Chapter 7
Arbuscular Mycorrhiza Mediated Control of Plant Pathogens

Ishwar Singh and Bhoopander Giri

Abstract The application of pesticides in agriculture significantly reduces crop losses by protecting the plant from several diseases, caused by a variety of attackers including fungi, bacteria, plant-parasite nematodes and insects. However, excessive use of these agrochemicals has become a serious cause of concern in agriculture as these not only pose a potential risk to beneficial soil microbes, which play a pivotal role in maintaining the soil-fertility but also, result in serious implications to human health and environment. Researchers are exploring environment-friendly approaches of plant protection that could minimize the side effects associated with the use of pesticides. The biocontrol is a process by which an undesirable organism is controlled with the help of another organism. Among soil microorganisms, arbuscular mycorrhizal fungi (AMF) have demonstrated a considerable potential to reduce crop damages from infectious organisms, whose applications in agriculture have not yet been adopted to a large extent. In view of the importance of AMF in agriculture, we have described the bioprotective role of AMF against various plant pathogens and the possible mechanisms involved in the biological control of crop diseases.

7.1 Introduction

The world's population is growing rapidly and has been predicted to exceed to even nine billion by the middle of this century (Rodriguez and Sanders 2015). Estimations indicate that the challenge to meet the ever-increasing demands of humankind will put a tremendous pressure on the global agriculture for almost doubling the food production. Unrestricted use of chemical pesticides and fertilizers for controlling plant pathogens and increasing food production has brought the world to the brink of an environmental catastrophe. According to the EU directive, in order to

---

I. Singh
Department of Botany, Hansraj College, University of Delhi, Delhi 110007, India

B. Giri (✉)
Department of Botany, Swami Shraddhanand College, University of Delhi, Delhi, India
e-mail: bhoopg@yahoo.com

A. Varma et al. (eds.), *Mycorrhiza - Nutrient Uptake, Biocontrol, Ecorestoration*,
https://doi.org/10.1007/978-3-319-68867-1_7

safeguard the human being and environmental health, and for the sustainable agriculture, it is of paramount importance to decrease the dependence of agrarian population on the use of agrochemicals for preventing the attack of harmful organisms and increasing crop production (EU Directive 2009/128/EC) (Berruti et al. 2016). Therefore, meeting the goal of forecasted agriculture production, it is imperative to implement alternative eco-friendly technologies, such as biocontrol agents, which is based on the sustainable utilization of natural resources. However, regardless of their massive potential, the use of these organisms has not been fully adopted by the farmers so far.

Amongst various biocontrol agents, arbuscular mycorrhizal fungi (AMF) appear to be most promising due to their well-established capability of increasing crop production by helping plants in combating various biotic and abiotic stresses. AMF belonging to the phylum Glomeromycota, develop mutual beneficial relationships with over 90% of terrestrial plants including agricultural and horticultural crops (Schüßler et al. 2001; Smith and Read 2008; Prasad et al. 2017). AM symbiotic association is believed to develop approximately 460 million years ago and perhaps played a major role in establishing the plants on land. In the plant root cortex, the fungal partner of this intimate association develops highly branched treelike structures termed as arbuscules (from Latin "*arbusculum*", meaning bush or little tree), which are the functional sites of nutrient exchange, and balloon-like structures termed as vesicles, which are the storage organ of reserve food (Balestrini et al. 2015). AMF form two types of mycelium system, the intraradical and the extraradical in the plant root and soil, respectively. The extraradical hyphae emerge out from the root system and acquire nutrients from the soil (Miller et al. 1995). AMF extraradical hyphae explore a large volume of soil by extending several meters (extend beyond 100 m) away from the host plant's roots; however, plant root hairs could extend one to 2 mm into the soil. The extensive extraradical mycelium formed by AMF connects many plant's roots to the hyphal network of the fungi (Miller et al. 1995). Further, the fungal hyphae being much thinner than plant roots penetrate the smaller pores more efficiently (Allen 2011). Mycorrhizal fungi have been found to be one of the most abundant organisms of the rhizosphere and play a vital role in the terrestrial ecosystems as several plant species depend on them for the acquisition of mineral nutrients from the soil (Remy et al. 1994). They establish a physical link between plants and soil, provide the host plant with mineral nutrients and improve plant growth and productivity. In exchange, the heterotrophic AMF receive photosynthate from the host plant for the fungal growth, survival, and reproduction (asexual) (Smith and Read 1997, 2008; Goltapeh et al. 2008). Indeed, AMF protect their host from abiotic and biotic stresses (Evelin et al. 2009; Auge et al. 2014; Cameron et al. 2013; Schouteden et al. 2015; Nath et al. 2016), therefore becoming a growing choice as a biofertilizer and bioprotectant (Ijdo et al. 2011; Berruti et al. 2016).

Many studies have shown that AMF improve plant's resistance that consequently reduce incidence as well as severity of plant diseases caused by a wide range of attackers including viruses, bacteria, nematodes and fungi. Although well-defined direct mechanisms are still unclear, several indirect mechanisms have been proposed by a number of researchers for increasing bioprotective ability of mycorrhizal plants. In the past decades, studied carried out to understand AMF-plant interactions in response to pathogen attack have proposed different mechanisms responsible for the increased tolerance to biotic stress in mycorrhizal plants (Cameron et al. 2013; Schouteden et al. 2015). The involvement of mycorrhizal fungi in the increased nutrient supply and altered rhizosphere microbial population, plant photosynthetic capacity, anatomy and architecture of the root system, root hydraulic conductivity, water use efficiency and antioxidants production seem to play a critical role in the AMF-mediated alleviation of biotic stresses. In this chapter, we have attempted to discuss the protective role of AMF towards different detrimental organisms belonging to fungi, bacteria, viruses and nematodes along with the possible mechanisms that may be employed in mycorrhizal plants with particular emphasis on the activation of defense mechanisms.

7.2 AMF Protection Against Plant Pathogens

Ample literature pertaining to the bioprotective role of AMF against various plant pathogens is available that has been reviewed time to time by various workers (Azcon-Aguilar and Barea 1996; Borowicz 2001; Akhtar and Siddiqui 2008; Veresoglou and Rillig 2012; Bagyaraj 2014; Pereira et al. 2016). Borowicz (2001) conducted a meta-analysis of data related to interactions between AM symbiosis and plant pathogens published between 1970 and early 1998, so that a general pattern, if possible, might be established. This analysis suggested the negative effect of AMF on the growth of pathogens and the nature of interaction between the two was influenced by the identity of the pathogen. AMF reduced pathogen growth in 50% of studies included in meta-analysis. AMF tended to decrease the harmful effects of fungal pathogens but to exacerbate the harmful effects of nematodes. Wherever, there was a negative effect on the growth of nematodes, the outcome depended upon mode of feeding of the nematode. AMF harmed sedentary endoparasitic nematodes but improved growth of migratory endoparasitic nematodes. In 16% of the total experiments included, both AMF and pathogens suffered reduced growth suggesting reciprocal suppression. Reciprocal suppression was more prominent when the pathogen was a fungus indicating that fungal pathogens in comparison to nematodes were more likely to compete with AMF. Another similar meta-analysis that included the wider data of period between 1978 and 2011 also provided unprecedentedly strong evidence of the ability of AMF to suppress plant pathogens. Additionally, the magnitude of the AM-induced decline in disease severity/nematode suppression ranged from 30 to 42% and 44–57% for fungal and nematode pathogens respectively, irrespective of pathogens' identity or lifestyle suggesting that through AMF, plants possibly receive similar protection from all pathogens rendering AM formulations a potentially broadly effective biocontrol agent. Although there were no differences in AMF effectiveness with respect to the identity of the plant pathogen, the identity of the AMF isolate had a dramatic effect on the level of pathogen protection. AMF efficiency differences with respect to nematode pathogens were mainly limited to the number of AM isolates present; by contrast, modification of the ability to suppress fungal pathogens could occur even through changing the identity of the Glomeraceae isolate applied. N-fixing plants received more protection from fungal pathogens than non-N-fixing dicotyledons; this was attributed to the more intense AMF colonization in N-fixing plants (Veresoglou and Rillig 2012). Considering the bioprotective potential of AMF against pathogens variable results have been reported and the effectiveness of AMF varies with the identity of pathogen and host, and different abiotic factors. The effect of AMF has been studied against various biotic disease causing agents including fungi, bacteria, viruses and nematodes. Since, AMF colonize the roots of higher plants therefore assuming the localized bioprotection most of the studies undertaken are related to soil-borne pathogens and relatively few studies have been conducted on shoot affecting pathogens. On the basis of published reports, it seems that AMF reduce the incidence of disease occurrence in underground parts of plants but enhance the severity of disease in above ground parts in case of certain pathogens (Dehne 1982). AMF species from the family Glomeraceae are more effective at reducing pathogen abundance in contrast to species belonging to family Gigasporaceae (Maherali and Klironomos 2007; Sikes 2010). Further, for promotion and inhibition of plant growth and growth of pathogens, respectively, AMF are known to act synergistically with other microorganisms dwelling in the rhizosphere, which are often termed as plant growth-promoting microorganisms (PGPMs). Amongst PGPMs, plant growth-promoting rhizobacteria (PGPR) such as species belonging to genera, *Pseudomonas*, *Paenibacillus, Rhizobium*, *Stenotrophomonas*, *Arthrobacter* and *Bacillus* and fungi like *Trichoderma* sp., *Gliocladium* sp. and *Aspergillus niger* have been reported to help AMF in reducing the disease severity (Lioussanne 2010; Bharadwaj et al. 2012; Singh et al. 2013; Singh 2015; Prasad et al. 2017; Naglaa et al. 2016; Pereira et al. 2016; Sharma and Sharma 2016). On the basis of information available about mycorrhizal interactions with different pathogens, some of the general conclusions that can be drawn are: (1) AMF either alone or in combination with other microorganisms can reduce damage caused by different pathogens, soil-borne plant pathogens in particular, (2) the abilities of the AM symbioses to enhance resistance or tolerance in roots vary among different AMF tested, (3) the effectiveness of the protection varies from pathogen to pathogen, and (4) protection is influenced by soil and other environmental conditions (Pozo and Azcon-Aguilar 2007). Thus, it can be expected that these interactions will vary with the host plant and the culture system.

