



Biocontrol of Soil Phytopathogens by Arbuscular Mycorrhiza – A Review

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1 Introduction

The use of benign microbes as control mechanism so called ‘Biocontrol’ to kill phytopathogens has been extensively studied wherein **biocontrol** implies to likely enemies of pests or pathogens to eradicate or control their population. It involves the prologue of foreign species that exists as expected in the environment. It has been considered as environmentally safe and the easier option accessible to protect plants against detrimental flora and fauna (Azcon-Aguilar and Barea 1992). Arbuscular mycorrhizal fungi (AMF) are organisms that have been used as biocontrol agents of plants. Mycorrhizae are ubiquitous soil-borne fungi and serve as prospective tools for sustainable agriculture. Mycorrhizae are generally associated with most terrestrial vascular plant species worldwide (Srnith and Read 2008; Brundrett 2009), being beneficial in improving plant growth and development (Jeffries et al. 2003). They belong to the Glomeromycota phylum (Schübler et al. 2001) and originated approximately 450my ago (Schübler and Walker 2011). They improve the growth of plant-root system and control plant pathogens (Gianinazzi and Schuepp 1994). Arbuscular mycorrhizal (AM) fungi influence plant augmentation and improvement. Their interactions with rhizosphere microorganisms influence the overall development of plants (Azcon-Aguilar and Barea 1992; Fitter and Sanders 1992). A harmful involvement between the host plant and the indigenous mycorrhizal fungi leads to solemn fatalities in crop yields, which indicate the connotation of AMF in agriculture (Caron 1989; Ravnskov and Jakobsen 1995; St-Arnaud et al. 1995; Frankenberger and Arshad 1995).

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Mycorrhizal fungi are the most influential group of soil microflora with reference to sustainability of ecosystem, once they establish mutualistic relationship with plants (Jeffries and Barea 2012). The rhizosphere is characterised by improved microbial activity owed to the root exudates (Grayston et al. 1997). Mycorrhizosphere include the fungal component of the symbiosis while plant roots in normal and semi-normal ecosystems are found to have mycorrhizal relations (Rambelli 1973).

The mycorrhizosphere is the area surrounding mycorrhizal fungus where the nutrients on the rampage as of the fungus raise the microbial actions (Linderman 1988). The mycorrhizosphere effect indicates the provoked changes in the plant biochemistry as a result of mycorrhizal-root immigration which causes a shift in the rhizosphere microflora that favours the absence or presence of pathogens (Paulitz and Linderman 1989). The mycorrhizosphere effect causes changes in root exudate composition mainly because of root membrane permeability. The root colonization with AM fungi has been shown to suppress harmful effects of fungi, stramenopiles, nematodes and bacteria ((Graham et al. 1981).

2 The Arbuscular Mycorrhizal Fungi

Mycorrhizal associations diverge broadly in structures and functionalities, but the AM are the most common interactions (Harrier 2001). These fungi are nonculturable and are obligate biotrophs, in view of the fact that these fungi can not inclusive their life cycle devoid of congregate a host. The study of these fungi and their biology and biotechnological applications has been hampered because of non-culturability (Schubler and Walker 2011; Barea et al. 2013). Six genera of AM fungi have been recognized based on phenetic characteristics of sexual spores and also based on various biochemical studies and molecular methods (Peterson et al. 2004). Various biochemical, molecular and immunological characteristics criteria employed for identification of AM fungi (Mukerji et al. 2002). AM fungi include genera such as *Glomus*, *Gigaspora*, *Sclerocystis*, *Acaulospora*, *Entrophospora* and *Scutellospora* (Garbaye 1994).

3 The AM Symbiosis

Srnith and Read (2008) reported that AM symbiosis is the most numerous type of mycorrhizal relationship wherein worldwide approximately 250 k species of plant, including angiosperms, petersengymnosperms and pteridophytes, tend to form such association. Herein, AM symbiosis initiates with the fungal infiltration in the root cortical cell walls followed by configuration of arbuscules -like structures (haustoria or coils) that interface with the host cytoplasm. These fungal structures help to augment exterior area for swap over of metabolites flanked by the plant and the fungus. Several mycorrhizal fungi are recognized to construct vesicles for storage. It has been revealed that in natural ecosystems plants colonised with mycorrhizal fungi

may incur 10–20% of the photosynthetically fixed carbon for their fungal symbionts (Johnson et al. 2002a, b).

