Arbuscular Mycorrhizal Fungi and Biological Control of Soil-Borne Plant Pathogens

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ABSTRACT

The role of arbuscular mycorrhizal fungi (AMF) in improving plant growth is now well documented. Most of the studies on AMF-root pathogens suggest that AMF decreased or mitigated the disease severity. Consistent reduction of disease symptoms has been described for fungal, bacterial and nematode pathogens. Studies conducted so far suggest that the mechanisms of suppression may be due to morphological, physiological and biological alterations in the host. Thickening of the cell walls through lignification and production of other polysaccharides in mycorrhizal plants preventing penetration and growth of pathogens like *Fusarium oxysporum* and *Phoma terrestris* have been demonstrated. Higher concentration of ortho-dihydroxy phenols present in mycorrhizal plants compared to non-mycorrhizal plants was found to be inhibitory to the root rot pathogen *Sclerotium rolfsii.* The activation of specific plant defence mechanisms as a response of AMF colonization is an obvious basis for the protective capacity of AMF. Among the compounds involved in plant defence studied in relationship to AMF formation are phytoalexins, enzymes of the phenylpropanoid pathway, chitinases, peroxidases, pathogenesis related (PR) proteins etc. Mycorrhizal plants harbour higher population of microorganisms in the rhizosphere thus making it difficult for the pathogen to compete and gain access to the root. Further mycorhizosphere supports higher population of antagonists and siderophore producers. Thus the possibility of biologically controlling the root pathogens with AMF looks promising.

Keywords: AMF, biocontrol, soil-borne plant pathogens

INTRODUCTION

Plant roots provide an ecological niche for many of the microorganisms that abound in soil. German botanist Albert Bernard Frank in 1885 introduced the Greek word mycorrhiza which literally means "fungus root". Most plant roots form mycorrhizal associations of one kind or the other with certain fungi in soil. These mycorrhizal fungi perform the function of root hairs. The symbiosis is so well balanced that, although many of the host cells are invaded by the fungal endophytes there is neither visible tissue damage nor any degree of pathogenicity towards its host. Mycorrhizal association generally enhances the growth and vigour of the host plants. Because of their wide spread occurrence in nature and their numerous benefits to plants, these fungi are currently attracting much attention in agricultural, horticultural, forestry research. Though there are different mycorrhizal associations, the most common type occurring in all ecological situations, especially in tropics, is the arbuscular mycorrhiza (AM) (Bagyaraj, 2006).

Arbuscular mycorrhizal fungi are geographically ubiquitous and occur over a broad ecological range. They are commonly found in association with agricultural crops, most shrubs, most tropical tree species and some temperate tree species. AM has been observed in 1000 genera of plants representing some 200 families. There are atleast 300,000 respective hosts in the world flora and around 230 species of AMF (Bagyaraj, 2011). AMF belong to the phylum *Glomeromycota*, which has a single class *Glomeromycetes* with four orders *Glomerales*, *Diversisporales*, *Paraglomerales* and *Archaeosporales*. There are 11 families, 17 genera and 228 species. The commonly occurring genera of AMF are *Glomus*, *Gigaspora*, *Acaulospora*, *Entrophospora* and *Scutellospora*. The AM endophytes are not host specific, although evidence is growing that certain endophytes may form preferential association with certain host plants. These fungi are obligate biotrophs.

Increased plant growth because of AM colonization is well documented. The increased plant growth is attributed to enhanced uptake of diffusion limited nutrients, hormone production, biological nitrogen fixation, drought resistance and suppression of root pathogens.

Biological control can be defined as the directed, accurate management of common components of ecosystems to protect plants against pathogens. Biological control of plant pathogens is currently accepted as a key practice in sustainable agriculture because it is based on the management of a natural resource, i.e., certain rhizosphere organisms. Thus biological control preserves environmental quality by reduction in chemical inputs and is characteristic of sustainable management practices (Barea and Jeffries, 1995). Several workers have reported that AMF can act as biocontrol agents for alleviating the severity of disease caused by root pathogenic fungi, bacteria and nematodes (Bagyaraj, 2016).

It is evident that an increased capacity for nutrient acquisition resulting from mycorrhizal association could help the resulting stronger plants to resist stress. However , AM symbiosis may also improve plant health through a more specific increase in protection (improved resistance and /or tolerance against biotic and abiotic stresses (Bethlenfalvay and Linderman,1992; Barea and Jeffries,1995). The study of a possible role for AM symbioses in protection against plant pathogens began in the 1970s, and a great deal of information has been published on the subject, however, the underlying mechanisms needs more investigation (Azcon-Aguilar and Barea, 1996). In this paper a brief account of AMF is given, followed by role played by them in controlling the root pathogens highlighting the mechanisms involved and suggesting the possible future line of work, wherever necessary.