7.2.1 Protection Against Fungal Pathogens

The interactions between AMF and fungal plant pathogens have been studied most extensively and majority of these are related to fungal root pathogens

(Whipps 2004). Consistent positive findings related to mycorrhizal plants and their root pathogens have been reported corroborating bioprotective effect of AMF against such pathogens; however, this consistency is missing against shoot pathogens and a lot of variability has been observed that varies with plant and pathogen involved (Ronsheim 2016). The majority of fungal pathogens that have been studied in relation to AMF belong to genera, *Alternaria*, *Aphanomyces*, *Botrytis*, *Colletotrichum*, *Cylindrocladium*, *Erysiphe, Fusarium*, *Gaeumannomyces*, *Macrophomina*, *Oidium*, *Phytophthora*, *Pythium*, *Rhizoctonia*, *Sclerotium* and *Verticillium* (Table 7.1).

7.2.2 Protection Against Bacterial Pathogens

There are relatively very few studies where biocontrol effect of AMF has been reported against various bacterial pathogens and majority of these suggest protective role of AMF (Table 7.2). AMF identity appeared to be playing an important role in providing bioprotection against foliar pathogen, *Pseudomonas syringae* pv. *glycinia* on soybean. Amongst AMF, *Entrophospora infrequens*, *Funneliformis mosseae*, *Claroideoglomus claroideum*, and *Racocetra fulgida*, only *E. infrequens* reduced the colonization of pathogen in host plant (Malik et al. 2016).

7.2.3 Protection Against Viral Pathogens

The impact of the AM symbiosis on infections caused by various viral pathogens is still largely uncertain and majority of studies conducted so far indicate negative impact where mycorrhizal colonization increases both multiplication of viruses and severity of the diseases (Dehne 1982; Miozzi et al. 2011), and AMF mediated protection against viral pathogens appeared to be a rare phenomenon (Maffei et al. 2014) (Table 7.3). Yellow mosaic virus infection in mycorrhizal mungbean had adverse effect on mycorrhizal colonization and reduced spore formation by AMF (Jayaram and Kumar 1995). Focusing on the disease symptoms, some of the viruses such as Tobacco mosaic virus (Jabaji-Hare and Stobbs 1984; Shaul et al. 1999), Potato virus Y (Sipahioglu et al. 2009), Citrus tristeza virus and Citrus leaf rurgose virus (Nemec and Myhre 1984), and Tomato spotted wilt virus (Miozzi et al. 2011) (TSWV) have been demonstrated to enhanced disease severity in the presence of mycorrhizal fungi (Table 7.3).

7.2.4 Protection Against Parasitic Nematodes

Nematodes are a diversified group of both free-living nematodes and parasitic nematodes of plants as well as animals that occur world over in various habitats.

Table 7.1 Effect of AMF on different pathogenic fungi in plants

Plant Pathogenic fungus	AM Fungi	Host-plant	Effect[a]	References
Alternaria triticina	*Glomus mosseae*	Wheat	+	Siddiqui and Singh (2005)
A. solani	*Glomus intraradices*	Tomato	+	Fritz et al. (2006)
Aphanomyces euteiches	*G. intraradices*	Pea	+	Bodker et al. (1998)
Botrytis cinerea	*G. mosseae*	Tomato	+	Fiorilli et al. (2011)
Colletotrichum gloeosporioides	*G. mosseae*	Strawberry	+	Li et al. (2010)
Cylindrocladium spathiphylli	*Glomus proliferum*, *G. intraradices*, *Glomus versiforme*	Banana	+	Declerck et al. (2002)
Erysiphe graminis	Unknown AMF	Barley	–	Gernns et al. (2001)
Fusarium oxysporum	*Glomus* sp., *G. intraradices*	Yellow foxtail, flax	+	Sikes (2010), Dugassa et al. (1996)
F. udum	*Gigaspora margarita*, *G. mosseae*	Pigeonpea	+	Siddiqui and Mahmood (1996)
Gaeumannomyces graminis	*G. mosseae*	Barley	+/–	Castellanos-Morales et al. (2011)
Macrophomina phaseolina	*Glomus fasciculatum*, *Glomus constrictum*, *Glomus etunicatum*, *G. intraradices*, *G. mosseae*, *G. margarita*, *Acaulospora* sp., *Sclerocystis* sp.	Chickpea	+	Siddiqui and Akhtar (2006), Shakoor et al. (2015)
Oidium lini	*G. intraradices*	Flax	–	Dugassa et al. (1996)
Phytophthora capsici	*G. mosseae*	Pepper	+	Ozgonen and Erkilic (2007), Pereira et al. (2016)
P. parasitica	*Glomus fasciculatus*, *G. mosseae*	Tomato, citrus	+	Pozo et al. (2002), Davis and Menge (1980)
P. fragariae	*G. etunicatum*, *Glomus monosporum*	Strawberry	+	Norman and Hooker (2000)
P. nicotianae	*G. intraradices*	Tomato	+	Lioussanne et al. (2008)
P. sojae	*G. intraradices*	Soybean	+	Yuanjing et al. (2013)
Pythium ultimum	*G. etunicatum*	Cucumber	+	Rosendahl and Rosendahl (1990)
Rhizoctonia solani	*G. etunicatum*, *G. intraradices*, *G. mosseae*	Potato, tomato	+	Yao et al. (2002), Kareem and Hassan (2014)

(continued)

Table 7.1 (continued)

Plant Pathogenic fungus	AM Fungi	Host-plant	Effect[a]	References
Sclerotium cepivorum	*Glomus* sp.	Onion	+	Torres-Barragan et al. (1996)
Sclerotium rolfsii	*G. fasciculatum*	Groundnut	+	Doley and Jite (2013)
Verticillium dahliae	*G. mosseae,* *G. vesiformae,* *Scutellospora sinuosa*	Cotton	+	Liu (1995)

[a] + means reduction in disease severity or reduced growth of the pathogen and − means enhanced disease severity or growth of the pathogen

Table 7.2 Effect of AMF against pathogenic bacteria in plants

Plant Pathogenic bacterium	AMF	Host-plant	Effect[a]	References
Pseudomonas syringae pv. *glycinia*	*Entrophospora infrequens*	Soybean	+	Malik et al. (2016)
Ralstonia solanaceraum	G. *mosseae*, *G. vesiforme,* *Scutellospora* sp., *G. margarita*	Tomato	+	Zhu and Yao (2004), Tahat et al. (2012)
Xanthomonas campestris pv. *alfalfae*	*G. intraradices*	*Medicago*	+	Liu et al. (2007)
Aster yellows phytoplasma	*G. mosseae*	Periwinkle	−	Kamińska et al. (2010)
Stolbur phytoplasma	*G. mosseae*	Tomato	+	Lingua et al. (2002)
Pear-decline phytoplasma	*G. intraradices*	Pear	+	García-Chapa et al. (2004)

[a] + means reduction in disease severity or reduced growth of the pathogen and − means enhanced disease severity or growth of the pathogen

The plant-parasitic nematodes (PPN) are mostly root pests of a wide range of important agricultural crops and on the basis of feeding strategy, have been classified into different groups viz., ectoparasites, endoparasites, migratory endoparasites, and sedentary parasites (Perry and Moens 2011). Ectoparasitic nematode such as *Xiphinema index* remains in the rhizosphere during feeding and acquire food from the epidermal or outer cortical cells of the roots with the help of the stylet. Endoparasitic nematodes, in contrast, completely enter the root during feeding. Migratory endoparasitic nematodes (e.g., *Radopholus* spp. and *Pratylenchus* spp.) during feeding inside root migrate inter or intracellularly thus, causing damage to the plant along their migration path (Jones et al. 2013). Sedentary endoparasitic nematodes such as cyst and root-knot nematodes are considered to be the most damaging pests of agricultural crops worldwide (Jones et al. 2013; Bartlem et al. 2014) which become sedentary with the onset of feeding in the vascular cylinder (Gheysen and Mitchum 2011). This last group includes various

Table 7.3 Effect of AMF against plant viruses

Plant virus	AMF	Host-plant	Effect[a]	References
Citrus tristeza virus	*G. etunicatum*	Sour orange	–	Nemec and Myhre (1984)
Citrus leaf rurgose virus	*G. etunicatum*	Duncan grapefruit	–	Nemec and Myhre (1984)
Potato virus Y	*G. intraradices*	Potato	–	Sipahioglu et al. (2009)
Tobacco mosaic virus	*Glomus* sp., *G. intraradices*	Tomato, tobacco	–	Jabaji-Hare and Stobbs (1984), Shaul et al. (1999)
Tomato yellow leaf curl Sardinia virus	*Funneliformis mosseae*	Tomato	+	Maffei et al. (2014)
Tomato spotted wilt virus	*F. mosseae*	Tomato	–	Miozzi et al. (2011)
Yellow mosaic virus	*Gigaspora gilmorei*, *Acaulospora marrowae*	Mungbean	–	Jayaram and Kumar (1995)

[a] + means reduction in disease severity or reduced growth of the pathogen and – means enhanced disease severity or growth of the pathogen

species of genus *Meloidogyne* such as *M. incognita* and *M. javanica* which, are notorious for severe damages in tobacco, tomato, sunflower and pepper (Wesemael et al. 2011). The direct damage caused by PPN can be aggravated by secondary infections of the wounded plant tissues by other pathogens, moreover, some PPN, like the migratory ectoparasitic *Xiphinema* spp. can transmit plant viruses (Hao et al. 2012). Losses in crops yields caused by PPN are expected to rise due to climate change and cropping systems intensification (Nicol et al. 2011). Considering the limitations of currently used nematicides there is a need for alternative nematode management strategies; the use of AMF has been proposed as one of the environment-friendly strategies to manage PPN. PPN suppressive ability of AMF is well reported and has been previously reviewed (Pinochet et al. 1996; Hol and Cook 2005). In vitro, greenhouse as well as field experiments have indicated protective efficacy of AMF against PPN in crop plants like banana, coffee and tomato (Vos et al. 2013; Alban et al. 2013; Koffi et al. 2013). The bioprotective potential of AMF has been tested in different crop plants with highly variable results against various root-feeding nematodes belonging mainly to the genera *Heterodera*, *Meloidogyne*, *Nacobbus*, *Pratylenchus, Radopholus, Rotylenchulus, Tylenchulus* and *Xiphinema* (Table 7.4).