The mycorrhizal fungi interact directly with the soil by producing extraradical hyphae that extend deep into the soil (Rhodes and Gerdemann 1975). Extra-radical hyphae raise the potential for nutrient and water uptake (Augé 2001). Hyphae of AM fungi form soil aggregates which play an important role in soil stabilisation (Tisdall and Oades 1979). The extraradical hyphae are responsible for acquisition of phosphorus and other mineral nutrients by plants (Read and Perez-Moreno 2003). These hyphae also improve mobilisation of organically bound nitrogen from plant litter (Hodge et al. 2001). Mycorrhizal fungi also alleviate negative effects of plant pathogens and toxic metals (Khan et al. 2000). The extraradical hyphae interact with other soil organisms either directly by physically and/or metabolically interacting with other organisms in the mycorrhizosphere or indirectly by changing host plant physiology. Extra-radical hyphae are surrounded by complex microbial communities that interact with the plant-mycorrhiza and sustain this relationship (Frey-Klett and Garbaye 2005). Thus, the establishment of the arbuscular mycorrhizal symbiosis affects the structure and diversity of microorganisms not only in the rhizosphere but also in other soil microhabitats.

4 Establishment of Arbuscular Mycorrhiza Fungi

Most vascular plants have exhibited mycorrhizal associations in both natural and agro-ecosystems (van der Heijden et al. 2015; Brundrett 2009; Jeffries and Barea 2012; Bonfante and Desirò 2015; López-Ráez et al. 2011a, b; Maillat et al. 2011). Gutjahr and Parniske 2013; Bonfante and Desirò 2015). Upon root colonization, the extraradical mycelium (ERM) is formed which is frequently considered as “branching absorbing structures”, (Bago et al. 1998). It is able to absorb and transport nutrients up to 25 cm distance (Jansa et al. 2003; Smith and Smith 2012).

5 Biocontrol of Phytopathogenic Fungi by AM Fungi

Phytopathogenic fungi contribute substantially to the overall loss in crop yield followed by plant pathogenic bacteria and viruses. The control of phytopathogens has always been practiced by agrochemical application, which are applied at various sites of plants. However, the constant use of such chemicals results in negative effects on the environment that affects water bodies, soil, plants, animals and human health (Bodker et al. 2002). Phytopathogenic microorganisms also develop resistance against these agrochemicals with the passage of time which makes it more difficult to control. Therefore, biological control as part of integrate pathogen management has been regarded as the most sustainable and a viable alternative to the indiscriminate use of agrochemicals.

The convenience of AM Fungi as biocontrol for controlling various phytopathogenic fungi has been widely accepted (Cordier et al. 1996; Bodker et al. 2002;

Harrier and Watson 2004; Azcon-Aguilar et al. 2002; Jaizme-Vega et al. 1998; Li et al. 1997; Pozo et al. 1999; Kulkarni et al. 1997), Prashanthi et al. (1997; Sharma et al. 1997). Feldmann and Boyle (1998) suggested that the crop loss due to phytopathogenic fungi could be reduced by an aggressively root colonizing AM Fungi. They observed an inverse relationship between *G. etunicatum* root colonization of begonia species and susceptibility to the powdery mildew fungus *Erysiphe cichoracearum*. Filion et al. (1999) found that extraradical mycelium of *G. intraradices* reduced the growth of *F. oxysporum* f. sp. *chrysanthemi*. They suggested that the chemical equilibrium of the mycorrhizosphere resulted in control of pathogen. In another study, Slezack et al. (2000) challenged pea with *Aphanomyces euteiches* and found that a fully established AMF symbiosis essential for protection against the pathogen. *Phytophthora* spp., have been commonly used as model fungi for demonstrating AMF-mediated plant disease control (Trotta et al. 1996). Caron and co-workers (1985) in their studies used the AMF species *G. intraradices* and pathogen *F. oxysporum* f. sp. *lycopersici* on tomato, and revealed that the combination of growth medium used, the application of Phosphorus and pretreatment with AM fungi could reduce disease severity. Newsham et al. (1995) reported that on pre-inoculating the annual grass *Vulpia ciliata* var. *ambigua* with *Glomus* sp. and re-introducing the grass into a natural grass population, there was a reduction in indigenous *F. oxysporum*. Torres-Barragan et al. (1996) in their study found that onion pretreated with *Glomus* sp. delayed the onset of onion white rot caused by *Sclerotium cepivorum* by two weeks in the field.

Hwang (1988) carried out a detailed study on interactions of mycorrhizal fungi and two wilt pathogens of alfalfa (*Medicago sativa*), *Verticillium albo-atrum* and *Fusarium oxysporum* f. sp. *medicaginis*, under controlled conditions over a 6-month period.