EFFECT OF AMF ON ROOT PATHOGENS

Most of the studies on AMF-root pathogens suggested that

AMF decreased or mitigated the disease severity. Several review articles have appeared on this topic (Schenck, 1987; Hooker *et al.*, 1994; Linderman, 1994; Azcon-aguilar and Barea, 1996; Harrier and Watson, 2004; Bagyaraj, 2006; St-Arnaud and Vujanovic, 2007; Tahat *et. al.*, 2010, Bagyaraj, 2016, Wani *et al.*, 2017). The main conclusion that can be drawn are: 1. AM associations can reduce damage caused by soil-borne plant pathogens, 2. The abilities of AM symbiosis to enhance resistance or tolerance in roots are not equal for the different AMF so far tested, 3. Protection is not effective for all pathogens, and 4. Protection is modulated by soil and other environmental conditions. Thus it can be expected that interactions between different AMF will vary with the host plant and the culture system. Recent studies have shown that AMF differ in their ability to protect plants against different soil-borne plant pathogens. The identity of AM fungal isolate has a dramatic effect on the level of protection against a particular pathogen (Wehner *et al.*, 2010; Veresoglou and Rillig, 2012, Kumar *et al.*, 2016). Consistent reduction of disease symptoms has been described for fungal pathogens such as *Phytophthora parasitica*, *P. cactorum*, *P. vignae*, *Gaeumannomyces graminis* var. *tritici*, *Fusarium oxysporum*, *Chalara* (*Thielaviopsis*) *basicola*, *Rhizoctonia solani*, *R. bataticola*, *Sclerotium rolfsii*, *Pythium ultimum*, *P. splendens*, *Dothiorella gregania*, *Botrytis fabae*, *Ganoderma pseudoferreum* and *Aphanomyces* spp., bacteria such as *Pseudomonas syringae* and *Ralstonia solanacearum* and nematodes such as *Meloidogyne avenaria*, *M. incognita*, *M. hapla*, *M. javanica*, *Tylenchulus semipenetrans, T. vulgaris, Pratylenchus brachyurus, P. zeae, Helichotylenchus dihystera* and *Radopholus similis* (Rabie,1998; Srivastava *et al.*, 2001; Bagyaraj, 2006; Tahat *et al.*, 2010; Bagyaraj and Chawla, 2012; Bagyaraj, 2016). Further integrating AMF and castor cake in the management of root-knot nematode on egg plant have shown that seedlings colonized with mycorrhiza were least infected by *M. incognita* when transplanted in soil which was amended with castor cake. Significant increases in colonization of *Glomus fasciculatum* on roots of egg plant and chlamydospore densities of mycorrhiza indicated favourable effects of castor cake amendment on the growth of *G. fasciculatum* (Rao *et al.*, 1998). Wilt disease complex of tomato caused by 3 pathogens *Ralstonia solanacearum*, *Fusarium oxysporum* f. sp. *lycopersici* and *Meloidogyne incognita* was found to be significantly reduced by the AM fungus *Glomus bagyarajii* among 11 AMF screened for this purpose (Lekshmi *et al.* 2014).

Another study with staggered inoculation of AMF and root pathogen brought out that application of AMF two weeks earlier than pathogen was better than simultaneous application of AMF and the pathogen in reducing the severity of disease. Application of the pathogen two weeks earlier than AMF was not effective in controlling the disease (Suresh and Bagyaraj, 1984). Vast (1997) studied the interaction of AMF of Arabica coffee and the chemical control of nematodes. It was found that when AMF were inoculated well in advance, it resulted in an enhanced tolerance of Arabica coffee cultivars susceptible to endoparasitic nematodes of *Pratylenchus* and *Meloidogyne* that are wide spread in Arabica plantations.

Most of the AM-root pathogen interaction studies have been conducted in crop plants. But the information available on forest tree species is scanty (Mohan and Verma, 1996). There are a large number of root pathogens causing disease of forest tree species, especially in the nursery (Bagyaraj and Kehri, 2012). Availability of healthy stock seedling for planting in the field is an important aspect of forest management. Hence there is a need to carry out more studies on the role of AMF in the control of root pathogens of forest tree species.

MECHANISMS OF SUPPRESSION OF ROOT PATHOGENS BY AMF

Studies conducted so far suggest that the mechanisms of suppression may be due to morphological, physiological and biological alterations in the host.