7.3 Mechanisms of Mycorrhiza-Mediated Disease Control

Mycorrhizal symbiosis largely influences plant growth and development, and also plays a pivotal role in the biocontrol of plant diseases directly or indirectly (Singh et al. 2000; Azcon-Aguilar et al. 2002; Whipps 2004; Xavier and Boyetchko 2004;

Table 7.4 Effect of AMF against different plant-parasitic nematodes

Plant parasitic nematode	AMF	Host-plant	Effect[a]	References
Heterodera cajani	*Glomus epigaeus*, *G. fasciculatum*, *G. margarita*	Cowpea, Pigeon pea	+	Jain and Sethi (1988), Siddiqui and Mahmood (1996)
H. glycines	Mixed AMF	Soybean	+	Tylka et al. (1991)
Meloidogyne arenaria	*G. etunicatum*, *G. margarita*, *G. fasciculatum*	Peanut, grapevine	−	Carling et al.(1996), Atilano et al. (1981)
M. hapla	*G. etunicatum*	*Pyrethrum*	+	Waceke et al. (2001)
	G. fasciculatum	Onion	−/No effect	Kotcon et al. (1985), MacGuidwin et al. (1985)
	G. intraradices	Tomato	+	Masadeh et al. (2004)
M. incognita	*Acaulospora laevis*	Tomato	+	Labeena et al. (2002)
	G. margarita	Black pepper, tomato	+	Anandaraj et al. (1990), Labeena et al. (2002)
	Glomus aggregatum	Mint	+	Pandey (2005)
	G. mosseae	Tomato, brinjal, okra, black gram	+	Rao et al. (1998), Sharma and Mishra (2003), Vos et al. (2013), Sankaranarayanan and Sundarababu (2010)
	G. fasciculatum	Tomato, brinjal, ginger, black gram	+	Sankaranarayanan and Sundarababu (1997), Borah and Phukan (2003), Nehra (2004), Kantharaju et al. (2005)
	Glomus coronatum	Tomato	+	Diedhiou et al. (2003)
	Glomus deserticola	Tomato	+	Rao et al. (1997)
	Glomus macrocarpum	Tomato	+	Labeena et al. (2002)
	G. etunicatum	Peach	No effect	Strobel et al. (1982)
	Sclerocystis dussi	Tomato	No effect	Labeena et al. (2002)
	G. intraradices	Cotton, chickpea	+	Siddiqui and Akhtar (2006)
M. javanica	*G. mosseae*, *G. macrocarpum*, *Glomus caledonicum*	Banana	+	Elsen et al. (2002)
	G. intraradices	Banana	No effect	Pinochet et al. (1997)
	Glomus manihotis, *G. margarita*, *G. gigantea*	Chickpea	+	Diederichs (1987)

(continued)

Table 7.4 (continued)

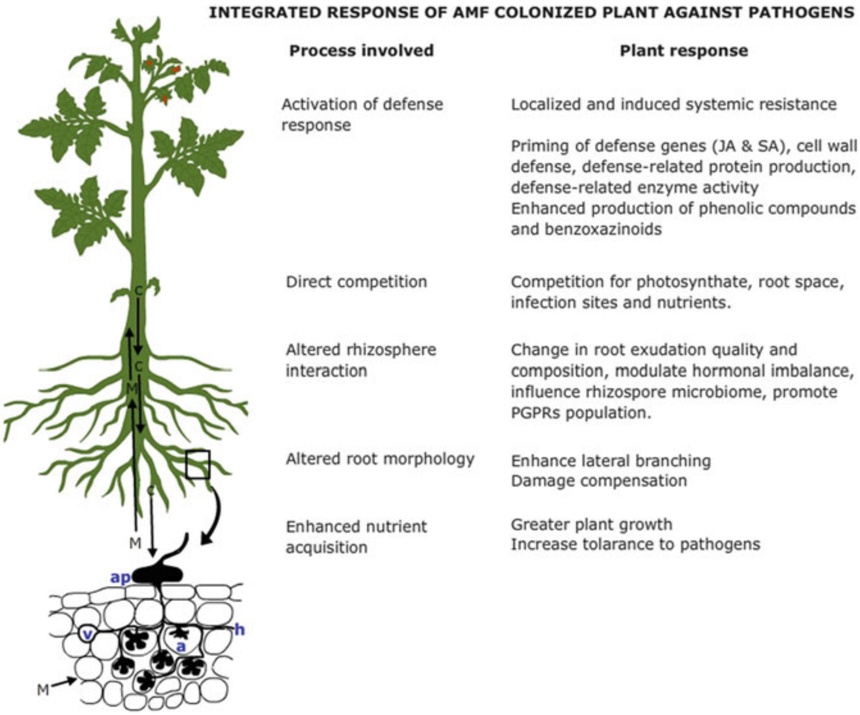
Plant parasitic nematode	AMF	Host-plant	Effect[a]	References
Nacobbus aberrans	*G. intraradices*	Tomato	+	Marro et al. (2014)
Pratylenchus brachyurus	*G. margarita*	Cotton	No effect	Hussey and Roncadori (1978)
P. coffeae	*G. intraradices*	Banana	+	Elsen et al. (2008)
Radopholus citrophilus	*G. intraradices*	Citrus	+	Smith and Kaplan (1988)
R. similis	*G. intraradices*	Banana	No effect/ +	O'Bannon and Nemec (1979), Elsen et al. (2008)
Rotylenchulus reniformis	*G. fasciculatum*	Tomato	+	Sitaramaiah and Sikora (1982)
Tylenchulus semipenetrans	*G. mosseae*	Citrus	+	O'Bannon et al. (1979)
Xiphinema index	*G. intraradices*	Grapevine	+	Hao et al. (2012)

[a] + means reduction in disease severity or reduced growth of the pathogen and − means enhanced disease severity or growth of the pathogen

St-Arnaud and Vujanovic 2007). In addition to improved plant nutrition, several other mechanisms such as damage compensation, direct competition for colonization sites or photosynthate, alteration in the root morphology, changes in rhizosphere microbial populations, biochemical changes associated with plant defense mechanisms and the activation of plant defense mechanisms have also been found to be involved in AMF-induced biocontrol of plant pathogens (Whipps 2004; Jung et al. 2012) (Fig. 7.1).

7.3.1 Improved Nutrient Status

Although the soluble nutrients such as N and K can be accessed by nonmycorrhizal plants, the less soluble or immobile nutrients like P are more difficult to be attained by plants. This problem further exaggerates under nutrient deficient conditions. Indeed, the extensive thread-like extraradical hyphae of AMF act as an extension of the plant's root system, extend several meters beyond the depletion zone, explore more soil volume and acquire both macro-and micro nutrients, therefore, improve nutrient status of their host plant. The nutritional aspect of plant-AMF interaction has been studied extensively from both physiological and molecular perspectives indicating that AMF considerably improve the acquisition of less soluble or immobile nutrients, mainly under stress conditions (Smith and Smith 2011). Nevertheless, mycorrhizal plants showed better survival and growth and increased resistance



INTEGRATED RESPONSE OF AMF COLONIZED PLANT AGAINST PATHOGENS

Process involved	Plant response
Activation of defense response	Localized and induced systemic resistance Priming of defense genes (JA & SA), cell wall defense, defense-related protein production, defense-related enzyme activity Enhanced production of phenolic compounds and benzoxazinoids
Direct competition	Competition for photosynthate, root space, infection sites and nutrients.
Altered rhizosphere interaction	Change in root exudation quality and composition, modulate hormonal imbalance, influence rhizospore microbiome, promote PGPRs population.
Altered root morphology	Enhance lateral branching Damage compensation
Enhanced nutrient acquisition	Greater plant growth Increase tolarance to pathogens

Fig. 7.1 An overview of the processes by which AMF can protect plants from pathogens. AMF facilitate host plant to acquire mineral nutrients (m) from soil and, in exchange, obtain carbon (c) from host plant. AM fungal hyphae enters plant root forming appressorium (ap) on the root surface and eventually vesicles (v) and arbuscules (a) in the root cortical cells by extending its hyphae. The fungus exerts a competition for photosynthate, infection sites and mineral nutrition with infectious organisms. AMF can control plant pathogens by increasing tolerance to pathogens, altering root morphology and rhizosphere interactions, and activating defense responses (ISR, MIR)

or tolerance to plant pathogens than that of the non-AMF plants, which could be ascribed to the increased nutrient status of mycorrhizal plants. However, it remains ambiguous whether the increased resistance against plant pathogens was a direct consequence of improved nutrient acquisition by mycorrhizal plants (Davis 1980; Declerck et al. 2002). Till the date, several reviews have been published advocating improved nutrients supply as one of the main mechanisms of AMF to control plant diseases (Azcon-Aguilar and Barea 1996; Xavier and Boyetchko 2004; Wehner et al. 2010; Schouteden et al. 2015), especially root-borne diseases (Bodker et al. 1998). On the other hand, there are a number of contradictory reports (Hooker et al. 1994; Linderman 1994). Davis (1980) provided an evidence of higher tolerance to citrus root rot disease induced by *Thielaviopsis* in AMF colonized than non-AMF citrus plants, conversely, non-AMF plants exhibited similar response to this pathogen when supplemented with additional dosage of phosphorus. Declerck et al. (2002) observed higher tolerance to *Cylindrocladium spathiphylli* in mycorrhizal as compared to non-mycorrhizal banana plants. The AMF isolates significantly improved growth and shoot P level of banana, and reduced root damage by *C. spathiphylli*, which may be correlated with the direct interaction between AMF and plant pathogen (Xavier and Boyetchko 2004). Caron et al. (1986) compared response between AMF and non-AMF tomato plants exposed to the *Fusarium oxysporum Schlecht* f. sp. *radicis-lycopersici*, a soil-borne pathogen, which can cause severe yield losses in tomato due to crown and root rot diseases. They observed a reduction in the *Fusarium* population and root rot incidences in the rhizosphere soil of AMF-colonized plants as compared to nonmycorrhizal control plants, and corroborated it with increased antagonistic activities in the mycorrhizosphere, an area influenced by AMF. They suggested that the disease suppression by AMF cannot be considered as a mere consequence of improved P nutrition; instead some other mechanisms may confer reduced disease incidences. A significant suppression in the symptoms of *A. solani* was observed in the mycorrhizal than non-mycorrhizal tomato plants by Fritz et al. (2006). Pettigrew et al. (2005) observed that plants with better nutrient status, growing in the cotton fields, which was infested with the sedentary semi-endoparasitic nematode *Rotylenchulus reniformis* were able to tolerate higher PPN population densities in their roots. Such findings indicate that the improved nutrition of the host plant could influence plant parasite nematode population densities either positively or negatively, however, no solid data are available to confirm a direct correlation between AMF-mediated increased nutrient status of host plant and the higher resistance against plant pathogens.

