interactions of arbuscular mycorrhizae, *Meloidogyne arenaria*, and phosphorus fertilization on peanut, *Mycorrhiza,* 1996, vol. 6, pp. 9–13.

11. Dos Anjos, É.C.T., Cavalcante, U.M.T., Gonçalves, D.M.C., Pedrosa, E.M.R., Santos, V.F., and Maia, L.C., Interactions between an arbuscular mycorrhizal fungus (*Scutellospora heterogama*) and the root-knot nematode (*Meloidogyne incognita*) on sweet passion fruit (*Passiflora alata*), *Braz. Arch. Biol. Technol.,* 2010, vol. 53, pp. 801–809.

12. Cordier, C., Pozo, M.J., Barea, J.M., Gianinazzi, S., and Gianinazzi-Pearson, V., Cell defense responses associated with localized and systemic resistance to *Phytophthora parasitica* induced in tomato by an arbuscular mycorrhizal fungus, *Mol. Plant Microbe Interact.,* 1998, vol. 11, pp. 1017–1028.

13. Filion, M., St-Arnaud, M., and Fortin, J.A., Direct interaction between the arbuscular mycorrhizal fungus *Glomus intraradices* and different rhizosphere microorganisms, *New Phytol.,* 2003, vol. 141, pp. 525–533.

14. Fritz, M., Jakobsen, I., Lyngkjaer, M.F., Thordal-Christensen, H., and Pons Kühnemann, J., Arbuscular mycorrhiza reduces susceptibility of tomatoto *Alternaria solani, Mycorrhiza,* 2006, vol. 16, pp. 413–419.

15. Gamalero, E., Pivato, B., Bona, E., Copetta, A., Avidano, L., and Lingua, G., Interactions between a fluorescent pseudomonad, anarbuscular mycorrhizal fungus and a hypo virulent isolate of *Rhizoctonia solani* affect plant growth and root architecture of tomato plants, *Plant Biosyst.,* 2010, vol. 144, pp. 582–591.

16. García-Garrido, J.M. and Ocampo, J.A., Regulation of the plant defense response in arbuscular mycorrhizal symbiosis, *J. Exp. Bot.,* 2002, vol. 53, pp. 1377–1386.

17. Gianinazzi, S., Gollotte, A., Binet, M.-N., van Tuinen, D., Redecker, D., and Wipf, D., Agroecology: The key role of arbuscular mycorrhizas in ecosystem services, *Mycorrhiza,* 2010, vol. 20, pp. 519–530.

18. Güimil, S., Chang, H.-S., Zhu, T., Sesma, A., Osbourn, A., Roux, C., Ioannidis, V., Oakeley, E.J., Docquier, M., Descombes, P., Briggs, S.P., and Paszkowski, U., Comparative transcriptomics of rice reveals an ancient pattern of response to microbial colonization, *Proc. Nat. Acad. Sci. U.S.A.,* 2005, vol. 102, pp. 8066–8070.

19. Gutjahr, C. and Paszkowski, U., Multiple control levels of root system remodelling in arbuscular mycorrhizal symbiosis, *Plant Sci.,* 2013, vol. 4, p. 204.

20. Hage-Ahmed, K., Moyses, A., Voglgruber, A., Hadacek, F., and Steinkellner, S., Alterations in root exudation of intercropped tomato mediated by the arbuscula rmycorrhizal fungus *Glomus mosseae* and the soil borne pathogen *Fusarium oxysporum* f.sp. *lycopersici, J. Phytopathol.,* 2013, vol. 161, pp. 763–773.

21. Hammer, E.C., Pallon, J., Wallander, H., and Olsson, P.A., Tit for tat? A mycorrhizal fungus accumulates phosphorus under low plant carbon availability, *FEMS Microbiol. Ecol.,* 2011, vol. 76, pp. 236–244.

22. Hause, B., Mrosk, C., Isayenkov, S., and Strack, D., Jasmonates in arbuscular mycorrhizal interactions, *Phytochemistry,* 2007, vol. 68, pp. 101–110.

23. Jaizme-Vega, M.C., Tenoury, P., Pinochet, J., and Jaumot, M., Interactions between the root-knot nematode *Meloidogyne incognita* and *Glomus mosseae* in banana, *Plant Soil,* 1997, vol. 196, pp. 27–35.

24. Johansson, J.F., Paul, L.R., and Finlay, R.D., Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture, *FEMS Microbiol. Ecol.,* 2004, vol. 48, pp. 1–13.

25. Jung, S.C., Martinez-Medina, A., Lopez-Raez, J.A., and Pozo, M.J., Mycorrhiza-induced resistance and priming of plant defenses, *J. Chem. Ecol.,* 2012, vol. 38, pp. 651–664.

26. Karagiannidis, N., Bletsos, F., and Stavropoulos, N., Effect of Verticillium wilt (*Verticillium dahliae* Kleb.) and mycorrhiza (*Glomus mosseae*) on root colonization, growth and nutrient uptake in tomato and egg plant seedlings, *Sci. Hortic.,* 2002, vol. 94, pp. 145–156.

27. Larsen, J. and Bodker, L., Interactions between pea root-inhabiting fungi examined using signature fatty acids, *New Phytol.,* 2003, vol. 149, pp. 487–493.

28. Lioussanne, L., Review. The role of the arbuscular mycorrhiza-associated rhizo bacteria in the biocontrol of soil borne phytopathogens, *Span. J. Agric. Res.,* 2010, vol. 8, pp. 3–5.