6 Biocontrol of Phytopathogenic Bacteria by AM Fungi

The AM fungi have been found to interact with diazotrophic bacteria, biological control agents, and other rhizosphere inhabitants (Nemec 1994) that often result insignificant alterations to plant growth and development. Filion et al. (1999) and Shalaby and Hanna (1998) suggested that interactions between mycorrhizal fungi and bacteria may have negative or beneficial effects or have neutral effect at all on the plant pathogens. Sharma et al. (1995) found that on inoculation of mulberry with *Glomus fasciculatum* or *G. mosseae* in combination with phosphorus the incidence of bacterial blight caused by *P. syringae* pv. *mori* was found to significantly reduce. In a study by Shalaby and Hanna (1998), it was found that *Glomus mosseae* prevented the infection of soybean plants by *P. syringae* by suppressing pathogen population in soybean. Li et al. (1997) also found in their study that *G. macrocarpum* alleviated the infection caused by *P. lacrymans* in eggplant and cucumber. Waschkies et al. (1994) reported that on AMF inoculation of grapevines, the fluorescent pseudomonads on the rhizoplane were reduced which in turn reduced the incidence of

grapevine replant disease. Similarly, root colonization by AMF caused a reduction in the colonization of apple seedling rootlets by actinomycetes causing replant disease (Otto and Winkler 1995).

7 Biocontrol of Phytopathogenic Viruses by AM Fungi

Mycorrhizae-mediated biocontrol of plant pathogenic viruses has been least studied. Earlier, Nemeč and Myhre (1984) demonstrated that mycorrhizal plants increase the rate of multiplication of viruses, increased leaf lesions are found on mycorrhizal plants than on nonmycorrhizal plants and the number of AMF spores in the rhizosphere are reduced considerably. (Shaul et al. 1999). Schonbeck and Spengler (1979) reported that mycorrhizal tobacco plants (*Nicotiana glutinosa* L.) exhibited higher levels of tobacco mosaic virus colonization following the inoculation of mycorrhizal as compared to nonmycorrhizal tobacco. Contrary, Ferraz and Brown (2002) reported that mung bean yellow mosaic bigeminivirus reduced the AM colonization and yield of mycorrhizal plants, while Takahashi et al. (1994) reported lack of response to viral infection by a mycorrhizal host. Jabaji-Hare and Stobbs (1984) used electron microscopy to observe interaction of AMF with plant viruses.

8 Biocontrol of Plant-Parasitic Nematodes by AM Fungi

Many species of plant-parasitic nematodes could be potential pests on agricultural crops (Ferraz and Brown (2002)). They are frequently found in the soil, but *Ditylenchus* spp. could act as aboveground pests and classified based on their feeding patterns (Perry and Moens 2011). The AMF has been deployed as biocontrol agents for nematodes (Jones et al. 2013; Gheysen and Mitchum 2011; Wesemael et al. 2011; Hao et al. 2012; Nicol et al. 2011; Alban et al. 2013; Salvioli and Bonfante 2013; Salvioli and Bonfante 2013).

9 Mechanisms of Mycorrhizae-Mediated Biocontrol

9.1 Higher Nutrient Uptake

The AMF has been suggested to improve phosphorus nutrition, enhance nitrogen uptake, or improve disease resistance in their host plants (Baum et al. 2015; Smith and Smith 2011; Gianinazzi et al. 2010; Singh et al. 2011; Fritz et al. 2006; Smith and Smith 2011). Nitrogen fixing bacteria or Phosphate solubilising bacteria have been found to synergistically interact with AM fungi and benefit plant development and growth (Puppi et al. 1994). Hodge et al. (2001) demonstrated the improved decay of plant litter in soil and N capture from the litter (^{15}N – ^{13}C labelled *Lolium perenne* leaves) in the presence of the AM symbiont *Glomus*. Minerdi et al. (2001)

reported the presence of genes for Nitrogen fixation in endosymbiotic *Burkholderia* in AM which makes it apparent that there may be a potential for enhanced nitrogen supply to mycorrhizal plants all the way through fixation of atmospheric Nitrogen.