7.3.2 Changes in the Root System Morphology

The interaction between mycorrhizal fungi and host plant modulates the plant root system and influence microbial activities in the rhizosphere, especially plant-pathogen interaction (Atkinson et al. 1994; Scannerini et al. 2001; Hodge et al. 2009). Consequently, the total root length may increase or remain unchanged as has been reported in *Vitis vinifera* and *Solanum lycopersicum* respectively (Schellenbaum et al. 1991; Berta et al. 2005). The number and length of the roots vary according to the different AMF associations and in comparison to the main roots, modifications occur in the lateral roots more frequently. Pre-inoculation with mycorrhizal fungi increases formation of lateral branching as a result increasing suitable sites for root colonization, which confers to a high branched root system; however, changes in the root architecture as a consequence of AMF colonization could provide a fewer sites for pathogen infection (Norman et al. 1996; Fusconi et al. 1999; Harrison 2005). The strigolactones, a group of sesquiterpene lactones have also been found to play an important role in the modulation of shoot and root architecture. Together with auxins, strigolactones favor lateral root formation and facilitates the root to explore new areas in the soil. Strigolactones-induced changes in root architecture could alter the dynamics of some pathogen infections; however, further experimentation is required to establish this correlation (Jung et al. 2012).

Mukherjee and Ane (2011) observed that germinating fungal spores of *Gigaspora margarita, G. rosea* and *Glomus intraradices* could induce lateral roots formation and increase the total length of the root system in *M. truncatula*, indicating that diffusible signals released by mycorrhizal fungal spores trigger the lateral root developmental program. The important role of AM symbiosis in lateral root development has also been confirmed by Paszkowski and Boller (2002) and Olah et al. (2005). They revealed that branching in *M. truncatula* is directly induced by AMF germinating spores and their exudates. Increased root branching has also been recorded in the case of monocots and dicots (herbaceous and woody plants) with a significant difference in the order of the roots involved (Berta et al. 1995; Scannerini et al. 2001). However, the tap root plants appear to be more benefited than fibrous root plants in terms of the biomass production and acquirement of mineral nutrients (Yang et al. 2014). The increased root branching in AMF-colonized plants may directly be attributed to the production and action of AMF exudates; while the indirect reason of increasing root branching could be ascribed to the increased mineral nutrition and modulation of hormonal balance (Fusconi 2014). Vos et al. (2014) suggested that increased root branching in AMF-colonized plants could increase the implication for infection by a pathogen; however, a clear correlation did not establish (Vierheilig et al. 2008).

The higher nutrient uptake capacity of mycorrhizal plants attributes to the vigorous root growth, which indeed exhibits higher resistance to plant parasite infection. Elsen et al. (2003a) demonstrated that in banana, migratory endoparasitic nematodes-*Radopholus similis* and *P. coffeae* reduced root branching whereas, same increased by mycorrhizal fungus, *Glomus mosseae*. On the other hand, there is a probability that higher root branching negatively impacts host plant as it increases potential infection sites, depending on the parasite and host plant species. Primary roots are the preferential sites of colonization by migratory endoparasitic nematodes, like *Radopholus similis*, whereas the sedentary endoparasitic root-knot and cyst nematodes prefer to infect the root elongation zone and the sites of lateral root formation (Stoffelen et al. 2000; Wyss 2002; Elsen et al. 2003b; Curtis et al. 2009). Instead, the strawberry plant, bearing highly branched root system, is primarily infected through the root tips by the pathogenic fungus *Phytophthora fragariae*; however, the mycorrhizal roots of strawberry plants showed lower infection as compared to non-mycorrhizal roots, which was indeed higher in the case of highly-branched root system. By the way, it is difficult to explain a uniform impact of altered root morphology in the biocontrol of plant disease, therefore, substantiates the speculations of the involvement of other mechanisms in the mycorrhiza-induced biocontrol of plant diseases (Fusconi et al. 1999; Gamalero et al. 2010).

7.3.3 Changes in the Rhizosphere Interactions

Lorenz Hiltner (1904), a German agronomist and plant physiologist, who coined the term “rhizosphere” and described it as an area around the plant root, which is directly influenced by root secretions and associated population of soil microorganisms (Hiltner 1904). The plant root secretions/exudates comprising of sugars and organic acids (Hage-Ahmed et al. 2013), amino acids (Harrier and Watson 2004), phenolic compounds (McArthur and Knowles 1992), flavonoids (Steinkellner et al. 2007) and plant hormones such as strigolactones, Jasmonic acid, salicylic acid and ethylene (Lopez-Raez et al. 2010; Jung et al. 2012). These compounds play an important role in plant–microbe interactions in the rhizosphere. Some of them are crucial for the initial phase of plant-microbes interactions, while others are required at the later stages of interaction (Bais et al. 2006; Hage-Ahmed et al. 2013).

Alteration in the root exudation patterns directly impacts the microbial population in the mycorrhizosphere. Many studies suggested that AMF alter root exudates quality and quantity (Bansal and Mukerji 1994) and influence the rhizosphere microbial communities, which in turn reduce pathogen populations (Citernesi et al. 1996; Larsen et al. 2003). However, the quality and effectiveness of root exudation indeed depend on the plant and AMF species involved as well as on the degree of root colonization (Scheffknecht et al. 2006; Lioussanne et al. 2008; Badri and Vivanco 2009; Kobra et al. 2009). The findings of Pozo and Azcon-Aguilar (2007) demonstrate the degree of root colonization, which is typically characterized by the presence of arbuscules, as an important requirement for the control of plant pathogen. The root exudates collected from 4 months old AMF-colonized roots was attractive for the zoospores of *Phytophthora nicotianae*, whereas concentrated exudates obtained from 6 months old AMF colonized roots was repulsive for the zoospores of *P. nicotianae*, as compared to exudates harvested from nonmycorrhizal plant roots. This shows that a change in the root exudation pattern in mycorrhizal tomato plants negatively impacts the infection potential of zoospores of *Phytophthora nicotianae*, indicating an obvious involvement of root exudates in the plant-pathogen interactions (Lioussanne et al. 2008). Lioussanne et al. (2008) suggested that modification in the exudates composition of older roots due to AMF colonization could provoke the repulsion of *P. nicotianae*, and therefore reduce the degree of infection. Nevertheless, a differential pattern was also observed in the root exudates of mycorrhizal and non-mycorrhizal plants (Jones et al. 2004; Scheffknecht et al. 2006, 2007). Vos et al. (2013) investigated the influence of a mycorrhizal fungus, *Glomus mosseae and mycorrhizal* root exudates on the *Meloidogyne incognita* penetration of tomato roots. They found that exudates from mycorrhizal tomatoes generally minimize nematode penetration in mycorrhizal plants and transiently inhibited nematodes proliferation as compared to the root exudates obtained from nonmycorrhizal tomatoes. The study showed that nematode penetration of tomato roots decreases in mycorrhizal tomato roots. Moreover, mycorrhizal root exudates could partially affect the motility of nematode; therefore reduce the *Meloidogyne incognita* penetration and subsequent proliferation in tomato roots. The root exudates obtained from AMF-colonized plants root served as chemoattractants for plant-growth-promoting rhizobacteria, *Azotobacter chroococcum* and *Pseudomonas fluorescens* (Sood 2003). Siasou et al. (2009) found that rhizosphere fluorescent *Pseudomonas* strains produce increasing amounts of antibiotic 2,4-diacetylphloroglucinol in the presence of AMF, *G. intraradices*, which confers plant protection against *Gaeumannomyces graminis* var. *tritici*. This shows that mycorrhizal root exudates positively influence rhizosphere microbial communities and help in the biocontrol of plant pathogens. On the basis of results of many studies, it could be tempting to speculate that mycorrhizal fungi show a protective effect against infectious organisms, which is more obvious in the case of soil-borne diseases, in different plant systems.

7.3.4 Direct Competition with Other Microorganisms

The AMF-host relationship is fundamentally characterized by the development of arbuscules in root cortical cells (Dehne 1982), which die eventually due to their short lifespan. The AMF and pathogenic microbes most probably depend on common resources such as host photosynthate, nutrition, infection-site and space within the plant root for their survival and multiplication (Smith and Read 1997; Whipps 2004); hence competition can occur for these resources between pathogens and mycorrhizal fungi. Indeed, competition can be beneficial in the case of mycorrhiza-colonized cells for the physical exclusion of pathogens (Xavier and Boyetchko 2004). Graham (2001) observed that the competition between plant pathogens and AMF could arise if the availability of carbon is limited, which further corroborates the observations of Vos et al. (2014). The reduced locations for pathogen infection within AMF-colonized root system were also observed by Vigo et al. (2000), which make it plausible that AMF directly compete for colonization sites with other soil microorganisms (Vos et al. 2014). One of the well-studied examples in this connection is the study conducted by Cordier and colleagues on AMF, *Glomus mosseae* and pathogenic fungus, *Phytophthora parasitica* in tomato plants. The study showed that cortical cells of mycorrhizal root did not allow pathogen to penetrate roots that demonstrated to be a localized resistance response (Cordier et al. 1998). Mycorrhizal root system has shown complete exclusion of the *Phytophthora parasitica* from arbusculized cells in tomato roots (Cordier et al. 1996). Therefore, the competition occurring between AMF and pathogens for acquiring host photosynthate, root space or locations could be a potential strategy to control microbial infection in AMF-colonized plants; however, the potentiality of this mechanism to be used as a strategy for control of plant diseases has not received much attention as the results of various studies conducted are not consistent (Pozo et al. 1999; Vos 2012).