Morphological alterations

It has been demonstrated that AM colonization induces remarkable changes in root system morphology, as well as in the meristematic and nuclear activities of root cells (Atkinson *et al.*, 1994).This might affect rhizosphere interactions and particularly pathogen-infection development. The most frequent consequence of AM colonization is an increase in branching, resulting in a relatively larger proportion of higher order roots in the root system (Hooker *et al.*, 1994). However the significance of this finding for plant protection has not yet been sufficiently considered. Another study brought out that root architecture plays an important role in AMF protecting plants against root pathogens (Sikes, 2010). More attention needs to be given to root system morphology in the future because it could modify the infection dynamics of the pathogen as well as the pattern of resistance of AM roots to pathogen attack.

Thickening of the cell walls through lignification and production of other polysaccharides in mycorrhizal plants preventing penetration and growth of pathogens like *Fusarium oxysporum* and *Phoma terrestris* have been demonstrated. A stronger vascular system observed in mycorrhizal plants will increase the flow of nutrients, impart greater mechanical strength and diminish the effect of vascular pathogens. Histopathological studies of nematode galls caused by *Meloidogyne* spp. showed that galls in mycorrhizal plants had fewer giant cells or syncitia, which are needed for the development of nematode larvae, compared to non-mycorrhizal plants. The nematodes in mycorrhizal plants were smaller and took a longer time to develop into adults (Bagyaraj, 1996).

Pioneering observations by Dehne (1982) illustrated how fungal root pathogens and AMF, although colonizing the same host tissues, usually develop in different root cortical cells, indicating some sort of competition for space. Cordier *et al.* (1996) working with AM-*Phytophthora* interaction observed that the pathogen does not penetrate cortical cells containing arbuscule; suggesting that localized competition for infection/colonization site does occur between the pathogen and the AM fungus.

Physiological and biochemical alterations

Improved nutrient status of the host plant: Increased nutrient uptake made possible by AM symbiosis results in

more vigorous plants. The plant itself may thus be more resistant to or tolerant of pathogen attack though this is true, some studies using non-mycorrhizal plants with tissue P concentration similar to that of mycorrhizal plants, indicated that non-P mediated mechanisms are also involved (Habte and Schmitt, 2005).

Competition for host photosynthates: It has been proposed that the growth of both the AMF and root pathogens depends on host photosynthates and that they compete for the carbon compounds reaching the root (Linderman, 1994). When AMF have primary access to photosynthates, the higher carbon demand may inhibit pathogen growth. However, there is little or no evidence that competition for carbon compounds is a generalized mechanism for pathogen biocontrol activity of AM symbiosis. Colonization of a plant by AMF alters the host physiology and in turn the root exudation pattern (Mada and Bagyaraj, 1993). Decreased root exudation in mycorrhizal plants increased membrane phospholipid content, possibly helps in reducing the infection by root pathogens.

Higher levels of phenols and amino acids: Higher concentration of ortho-dihydroxy phenols present in mycorrhizal plants compared to non-mycorrhizal plants was found to be inhibitory to the root-rot pathogen *Sclerotium rolfsii*. Higher levels of amino acid arginine in the root extracts of mycorrhizal plants were found to reduce *Thielaviopsis basicola* chlamydospore production. Increased phenylalanine and serine in tomato roots due to inoculation with *G. fasciculatum* was found to be inhibitory to root knot nematodes (Bagyaraj and Chawla, 2012).

Activation of plant defence mechanisms: During their life cycle plants evolve a number of defence responses elicited by various signals, including those associated with pathogen attack (Huynh *et al.,* 1992). The activation of specific plant defence mechanisms as a response to AM colonization is an obvious basis for the protective capacity of AMF. Among the compounds involved in plant defence (Bowles,1990) studied in relationship to AM formation are phytoalexins, enzymes of the phenylpropanoid pathway, chitinases, -1,3-glucanases, peroxidases, pathogenesis related proteins, callose, hydroxyproline rich glycoproteins (HRGP) and phenolics (Gianinazzi Pearson *et al*., 1994; Li *et al.,* 2006; Bagyaraj and Chawla, 2012; Mustafa *et al.,* 2017). Another study showed that application of a consortium of five AMF enhanced polyphenol oxidase, phenylalanine ammonium-lyase and peroxidases in the common bean plant and thus protected it against *Fusarium* wilt (Al-Askar and Rashad, 2010).

Phytoalexins, low-molecular-weight toxic compounds usually accumulating with pathogen attack and released at the sites of infection, were detected during the later stages of AM formation (Morandi *et* al., 1984). There seems to be a similar low activation of the phenylpropanoid-related enzymes. In particular, both phenylalanine ammonium-lyase, the first enzyme of the phenylpropanoid pathway, and the chalcon isomerase, the second enzyme specific for flavanoid /isoflavanoid biosynthesis, increased in amount and activity during early colonization of plant roots by *Glomus intraradices*, but then decreased sharply to levels at or below those in uninoculated controls (Volpin *et al.,* 1995). These results suggest that AMF initiate a host defence response, which is subsequently suppressed. Pathogenesis related proteins and HRGP are synthesized only locally and in very low amount in response to AM colonization.