9.2 Altered Root Morphology

The AMF symbiotic plants often show increased root growth and branching (Gutjahr and Paszkowski 2013). The root morphology responses resulting from AMF colonization depend on plant characteristics, with tap roots profit more from AM fungi than fibrous roots in terms of gained biomass and nutrient acquisition (Yang et al. 2014). Increased root branching observed in mycorrhizal plants have implications for pathogen infection as well (Vos et al. 2014). The mycorrhizal fungi increase host tolerance of pathogen attack by compensating for the loss of root biomass and functions caused by soilborne pathogenic fungi and nematodes which could be an indirect contribution to the biological control through the conservation of root system function through mycorrhizal arbuscules formation (Linderman 1994; Stoffelen et al. 2000; Norman et al. 1996; Elsen et al. 2003)

9.3 Competition for Nutrients and Space

The basis for interface between AMF and soil microorganisms is largely the physical opposition between mycorrhizal fungi and rhizosphere microorganisms to occupy more space in the roots (Bansal and Mukerji 1996). The pathogen suppression in mycorrhizal plants is mainly due to the competition for nutrients such as carbon by mycorrhiza fungi and rhizosphere soil microorganisms with the same physiological requirements (Jung et al. 2012; Vos et al. 2014). Hammer et al. (2011) stated that there is 4–20% carbon transfer of the total assimilated carbon from the host plant to the AMF. Cordier et al. (1998) reported that *Phytophthora* could not penetrate in arbuscule containing tomato plant. Lerat et al. (2003) reported that different AMF species mediate different levels of biocontrol as there is a difference in carbon sink strength between different AMF species. Vos (2012) reported that the AM fungus *Rhizophagus irregularis* was not having a stronger biocontrol effect on plant parasitic nematodes *Rhadinopholus similis* and *Pratylenchus coffeae* in banana nor on *Meloidogyne incognita* in tomato despite its higher carbon sink strength compared to *Funneliformis mosseae*.

9.4 Systemic Induced Resistance

From the biocontrol point of view AMF has been used to develop systemic induced resistance (SIR) in plants (Trotta et al. 1996; Cordier et al. 1998). The SIR is defined as the unrelenting induction of resistance or tolerance to infection in plants by

inoculating with a pathogen, exposing to an environmental influence or treating with a chemical, with or without antimicrobial activity (Handelsman and Stabb 1996). Jones and Dangl (2006) and Zamioudis and Pieterse (2012) demonstrated that the disease resistance by AMF is mainly due to action of MAMPs. Bodker et al. (1998) reported SIR factor by *G. intraradices* in pea plant for resistance to *A. euteiches*. The AMF-mediated SIR protected potatoes against post-harvest suppression of potato dry rot, wherein dry rot in *G. intraradix*-inoculated potato was reduced by up to 90% compared to uninoculated control (Brendan et al. 1996).

9.5 Altered Rhizosphere Interactions

The AMF symbiosis leads to an changed root exudation composition and distribution in host plants rhizosphere (Jones et al. 2004; Hage-Ahmed et al. 2013; Harrier and Watson 2004; McArthur and Knowles 1992; Steinkellner et al. 2007; López-Ráez et al. 2011a, b. The root exudation may or may not be AMF specific (Kobra et al. 2009; Lioussanne et al. 2008). It helps in autoregulation of symbiosis interaction between plant and AMF (Schaarschmidt et al. 2013; Vierheilig et al. 2008; Pozo and Azcón-Aguilar 2007). Lioussanne et al. (2008) observed that the depending on the maturity level of the AM fungi colonization the attraction of *Phytophthora nicotianae* zoospores toward *R. irregularis* colonized root exudates changed to repellency. The bacterial colonization in rhizosphere induced by AMF reported in recent period (Nuccio et al. 2013; Philippot et al. 2013; Zamioudis and Pieterse 2012; Sood 2003; Druzhinina et al. 2011; Sikora et al. 2008).

9.6 Phytoalexins and Phytoanticipins

Under response to pathogen attack plants produce phytoalexins which are natural products and exhibited antagonistic activity against microflora and –fauna and plant *per se*. They are lipophilic in natures that have the ability to cross the plasma membrane and act inside the cell (Braga et al. 1991). Based on earlier researches it has been demonstrated that phytoalexins are produced in response to microbial infection (Paxton 1981; Wyss et al. 1991) whereas phytoanticipins considered as the storage products in plant cells that produced in anticipation of or prior to pathogen attack (VanEtten et al. 1995). Upon mycorrhiza fungal colonization of roots there is an increase in the level of lignin, syringic, ferulic or coumaric acids and phenolics namely, isoflavonoids or flavonoids (Morandi 1996).