Since PPN also colonize plant root, therefore, the competition for space and infection loci appears to be involved in AMF-nematodes interactions. It becomes very difficult for migratory endo-parasitic nematodes to survive in the presence of mycorrhizal arbuscules, which largely develop in the root cortical cells, where these nematodes feeds upon (Jung et al. 2012; Schouteden et al. 2015). Moreover, the competition for the space between AMF and sedentary endo-parasitic nematodes becomes important if feeding cells extend into the host cortical cells. However, cyst nematodes are meagerly affected by AMF colonization as these nematodes are restricted to the endodermal cells only (Schouteden et al. 2015). Indeed, the formation of mycorrhizal fungi may also be affected by PPN infection as the competition for the nutrients and space arises between them as substantiated by Hol and Cook (2005) who reported reduced AMF colonization due to the attack of migratory and sedentary endoparasitic and ectoparasitic nematodes. Elsen et al. (2003b) observed that mycorrhizal inoculation of *Musa* with *Glomus mosseae* gives rise to a significantly higher plant growth even in the presence of nematodes under greenhouse conditions. Although nematodes decreased the root branching, the population densities of them drastically decreased in the presence of *Glomus mosseae*, and a decrease in root branching seems to be compensated by the AMF inoculation. A negative effect of burrowing nematode *Radopholus similis* and *Pratylenchus coffeae* infection was observed on the frequency of *Glomus mosseae* colonized *Musa* roots (Elsen et al. 2003a, b); however, such effect did not observe in the case of the intensity. In an *in vitro* experiment, carried out by Elsen et al. (2003c), the interaction between AMF and *P. coffeae* on transformed carrot roots in root organ culture did not influence the root colonization by mycorrhizal fungus *Glomus intraradices* (Elsen et al. 2003c), which substantiate the findings of recent study on *in vitro* mycorrhizal banana plantlets and *R. similis* (Koffi et al. 2013). Dos Anjos et al. (2010) observed that the establishment of mycorrhiza prior to the nematode infection could reduce both severity symptoms and reproduction of *Meloidogyne incognita*. Based on the findings, Alban et al. (2013) concluded that pre-inoculation of coffee plants with AMF could develop stronger and healthier plants, which resist *Meloidogyne exigua* infestation and subsequently reduce the rate of infestation. Lower nematode infestation in AMF colonized plants could be attributed to the lignifications of the plant cell wall cuticle, which is not easy to penetrate by nematodes to enter into plant roots. They highlighted that as compared to nematodes, AMF colonize plant root faster, giving them an advantage in their development inside the root, for that reason occupying more root space and eventually lower the nematode infestation rates.

7.4 The Activation of Defense Mechanisms in Response to AMF Formation

For the biological control of plant diseases, it is expected that arbuscular mycorrhizal fungi could apply more than one mechanism to restrain the adverse effects of the causal organisms. As above mentioned mechanisms do not elucidate satisfactorily the mycorrhiza-induced biocontrol of certain plant diseases, therefore, researchers have explored possibilities of other mechanism like the activation of plant defense compounds in response to AMF formation in plant roots. It has been observed that, in response to mycorrhizal colonization, though a weak or very local and transient, activation of specific plant defense compounds takes place which, elicits the specific defense reactions and makes the plants proactive against attackers/pathogens (Gianinazzi-Pearson et al. 1994; Koide and Schreiner 1992). The chemicals produced under plant defense mechanism are diversified groups of biochemicals which are synthesized mostly as secondary metabolites (Singh 2017). Some of such chemicals like, phytoalexins, chitinases, β-1,3-glucanases, pathogenesis-related proteins, callose, hydroxyproline-rich glycoproteins, phenolic compounds and enzymes of the phenylpropanoid pathway have been reported to be involved in the activation of plant defense as a result of AMF colonization (Gianinazzi-Pearson et al. 1994; Azcon-Aguilar and Barea 1996).

In the past decades, the changing host plant physiology (including plant nutrition) as a consequence of plant-AMF interactions and the plant signal transduction pathways controlling this intimate association have largely been the central point of research. Conversely, a little attention has been paid to understand the contribution of AMF for non-nutritional benefits, such as suppression of plant diseases or induction of plant resistance against plant diseases/attackers. It is well established that plant roots exude different chemical compounds (secondary metabolites), which usually signaling an array of soil microorganisms, predominantly occurring in the rhizosphere. The pioneer observations of Akiyama et al. (2005) and successive publications have established that strigolactones, a group of carotenoids-derived signaling molecules that are released by the host plant root promote AMF-hyphal branching and facilitate AMF establishment in the plant root. The production of strigolactones generally increases in the early phase of root colonization but, it decreases in a well-established mycorrhizal symbiosis (Jung et al. 2012). The root exudates released by AMF-colonized plants seems to prime microbial activities in the rhizosphere and thereby induce a ‘mycorrhizosphere effect’ (Linderman 1988; Giri et al. 2005).

Like certain other soil microbes, mycorrhizal fungi also exhibit the ability to reduce the impacts of plant pathogens through induced systemic resistance (Pozo and Azcon-Aguilar 2007). The induced systemic resistance (ISR) is typically a sustained induction of resistance in plants against pathogens, which is induced by the non-pathogenic rhizosphere microorganisms such as PGPR, mycorrhizal fungi or endophytes (Trotta et al. 1996; Cordier et al. 1998; Pineda et al. 2010). ISR protect plants from the infection of different plant pathogens including bacteria, fungi, viruses, nematodes and insects and is mediated by the priming of defense genes that demonstrate a higher expression systemically in the leaves only after the pathogen attack (van Wees et al. 2008; Pineda et al. 2010). ISR often exhibits increased plant-sensitivity towards the plant growth regulators such as jasmonic acid (JA) and ethylene (ET) (Pineda et al. 2010).

In the AMF-colonized plants, both localized and induced systemic resistance has been observed against detrimental organisms. Cordier et al. (1998), in split root experiment observed the protective role of AMF, *Glomus mosseae* against *Phytophthora parasitica* as it hindered the development and proliferation of causal organisms in tomato roots. They suggested that root cortical cells become immunized on AMF colonization resulting in a localized plant cell resistance, likely due to the formation of cell wall appositions supported by callose (adjacent to intercellular hyphae) and phenolic compounds, and plant cell defense responses. Induced systemic resistance in nonmycorrhizal root parts of the mycorrhizal plants could attribute to the host wall-thickenings containing non-esterified pectins and pathogenesis-related (PR)-1a protein and formation of callose rich jacket around the hyphae of *P. parasitica* (Cordier et al. 1998). Liu et al. (1995) found more than ten types of pathogenesis-related (PR) proteins in cotton plants, moreover, the content of PR proteins increased on AMF inoculation. The growth of hyphae and conidia of *Verticillium dahlia* were found to be hampered at certain concentrations in mycorrhizal plants, which subsequently helped in the reduction of disease incidences and index of verticillium wilt and in the promotion of seedling growth and yield of cotton seed. Indeed, the higher MIR response against *V. dahlia* could be an effect of the increased content of PR proteins in cotton plants on mycorrhization.

Mycorrhiza-induced resistance (MIR) against many plant pathogens has been demonstrated by researchers that seems to be based more on the priming of jasmonic acid-dependent defense (JADD) responses (Pozo and Azcon-Aguilar 2007) than accumulation of salicylic acid (Khaosaad et al. 2007) as there are reports suggesting negative impact of salicylic acid on mycorrhizal colonization (Hause et al. 2007; Jung et al. 2012; Miransari and Smith 2014). Priming can be explained as a pre-conditioning of plant tissues that allows the plant to activate defense responses faster and stronger against a broad range of plant pathogens/attackers. Such a pre-conditioning can be elicited by certain chemical compounds and different microorganisms (Pineda et al. 2010). Priming seems to be a plausible mechanism operating in MIR. The MIR-regulated bioprotection of crop plants has been reported in the case of *Gaeumannomyces graminis* var. *tritici*, which causes Take-all disease in barley (Khaosaad et al. 2007). Aberra et al. (1998) also observed similar results in the case of a sterile red fungus, which suppressed the infection of wheat roots by *Gaeumannomyces graminis* var. *tritici*. Benhamou et al. (1994) observed strong defense reactions at the sites challenged by *Fusarium oxysporum* f. sp. *chrysanthemi* in mycorrhizal transformed carrot roots. The protective ability of mycorrhizal fungi in grapevine roots against *Meloidogyne incognita*, has been found to be associated with primed expression of a chitinase gene (VCH3) (Li et al. 2006). Moreover, mycorrhiza-induced resistance against *Fusarium oxysporum* in mycorrhizal date palm trees and *Colletotrichum* in cucumber seem to be associated with the primed-accumulation of the phenolic compounds (Jaiti et al. 2008), and callose deposition (Lee et al. 2005), respectively.