29. Liu, J., Blaylock, L.A., Endre, G., Cho, J., Town, C.D., Vand, EnboschK.A., and Harrison, M.J., Transcript profiling coupled with spatial expression analyses reveals genes involved in distinct developmental stages of an arbuscular mycorrhizal symbiosis, *Plant Cell,* 2003, vol. 15, pp. 2106–2123.

30. Maeder, P., Fliessbach, A., Dubois, D., Gunst, L., Fried, P., and Niggli, U., Soil fertility and biodiversity in organic farming, *Science,* 2002, vol. 296, pp. 1694–1697.

31. Maherali, H. and Klironomos, J., Influence of phylogeny on fungal community assembly and ecosystem functioning, *Science,* 2007, vol. 316, pp. 1746–1748.

32. Meyer, J.R. and Linderman, R.G., Response of subterranean clover to dual inoculation with *vesicular-arbuscular mycorrhizal* fungi and a plant growth-promoting bacterium, *Pseudomonas putida, Soil Biol. Biochem.,* 1986, vol. 18, pp. 185–190.

33. Parniske, M., Arbuscular mycorrhiza: The mother of plant root endosymbioses, *Nat. Rev. Microbiol.,* 2008, vol. 6, pp. 763–775.

34. Paszkowski, U., Mutualism and parasitism: The yin and yang of plant symbioses, *Curr. Op. Plant Biol.,* 2006, vol. 9, pp. 364–370.

35. Pettigrew, W.T., Meredith, W.R., and Young, L.D., Potassium fertilization effects on cotton lint yield, yield components, and reni form nematode populations, *Agron. J.,* 2005, vol. 97, pp. 1245–1251.

36. Pieterse, C.M.J., Zamioudis, C., Berendsen, R.L., Weller, D.M., van Wees, S.C.M., and Bakker, P.A.H.M., Induced systemic resistance by beneficial microbes, *Annu. Rev. Phytopathol.,* 2014, vol. 52, pp. 347–375.
37. Pozo, M.J. and Azcon-Aguilar, C., Unraveling mycorrhiza-induced resistance, *Curr. Opin. Plant Biol.,* 2007, vol. 10, pp. 393–398.
38. Román, M., Fernández, I., Wyatt, T., Sahrawy, M., Heil, M., and Pozo, M.J., Elicitation of foliar resistance mechanisms transiently impairs root association with arbuscular mycorrhizal fungi, *J. Ecol.,* 2011, vol. 99, pp. 36–45.
39. Sieverding, E., *Vesicular-Arbuscular Mycorrhiza Management in Tropical Agrosystems,* Eschborn, 1991.
40. Sikes, B.A., Cottenie, K., and Klironomos, J.N., Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas, *J. Ecol.,* 2009, vol. 97, pp. 1274–1280.
41. Smith, G.S., The role of phosphorous nutrition in interactions of vesicular arbuscular mycorrhizal fungi with soilborne nematodes and fungi, *Phytopathology,* 1988, vol. 78, pp. 371–374.
42. Smith, S.E. and Read, D.J., *Mycorrhizal Symbiosis,* London: Academic Press, 2008, 3rd ed.
43. Smith, S.E., Facelli, E., Pope, S., and Smith, F.A., Plant performance in stressful environments: Interpreting new and established knowledge of the roles of arbuscular mycorrhizas, *Plant Soil,* 2010, vol. 326, pp. 3–20.
44. Smith, F.A. and Smith, S.E., What is the significance of the arbuscular mycorrhizal colonisation of many economically important crop plants?, *Plant Soil,* 2011a, vol. 348, pp. 63–79.
45. Smith, S.E. and Smith, F.A., Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales, *Annu. Rev. Plant Biol.,* 2011b, vol. 62, pp. 227–250.
46. Vierheilig, H., Steinkellner, S. and Khaosaad, T., The biocontrol effect of mycorrhization on soil borne fungal pathogens and the autoregulation of the AM symbiosis: One mechanism, two effects?, in *Mycorrhiza,* Varma, A., Ed., Berlin: Springer-Verlag, 2008, pp. 307–320.
47. Toljander, J.F., Lindahl, B.D., Paul, L.R., Elfstr, M.A., and Finlay, R.D., Influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure, *FEMS Microbiol. Ecol.,* 2007, vol. 61, pp. 295–304.
48. Vigo, C., Norman, J.R., and Hooker, J.E., Biocontrol of the pathogen *Phytophthora parasitica* by arbuscular mycorrhizal fungi is a consequence of effects on infection loci, *Plant Pathol.,* 2000, vol. 49, pp. 509–514.
49. Vos, C.M., Yang, Y., De Coninck, B., and Cammue, B.P.A., Fungal(-like) biocontrol organisms in tomato disease control, *Biol. Control,* 2014, vol. 74, pp. 65–81.
50. Whipps, J.M., Prospects and limitations for mycorrhizas in biocontrol of root pathogens, *Can. J. Bot.,* 2004, vol. 1227, pp. 1198–1227.
51. Yang, H., Zhang, Q., Dai, Y., Liu, Q., Tang, J., and Bian, X., Effects of arbuscular mycorrhizal fungi on plant growth depend on root system: A meta-analysis, *Plant Soil,* 2014, vol. 389, pp. 361–374.

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