As a result of pathogen invasion (*F. oxysporum*), Dehne and Schonbeck (1979) explored the phytoalexins synthesis in mycorrhizal tomato plants where the plants were inoculated with *G. mosseae*. Upon treatment it has been reported that plants showed greater resistance to the *F. oxysporum* which lead to enhanced phenylalanine and beta-glucosidase activity along with total phenol content in their roots

compared to control plants (Dehne and Schonbeck (1979). Sundaresan et al. (1993) reported *in vitro* inhibition of *F. oxysporum* by a purified ethanol root fraction of mycorrhizal cowpea. Caron et al. 1986 recommended that phytoalexins neutralize the antagonistic effects of pathogens in mycorrhizal plants as compared to control

9.7 Hydrolases

The AMF mediated biocontrol has explored the subsistence of defense-related genes in mycorrhizal plants (Lambais and Mehdy 1995). Pozo et al. (2002) reported that entry of mycorrhizal fungi into tomato roots induced fabrication of hydrolytic enzymes such as chitinase, chitosanase, b-glucanase, and superoxide dismutase to host defense mechanism against *Pseudomonas parasitica*. Graham and Graham (1991) reported constructive relationship between the level of glucanase activity in host tissues and resistance to phytopathogens.

9.8 Antibiosis

Earlier it has been reported that under non influential impact of pH the AMF namely, *G. intraradices* produced unidentified antimicrobial substance that helps in control of conidial germination of *F. oxysporum* f. sp. *Chrysanthemi* (Filion et al. 1999). Likewise, Budi et al. (1999) recovered a bacterium viz., *Paenibacillus* sp. strain from the rhizosphere of *Sorghum bicolor* plants inoculated with *G. mosseae* that showed noteworthy inhibitory activity against *Phytophthora parasitica*.

10 Challenges and Future Perspectives in AM Fungi Mediated Biocontrol

The worth of AMF for controlling of phytopathogens usually measured to be high, but there are restrictions in use of AMF as biological agents for control of phyto-diseases under field conditions. Budi et al. (1999) reported that there are few important consideration to deploy AMF in the field that include firstly, the production of large quantities of AMF quorum and secondly, occurrence of negative interactions between the introduced AMF and the indigenous AMF and microbial community. A host which is greatly mycotrophic or host cultivar may be considered as more appropriate for AMF propagation and imitation than one that is not highly mycotrophic (Bever et al. 1996; Xavier 1999). High soil Phosphorous levels also affect AM fungal colonization in host plants (Ratnayake et al. 1978; Bever et al. 1996).Bever et al. (1996) demonstrated that abundantly diverse AMF community ensures efficient biocontrol of phytopathogens. The diversity of AMF in soils has affected by the preference of host genotype and rotation, levels of fertilizer deployment

(McGonigle and Miller 1996), tillage (McGonigle and Miller 1993), pesticide submission (Schreiner and Bethlenfalvay 1997), and the effect of associated quorum of microflora (Xavier and Germida 2003). Further, Johnson et al. (1992) emphasized that continuous cropping selectively improves the proliferation of AMF that lead to alterations in mycorrhizal biodiversity in the rhizosphere. Likewise, Xavier (1999) observed that use of sole meticulous AMF host out of an indigenous AMF residents resulting in the selective fortification of certain AMF species above others.

The approaches involve AM fungi have been deployed as biocontrol of phytopathogens. Sikora (1997) has been anticipated a holistic approach “natural system administration that derived biologically” for humanizing plant roots that adopts specific cropping patterns that uphold plant protection mechanisms such as tolerance and/or resistance to phytopathogens. This has been considered as practicable substitute to integrated pest administration and inundative approaches to the nonrhizospheric soil for biological control purposes, and underlines the implication of mycorrhizae in root growth and development. In addition, Bagyaraj (1984) recommended that assortment of AMF species for a preferred activity must be based on their capability for continued existence, forceful colonization of host roots and efficacy. It has been shown that AMF species originally recovered from test host roots are benign for numerous plant species (Vinayak and Bagyaraj 1990). It has been observed that inoculating plants with AM fungi induce resistance in plants. Cordier et al. (1998) pointed out that “priming” plants against phytopathogens by AMF inocula helps in protection of plants by employing systemic induced resistance. Herein, the inoculum wants to be functional to plantlets fashioned all the way through tissue culture technique. Boyetchko (1996) reported that an appliance of the bioagent prior to transplanting eliminates the requirement for composite formulations and relevance techniques then exhibits greater biocontrol commotion, reduces costs whereby reflects environment-friendly approach.

11 Conclusions

The AMF not only act as biocontrol of phytopathogens caused by detrimental flora and fauna, it also enhances crop efficiency using offered assets, avoiding battle development to chemicals and maintaining effluence conforming to sustenance of agroecosystem. It is speculated that in the near future, task of AM fungi must become one of the practicable and ecosystem friendly solutions to supervise plant diseases and reducing pathogen occurrence and quorum.

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