Fritz et al. (2006) conducted an experiment to understand the influence of mycorrhizal fungi on the development of early blight in tomato, caused by a necrotrophic fungus, *Alternaria solani*. The mycorrhizal tomato plants showed a significant reduction in disease symptoms as compared to the non-mycorrhizal plants. Although the increased nutrient supply considerably influenced disease severity in mycorrhizal than non-mycorrhizal plants, the defensive role of AMF against causal organisms could be due to mycorrhiza-induced resistance. Recently, Cameron et al. (2013) presented a four-phase spatiotemporal model demonstrating MIR as a cumulative outcome of direct interactions between mycorrhizal fungi and plant, and responses to ISR-eliciting rhizobacteria present in the mycorrhizosphere. They highlighted that at the early stage of colonization, strigolactones present in the exudates of host plant roots, promote hyphal branching and AMF establishment. At the onset of mycorrhizal symbiosis, microbe-associated molecular patterns (MAMPs) from the fungus are recognized by the plant's innate immune system that leads to a weak and transient MAMP-triggered immunity (MTI) response as well as the activation of long-distance signals in the xylem, which could prime the salicylic acid-dependent defense (SADD) responses. The AMF-regulated induction of the specific effector molecules suppresses MTI locally. Mycorrhizal symbiosis elicits the production of abscisic acid that systemically transports to the shoot tissues through xylem and can prime cell wall defense responses. With the development of arbuscules in the root cortical cells, the increased supply of sugar and mineral nutrition, particularly phosphorus modulates root metabolisms and thereby the chemical composition of root exudates. Such modifications in the root exudates chemical composition indeed influence mycorrhizosphere populations, which could allow the selection of growth-promoting rhizosphere microbes/bacteria that metabolize AMF root exudates and convey ISR-eliciting signals at the root surface and/or AMF hyphae, resulting in the long-distance signals, which could credit the priming of JA-dependent defense and ET-dependent defense responses and eventually triggers the ISR in mycorrhizal plants (Cameron et al. 2013). Although the well-defined roles of jasmonic acid in MIR against detrimental organisms are not well known, Pozo and Azcon-Aguilar (2007) proposed that the active suppression of components involved in the SA-dependent defense pathway could lead to the induction of MIR and the priming of JA-dependent defense responses (Pozo and Azcon-Aguilar 2007; Hause et al. 2007). Although salicylic acid has been proved to be a key regulator of plant defense against biotrophs (Glazebrook 2005), it could have negative impact on AMF formation in the host roots (García-Garrido and Ocampo 2002; Lopez-Raez et al. 2010). Therefore, it is possible that AMF suppress certain components of SA-dependent responses in the host plant in order to accomplish a compatible interaction. Dumas-Gaudot et al. (2000) also observed a delay in the accumulation of PR-1 proteins (common markers of SA-dependent responses) in mycorrhizal roots. Nevertheless, the beneficial microbes (PGPR)-induced systemic resistance, regulated by JA-dependent and ethylene-dependent signaling pathways, and associated with priming for enhanced defense against plant pathogens has been observed by van Wees et al. (2008). These findings tempting to consider that the JA is a key regulator in the AMF symbiosis (Hause et al. 2007; Hause and Schaarschmidt 2009). The higher levels of JA have been confirmed in mycorrhizal tomato roots (Lopez-Raez et al. 2010), which remains unchanged in the shoots (Pozo et al. 2010). Pozo et al. (2010) recorded rather low, but a significant increase in the expression of marker genes for JA responses and a strong induction of JA-regulated genes in *Glomus mosseae*-colonized tomato plants.

Confirming a priming response in tomato plant they further validated the MIR response against *Botrytis cinerea* directly related to the priming of JA-dependent defense responses.

7.5 Conclusions and Outlook

Arbuscular mycorrhizal fungi have been found to protect several plant species against many pathogens including viruses, phytoplasmas, bacteria, fungi, and plant-parasite nematodes. The suppression of both necrotrophic and biotrophic pathogens and consequently reduction in the severity of disease symptoms either directly or indirectly has also been observed in majority of AMF-colonized plants. However, soil-borne root attackers appear to be affected more than shoot attackers. One of the reasons of such a generalization is availability of relatively few reports pertaining to air-borne pathogens. The protective action mechanism of AMF is not fully understood and based on the investigations done so far appears to be multi-targeted. The primary protection mechanism is increased resistance of crop plants as a result of AMF-mediated improved nutrient status. However, studies indicate the involvement of other mechanisms such as changes in the chemical composition of root exudates, modulation of rhizosphere microbial activities and the activation of plant defense responses in mycorrhiza-induced protection against different attackers. Indeed, the actual use of AMF as a bio-control agent remains to be popularized for agricultural practices.

Acknowledgements Authors duly acknowledge the support provided by Dr. Bhawna Saxena, Swami Shraddhanand College, University of Delhi, Delhi, India throughout the preparation of Manuscript.

References

Aberra MB, Seah S, Sivasithamparam K (1998) Supression of the takeall fungus (*Gaeumannomyces graminis* var. *tritici*) by a sterile red fungus through induced resistance in wheat (*Triticum aestivum*) seedling roots. Soil Biol Biochem 30:1457–1461

Akhtar MS, Siddiqui MA (2008) Arbuscular mycorrhizal fungi as potential bioprotectants against plant pathogens. In: Siddiqui ZA, Akhtar S, Futai K (eds) Mycorrhizae: sustainable agriculture and forestry. Springer, Netherlands, pp 61–98

Akiyama K, Ki M, Hayashi H (2005) Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature 435:824–827

Alban R, Guerrero R, Toro M (2013) Interactions between a root-knot nematode (*Meloidogyne exigua*) and arbuscular mycorrhizae in coffee plant development (*Coffea arabica*). Am J Plant Sci 4:19–23

Allen MF (2011) Linking water and nutrients through the vadose zone: a fungal interface between the soil and plant systems: linking water and nutrients through the vadose zone: a fungal interface between the soil and plant systems. J Arid Land 3:155–163

Anandaraj M, Ramana KV, Sharma, YR (1990) Interaction between vesicular arbuscular mycorrhizal fungi and *Meloidogyne incognita* in black pepper. In: Bagyaraj DJ, Manjunath A (eds) Mycorrhizal symbiosis and plant growth, Proc Sec Nat Conf on Mycorrhiza, 21–23 November, Banglore, India, pp 110–112

Atilano RA, Menge JA, Vangundy SD (1981) Interaction between *Meloidogyne arenaria* and *Glomus fasciculatus* in grape. J Nematol 13:52–57

Atkinson D, Berta G, Hooker JE (1994) Impact of mycorrhizal colonisation on root architecture, root longevity and the formation of growth regulators. In: Gianinazzi S, Schüepp H (eds) Impact of arbuscular mycorrhizas on sustainable agriculture and natural ecosystems. Birkhäuser, Basel, pp 89–99

Auge RM, Toler HD, Saxton AM (2014) Arbuscular mycorrhizal symbiosis and osmotic adjustment in response to NaCl stress: a meta-analysis. Front Plant Sci 5:562–574

Azcon-Aguilar C, Barea JM (1996) Arbuscular mycorrhizas and biological controlof soil-borne plant pathogens – An overview of the mechanisms involved. Mycorrhiza 6:457–464

Azcon-Aguilar C, Jaizme-Vega MC, Calvet C (2002) The contribution of arbuscular mycorrhizal fungi to the control of soil-borne plant pathogens. In: Gianinazzi S, Schüepp H, Barea JM, Haselwandter K (eds) Mycorrhizal technology in agriculture. Birkhäuser, Basel, pp 187–197

Badri DV, Vivanco JM (2009) Regulation and function of root exudates. Plant Cell Environ 32:666–681

Bagyaraj DJ (2014) Mycorrhizal fungi. Proc Ind Nat Sci Acad 80:415–428

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 57:233–266

Balestrini R, Lumini E, Borriello R, Bianciotto V (2015) Plant-soil biota interactions. In: Paul EA (ed) Soil microbiology, ecology and biochemistry. Academic Press/Elsevier, Burligton, MA/Oxford, pp 311–338

Bansal M, Mukerji KG (1994) Positive correlation between VAM induced changes in root exudation and mycorrhizosphere mycoflora. Mycorrhiza 5:39–44

Bartlem DG, Jones MGK, Hammes UZ (2014) Vascularization and nutrient delivery at root-knot nematode feeding sites in host roots. J Exp Bot 65:1789–1798. https://doi.org/10.1093/jxb/ert415

Benhamou N, Fortin JA, Hamel C, St-Arnaud M, Shatilla A (1994) Resistance responses of mycorrhizal Ri T-DNA-transformed carrot roots to infection by *Fusarium oxysporum* f. sp *chrysanthemi*. Phytopathol 84:958–968

Berruti A, Lumini E, Balestrini R, Bianciotto V (2016) Arbuscular mycorrhizal fungi as natural biofertilizers: Let's benefit from past successes, review. Front Microbiol 6:1559. https://doi.org/10.3389/fmicb.2015.01559

Berta G, Trotta A, Fusconi A, Hooker M, Munro D, Atkinson M, Govionetti S, Morini P, Fortuna B, Tisserant V, Gianinazzi-Pearson V, Gianinazzi S (1995) Arbuscular mycorrhizal induced changes to plant growth and root system morphology in *Prunus cerasifera*. Tree Physiol 15:281–293

Berta G, Sampo S, Gamalero E, Massa N, Lemanceau P (2005) Suppression of *Rhizoctonia* root-rot of tomato by *Glomus mossae* BEG12 and *Pseudomonas fluorescens* A6RI is associated with their effect on the pathogen growth and on the root morphogenesis. Euro J Plant Pathol 111:279–288

Bharadwaj DP, Sadhna Alström S, Lundquist P (2012) Interactions among *Glomus irregulare*, arbuscular mycorrhizal spore-associated bacteria, and plant pathogens under in vitro conditions. Mycorrhiza 22:437–447

Bodker L, Kjoller R, Rosendahl S (1998) Effect of phosphate and arbuscular mycorrhizal fungus *Glomus intraradices* on disease severity of root rot of peas (*Pisum sativum*) caused by *Aphanomyces euteiches*. Mycorrhiza 8:169–174

Borah A, Phukan PN (2003) Effect of interaction of *Glomus fasciculatum* and *Meloidogyne incognita* on growth of brinjal. Ann Plant Prot Sci 11:352–354

Borowicz VA (2001) Do arbuscular mycorrhizal fungi alter plant–pathogen relations? Ecology 82:3057–3068

Cameron D, Neal A, van Wees S, Ton J (2013) Mycorrhiza-induced resistance: more than the sum of its parts? Trends Plant Sci 18:539–545

Carling DE, Roncadori RW, Hussey RS (1996) Interactions of arbuscular mycorrhizae, *Meloidogyne arenaria*, and phosphorus fertilization on peanut. Mycorrhiza 6:9–13

Caron M, Fortin JA, Richard C (1986) Effect of inoculation sequence on the interaction between *Glomus intraradices* and *Fusarium oxysporum* f. sp. *radicis-lycopersici* in tomatoes. Can J Plant Pathol 8:12–16

Castellanos-Morales V, Keiser C, Cardenas-Navarro R, Grausgruber H, Glauninger J, Garcia-Garrido JM, Steinkellner S, Sampedro I, Hage-Ahmed K, Illana A, Ocampo JA, Vierheilig H (2011) The bioprotective effect of AM root colonization against the soil-borne fungal pathogen *Gaeumannomyces graminis* var. *tritici* in barley depends on the barley variety. Soil Biol Biochem 43:831–834

Citernesi AS, Fortuna P, Filippi C, Bagnoli G, Giovannetti M (1996) The occurrence of antagonistic bacteria in *Glomus mosseae*pot cultures. Agronomie 16:671–677