Electrophoretic analysis of soluble extracts from AM roots has demonstrated that the host plant produces a number of new proteins (endomycorrhizins) in response to AM colonization (Gianinazzi Pearson and Gianinazzi, 1995). New polypeptides are synthesized during AM infection and others disappear (Dumas Gaudot *et al.,* 1994). However, this altered pattern of protein synthesis in the plant is not necessarily related to defence reactions. This is a research area deserving further attention. It can be said that plant defence mechanisms are activated to a very little extent by AM colonization. However, these compounds could sensitize the roots to pathogens and enhance mechanisms of defence to subsequent pathogen infection (Azcon Aguilar and Barea, 1996; Bagyaraj, 2006). Current research using molecular biology techniques and immunological and histochemical analyses will probably provide more information about these mechanisms.

Biological alterations

Mycorrhizal plants harbour higher population of microorganisms in the rhizosphere thus making it difficult for the pathogen to compete and gain access to the root. Caron (1989) reported a reduction in *Fusarium* population in the soil surrounding mycorrhizal tomato roots as compared with the soil of non-mycorrhizal controls. Secilia and Bagyaraj (1987) isolated more pathogen-antagonistic actinomycetes from the rhizosphere of AM plants than from non-mycorrhizal controls, an effect that also depended on the AM fungus involved. Microorganisms producing siderophores, which are low molecular weight chelating agents that have high affinity for ferric iron and thus fungistatic to many pathogens, were observed in higher numbers in the rhizosphere of mycorrhizal plants. The prophylactic ability of some AMF could be exploited in association with other rhizosphere microorganisms known to be antagonistic to root pathogens that are being used as biological control agents (Azcon Aguilar and Barea, 1996).

Earlier studies suggest that microbial antagonists of fungal pathogens, either fungi or plant growth promoting rhizomicroorganisms (PGPR) do not antagonize AMF. Moreover they can improve the development of the mycosymbiont and facilitate AM formation (Lioussanne *et al.*, 2009). Synergistic interactions between AMF and PGPR or other soil microorganisms may enhance bioprotection against soil-borne plant diseases. For example, Siddiqui and Mahmood (1998) demonstrated that the combination inoculation of *G. mosseae* and *P. fluorescens* caused a greater reduction in galling and nematode reproduction than when they were used alone. The mechanisms used by PGPR to protect plants against pathogens are well known: competition for space and nutrients, modification of Fe and Mn availability, liberation of antibiotics and HCN, plant growth promotion by modification of plant hormone balance, and stimulation of systemic and localized plant defence mechanisms (Lioussanne *et al.*, 2009).

Paenibacillus sp. strain B2 along with *G. mosseae* protected sorghum plants more effectively against the pathogen *Phytophthora nicotianae* compared to *G. mosseae* alone (Budi *et al.*, 2000). Wilt disease complex of the medicinal plant *Coleus forskohlii* caused by *Fusarium chlamydosporum, Pseudomonas fluorescens* and *Meloidogyne incognita is* very serious in India. Inoculation with the AM fungus *G. fasciculatum* together with *P. fluorescens* and *Trichoderma viride* was found to increase root yield and root forskolin concentration, and reduce the severity of the disease significantly under field conditions compared to inoculation with only *G. fasciculatum* (Singh *et al.*, 2012). In a recent study we observed that wilt disease complex of capsicum caused by *Phytophthora capsici + Ralstonia solanacearum + Meloidogyne incognita* is reduced by about 50% through inoculation with the microbial consortium consisting of *Glomus bagyarajii + Pseudomonas fluorescens + Paecilomyces lilacinus* under field conditions (unpublished). This brings out that microbial consortia consisting of effective AMF and PGPR can be judiciously selected for controlling soil-borne plant diseases. Therefore, the management of these interactions improving plant growth and health, in an integrated approach, should be one of the targets for future research.

CONCLUSIONS

It can be concluded that AMF has the potential to alleviate the severity of disease caused by soil-borne plant pathogens. Like most instances of biological control AMF cannot offer complete immunity against the soil-borne plant pathogens. They could only impart a degree of resistance against these pathogens. The diversity of interactions between AMF and soil-borne plant pathogens show that each pathogen-AMF-plant combination is unique which is further influenced by the environment. However, the possibility of biologically controlling these pathogens with AMF alone or together with PGPR looks promising. Most of the soil-borne pathogens are currently controlled only with expensive physical or chemical soil treatments. Thus, AMF offer an alternative approach and we should pursue their potential as biocontrol agents. Further, most of the studies, barring few investigations, have been conducted in pots and hence there is a need for exploiting this potential under field conditions.

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