Cordier C, Gianinazzi S, Gianinazzi-Pearson V (1996) Colonisation patterns of root tissues by fungus *Glomus mosseae* in tomato plants. Plant Soil 185:199–209

Cordier C, Pozo MJ, Barea JM, Gianinazzi S, Gianinazzi-Pearson V (1998) Cell defense responses associated with localized and systemic resistance to *Phytophthora* induced in tomato by an arbuscular mycorrhizal fungus. Mol Plant Microbe Interact 11:1017–1028

Curtis R, Robinson A, Perry R (2009) Hatch and host location. In: Perry RN, Moens M, Starr JL (eds) Root-knot Nematodes. CAB International, Wallingford, pp 139–162

Davis RM (1980) Influence of *Glomus fasciculatus* on *Thielaviopsis basicola* root rot of citrus. Plant Dis 64:839–840

Davis RM, Menge JA (1980) Influence of *Glomus fasciculatus* and soil phosphorus on *Phytophthora* root rot of citrus. Phytopathol 70:447–452

Declerck S, Risede JM, Rufyikiri G, Delvaux B (2002) Effects of arbuscular mycorrhizal fungi on the severity of root rot of bananas caused by *Cylindrocladium spathiphylli*. Plant Pathol 51:109–115

Dehne HW (1982) Interaction between vesicular-arbuscular mycorrhizal fungi and plant pathogens. Phytopathol 72:1115–1119

Diederichs C (1987) Interaction between five endomycorrhizal fungi and root-knot nematode and *Meloidogyne hapla* on *Allium cepa* in organic soils. J Nematol 17:55–60

Diedhiou PM, Hallmann J, Oerke EC, Dehne HW (2003) Effects of arbuscular mycorrhizal fungi and a non-pathogenic *Fusarium oxysporum* on *Meloidogyne incognita* infestation of tomato. Mycorrhiza 13:199–204

Doley K, Jite PK (2013) Management of stem-rot of groundnut (*Arachis hypogaea* L.) cultivar in field. Not Sci Biol 5:316–324

Dos Anjos ÉCT, Cavalcante UMT, Gonçalves DMC, Pedrosa EMR, dos Santos VF, Maia LC (2010) 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 53:801–809

Dugassa GD, von Alten H, Schonbeck F (1996) Effects of arbuscular mycorrhiza (AM) on health of *Linum usitatissimum* L infected by fungal pathogens. Plant Soil 185:173–182

Dumas-Gaudot E, Gollotte A, Cordier C, Gianinazzi S, Gianinazzi-Pearson V (2000) Modulation of host defense systems. In: Kapulnik Y, Douds DD Jr (eds) Arbuscular mycorrhizas: physiology and function. Kluwer, Dordrecht, pp 173–200

Elsen A, Declerck S, De Wasele D (2002) Effects of three arbuscular mycorrhizal fungi on root knot nematode (*Meloidogyne* spp.) infection of *Musa*. Infomusa 11:21–23

Elsen A, Baimey H, Swennen R, De Waele D (2003a) Relative mycorrhizal dependency and mycorrhiza-nematode interaction in banana cultivars (*Musa* spp.) differing in nematode susceptibility. Plant Soil 256:303–313

Elsen A, Beeterens R, Swennen R, De Waele D (2003b) Effects of an arbuscular mycorrhizal fungus and two plant-parasitic nematodes on *Musa* genotypes differing in root morphology. Biol Fertil Soils 38:367–376

Elsen A, Declerck S, De Waele D (2003c) Use of root organ cultures to investigate the interaction between *Glomus intraradices* and *Pratylenchus coffeae*. Appl Environ Microbiol 69:4308–4311

Elsen A, Gervacio D, Swennen R, De Waele D (2008) AMF-induced biocontrol against plant-parasitic nematodes in *Musa* sp.: a systemic effect. Mycorrhiza 18:251–256

Evelin H, Kapoor R, Giri B (2009) Arbuscular mycorrhizal fungi in alleviation of salt stress: a review. Ann Bot 104:1263–1280

Fiorilli V, Catoni M, Francia D, Cardinale F, Lanfranco L (2011) The arbuscular mycorrhizal symbiosis reduces disease severity in tomato plants infected by *Botrytis cinerea*. J Plant Pathol 93:237–242

Fritz M, Jakobsen I, Lyngkjaer MF, Thordal-Christensen H, Pons-Kühnemann J (2006) Arbuscular mycorrhiza reduces susceptibility of tomato to *Alternaria solani*. Mycorrhiza 16:413–419

Fusconi A (2014) Regulation of root morphogenesis in arbuscular mycorrhizae: what role do fungal exudates, phosphate, sugars and hormones play in lateral root formation? Ann Bot 13:19–33

Fusconi A, Gnavi E, Trotta A, Berta G (1999) Apical meristems of tomato roots and their modifications induced by arbuscular mycorrhizal and soilborne pathogenic fungi. New Phytol 142:505–516

Gamalero E, Pivato B, Bona E, Copetta A, Avidano L, Lingua G (2010) Interactions between a fluorescent pseudomonad, an arbuscular mycorrhizal fungus and a hypovirulent isolate of *Rhizoctonia solani* affect plant growth and root architecture of tomato plants. Plant Biosyst Int J Deal Asp Plant Biol 144:582–591

García-Chapa M, Batlle A, Laviña A, Camprubí A, Estaún V, Calvet C (2004) Tolerance increase to pear decline phytoplasma in mycorrhizal OHF-333 pear rootstock. Acta Hortic (ISHS) 657:437–441

García-Garrido JM, Ocampo JA (2002) Regulation of the plant defence response in arbuscular mycorrhizal symbiosis. J Exp Bot 53:1377–1386

Gernns H, Von Alten H, Poehling HM (2001) Arbuscular mycorrhiza increased the activity of a biotrophic leaf pathogen-is a compensation possible? Mycorrhiza 11:237–243

Gheysen G, Mitchum MG (2011) How nematodes manipulate plant development pathways for infection. Curr Opin Plant Biol 14:415–421. https://doi.org/10.1016/j.pbi.2011.03.012

Gianinazzi-Pearson V, Gollotte A, Dumas-Gaudot E, Franken P, Gianinazzi S (1994) Gene expression and molecular modifications associated with plant responses to infection by arbuscular mycorrhizal fungi. In: Daniels M, Downic JA, Osbourn AE (eds) Advances in molecular genetics of plant-microbe interactions. Kluwer, Dordrecht, pp 179–186

Giri B, Giang PH, Kumari R, Prasad R, Sachdev M, Garg AP, Oelmuller R, Varma A (2005) Mycorrhizosphere: strategies and functions. In: Buscot F, Varma A (eds) Microorganisms in soils: roles in genesis and functions. Springer, Heidelberg, pp 213–252

Glazebrook J (2005) Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. Annu Rev Phytopathol 43:205–227

Goltapeh EM, Danesh YR, Prasad R, Varma A (2008) Mycorrhizal fungi: what we know and what should we know. In: Varma A (ed) Mycorrhiza, 3rd edn. Springer, Heidelberg, pp 3–28

Graham JH (2001) What do root pathogens see in mycorrhizas? New Phytol 149:357–359

Hage-Ahmed K, Moyses A, Voglgruber A, Hadacek F, Steinkellner S (2013) Alterations in root exudation of intercropped tomato mediated by the arbuscular mycorrhizal fungus *Glomus mosseae* and the soilborne pathogen *Fusarium oxysporum* f.sp. *lycopersici*. J Phytopathol 161:763–773

Hao Z, Fayolle L, van Tuinen D, Chatagnier O, Xiaolin L, Gianinazzi S, Gianinazzi-Pearson V (2012) Local and systemic mycorrhiza-induced protection against the ectoparasitic nematode

Xiphinema index involves priming of defence gene responses in grapevine. J Exp Bot 63:3657–3672

Harrier LA, Watson CA (2004) The potential role of arbuscular mycorrhizal (AM) fungi in the bioprotection of plants against soil-borne pathogens in organic and/or other sustainable farming systems. Pest Manag Sci 60:149–157

Harrison MJ (2005) Signaling in the arbuscular mycorrhizal symbiosis. Annu Rev Microbiol 59:19–42

Hause B, Schaarschmidt S (2009) The role of jasmonates in mutualistic symbioses between plants and soil-borne microorganisms. Phytochem 70:1589–1599

Hause B, Mrosk C, Isayenkov S, Strack C (2007) Jasmonates in arbuscular mycorrhizal interactions. Phytochem 68:101–110

Hiltner L (1904) Uber neuere Erfahrungen und Probleme auf dem Gebiete der Bodenbakteriologie unter besonderden berucksichtigung und Brache. Arb Dtsch Landwirtsch Gesellschaft 98:59–78

Hodge A, Berta G, Doussan C, Merchan F, Crespi M (2009) Plant root growth, architecture and function. Plant Soil 321:153–187

Hol WHG, Cook R (2005) An overview of arbuscular mycorrhizal fungi-nematode interactions. Basic Appl Ecol 6:489–503

Hooker JE, Jaizme-Vega M, Atkinson D (1994) Biocontrol of plant pathogens using arbuscular mycorrhizal fungi. In: Gianinazzi S, Schüepp H (eds) Impact of arbuscular mycorrhizas on sustainable agriculture and natural ecosystems. Birkhäuser, Basel, pp 191–200

Hussey R, Roncadori R (1978) Interaction of *Pratylenchus brachyurus* and *Gigaspora margarita* on cotton. J Nematol 10:16–20

Ijdo M, Cranenbrouck S, Declerck S (2011) Methods for large-scale production of AM fungi: past, present, and future. Mycorrhiza 21:1–16

Jabaji-Hare SH, Stobbs LW (1984) Electron microscopic examination of tomato roots coinfected with *Glomus* sp. and tobacco mosaic virus. Phytopathol 74:277–279

Jain RK, Sethi CL (1988) Influence of endomycorrhizal fungi *Glomus fasciculatum* and *G. epigaeus* on penetration and development of *Heterodera cajani* on cowpea. Ind J Nematol 18:89–93

Jaiti F, Kassami M, Meddich A, El Hadrami I (2008) Effect of arbuscular mycorrhization on the accumulation of hydroxycinnamic acid derivatives in date palm seedlings challenged with *Fusarium oxysporum* f. sp. *albedinis*. J Phytopathol 156:641–646

Jayaram J, Kumar D (1995) Influence of mungbean yellow mosaic virus on mycorrhizal fungi associated with *Vigna radiata* var. PS 16. Ind Phytopathol 48:108–110

Jones DL, Hodge A, Kuzyakov Y (2004) Plant and mycorrhizal regulation of rhizodeposition. New Phytol 163:459–480

Jones JT, Haegeman A, Danchin EGJ, Gaur HS, Helder J, Jones MG, Kikuchi T, Manzanilla-López R, Palomares-Rius JE, Wesemael WM, Perry RN (2013) Top 10 plant-parasitic nematodes in molecular plant pathology. Mol Plant Pathol 14:946–961

Jung SC, Martinez-Medina A, Lopez-Raez JA, Pozo MJ (2012) Mycorrhiza-induced resistance and priming ofplant defenses. J Chem Ecol 38:651–664

Kamińska M, Klamkowski K, Berniak H, Sowik I (2010) Response of mycorrhizal periwinkle plants to aster yellows phytoplasma infection. Mycorrhiza 20:161–166

Kantharaju V, Krishnappa K, Ravichardra NG, Karuna K (2005) Management of root-knot nematode, *Meloidogyne incognita* on tomato by using indigenous isolates of AM fungus, *Glomus fasciculatum*. Ind J Nematol 35:32–36

Kareem TA, Hassan MS (2014) Evaluation of *Glomus mosseae* as biocontrol agents against *Rhizoctonia solani* on Tomato. J Biol Agric Healthcare 4:15–19

Khaosaad T, García-Garrido JM, Steinkellner S, Vierheilig H (2007) Take-all disease is systemically reduced in roots of mycorrhizal barley plants. Soil Biol Biochem 39:727–734

Kobra N, Jalil K, Youbert G (2009) Effects of three *Glomus* species as biocontrol agents against *Verticillium*-induced wilt in cotton. J Plant Prot Res 49:185–189

Koffi MC, Vos C, Draye X, Declerck S (2013) Effects of *Rhizophagus irregularis* MUCL 41833 on the reproduction of *Radopholus similis* in banana plantlets grown under in vitro culture conditions. Mycorrhiza 23:279–288. https://doi.org/10.1007/s00572-012-0467-6

Koide RT, Schreiner RP (1992) Regulation of the vesicular arbuscular mycorrhizal symbiosis. Annu Rev Plant Physiol Plant Mol Biol 43:557–581

Kotcon JB, Bird GW, Rose LM, Dimoff K (1985) Influence of *Glomus fasciculatum* and *Meloidogyne hapla* on *Allium cepa* in organic soils. J Nematol 17:55–60

Labeena P, Sreenivasa MN, Lingaraju S (2002) Interaction effects between arbuscular mycorrhizal fungi and root-knot nematode *Meloidogyne incognita* on tomato. Ind J Nematol 32:118–120

Larsen J, Ravnskov S, Jakobsen I (2003) Combined effect of an arbuscularmycorrhizal fungus and a biocontrol bacterium against *Pythium ultimum* in soil. Folia Geobotanica 38:145–154

Lee CS, Lee YJ, Jeun YC (2005) Observations of infection structures on the leaves of cucumber plants pre-treated with arbuscular mycorrhiza *Glomus intraradices* after challenge inoculation with *Colletotrichum orbiculare*. Plant Pathol J 21:237–243

Li HY, Yang GD, Shu HR, Yang YT, Ye BX, Nishida I, Zheng CC (2006) Colonization by the arbuscular mycorrhizal fungus *Glomus versiforme*induces a defense response against the root-knot nematode *Meloidogyne incognita* in the grapevine (*Vitis amurensis* Rupr), which includes transcriptional activation of the class III chitinase gene VCH3. Plant Cell Physiol 47:154–163

Li HY, Yanagi A, Miyawaki Y, Okada T, Matsubara Y (2010) Disease tolerance and changes in antioxidative abilities in mycorrhizal strawberry plants. J Jpn Soc Hortic Sci 79:174–178

Linderman RG (1988) Mycorrhizal Interactions with the rhizosphere microflora–the mycorrhizosphere effect. Phytopathol 78:366–371

Linderman RG (1994) Role of VAM fungi in biocontrol. In: Pfleger FL, Linderman RG (eds) Mycorrhizae and plant health. APS, St Paul, pp 1–26

Lingua G, D'Agostino G, Massa N, Antosiano M, Berta G (2002) Mycorrhiza-induced differential response to a yellows disease in tomato. Mycorrhiza 12:191–198

Lioussanne L (2010) The role of the arbuscular mycorrhiza-associated rhizobacteria in the biocontrol of soilborne phytopathogens. Span J Agric Res 8(S1):S51–S61

Lioussanne L, Jolicoeur M, St-Arnaud M (2008) Mycorrhizal colonization with *Glomus intraradices* and development stage of transformed tomato roots significantly modify the chemotactic response of zoospores of the pathogen *Phytophthora nicotianae*. Soil Biol Biochem 40:2217–2224

Liu RJ (1995) Effect of vesicular-arbuscular mycorrhizal fungi on Verticillium wilt of cotton. Mycorrhiza 5:293–297

Liu RJ, Li HF, Shen CY, Chiu WF (1995) Detection of pathogenesis-related proteins in cotton plants. Physiol Mol Plant Pathol 47:357–363

Liu J, Maldonado-Mendoza I, Lopez-Meyer M, Cheung F, Town CD, Harrison MJ (2007) Arbuscular mycorrhizal symbiosis is accompanied by local and systemic alterations in gene expression and an increase in disease resistance in the shoots. Plant J 50:529–544

Lopez-Raez JA, Verhage A, Fernandez I, Gracia JM, Azcon-Aguilar C, Flors V (2010) Hormonal and transcriptional profiles highlight common and differential host responses to arbuscular mycorrhizal fungi and the regulation of the oxylipin pathway. J Exp Bot 61:2589–2601

MacGuidwin A, Bird G, Safir G (1985) Influence of *Glomus fasciculatum* on *Meloidogyne hapla* infecting *Allium cepa*. J Nematol 17:389–395

Maffei G, Miozzi L, Fiorilli V, Novero M, Lanfranco L, Accotto GP (2014) The arbuscular mycorrhizal symbiosis attenuates symptom severity and reduces virus concentration in tomato infected by Tomato yellow leaf curl Sardinia virus (TYLCSV). Mycorrhiza 24:179–186

Maherali H, Klironomos JN (2007) Influence of phylogeny on fungal community assembly and ecosystem functioning. Science 316:1746–1748

Malik RJ, Dixon MH, Bever JD (2016) Mycorrhizal composition can predict foliar pathogen colonization in soybean. Biol Control 103:46–53

Marro N, Lax P, Cabello M, Doucet ME, Becerra AG (2014) Use of the arbuscular mycorrhizal fungus *Glomus intraradices* as biological control agent of the nematode *Nacobbus aberrans* parasitizing tomato. Braz Arch Biol Technol 57:668–675

Masadeh B, von Alten H, Grunewaldt-Stoecker G, Sikora RA (2004) Biocontrol of root knot nematodes using the arbuscular mycorrhizal fungus *Glomus intraradices* and the antagonistic *Trichoderma viridae* in two tomato cultivars differing in their suitability as hosts for the nematodes. J Plant Dis Prot 111:322–333

McArthur DA, Knowles NR (1992) Resistance responses of potato to vesicular-arbuscular mycorrhizal fungi under varying abiotic phosphorus levels. Plant Physiol 100:341–351

Miller RM, Reinhardt DR, Jastrow JD (1995) External hyphalproduction of vesicular-arbuscular mycorrhizal fungi in pastureand tallgrass prairie communities. Oecologia 103:17–23

Miozzi L, Catoni M, Fiorilli V, Philip MM, Accotto GP, Lanfranco L (2011) Arbuscular mycorrhizal symbiosis limits foliar transcriptional responses to viral infection and favors long-term virus accumulation. Mol Plant Microbe Interact 24:1562–1572

Miransari M, Smith DL (2014) Plant hormones and seed germination. Environ Exp Bot 99:110–121

Mukherjee KG, Ane JM (2011) Germinating spore exudates from arbuscular mycorrhizal fungi: molecular and developmental responses in plants and their regulation by ethylene. Mol Plant Microbe Interact 24:260–270

Naglaa ASM, Essa TA, Manal AHE, Kamel SM (2016) Efficacy of free and formulated arbuscular mycorrhiza, *Trichoderma viride* and *Pseudomonas fluorescens* on controlling tomato root rot diseases. Egypt J Biol Pest Control 26:477–486

Nath M, Bhatt D, Prasad R, Gill SS, Anjum NA, Tuteja N (2016) Reactive oxygen species generation-scavenging and signaling during plant-arbuscular mycorrhizal and *Piriformospora indica* interaction under stress condition. Front Plant Sci 7:1574. https://doi.org/10.3389/fpls.2016.01574

Nehra S (2004) VAMF and organic amendments in the management of *Meloidogyne incognita* infected ginger. J Ind Bot Soc 83:90–97

Nemec S, Myhre D (1984) Virus-*Glomus etunicatum* interactions in Citrus rootstocks. Plant Dis 68:311–314

Nicol JM, Turner SJ, Coyne DL, den Nijs L, Hockland S, Tahna Maafi Z (2011) Current nematode threats to world agriculture. In: Jones J, Gheysen G, Fenoll C (eds) Genomics and molecular genetics of plant-nematode interactions. Springer, Heidelberg, pp 21–44

Norman JR, Hooker JE (2000) Sporulation of *Phytophthora fragariae* shows greater stimulation by exudates of non-mycorrhizal than by mycorrhizal strawberry roots. Mycol Res 104:1069–1073

Norman J, Atkinson D, Hooker J (1996) Arbuscular mycorrhizal fungal-induced alteration to root architecture in strawberry and induced resistance to the root pathogen *Phytophthora fragariae*. Plant Soil 185:191–198

O'Bannon J, Nemec S (1979) The response of Citrus limon seedlings to a symbiont, *Glomus etunicatus*, and a pathogen, *Radopholus similis*. J Nematol 11:270–275

O'Bannon J, Inserra R, Nemec S, Vovlas N (1979) The influence of *Glomus mosseae* on *Tylenchulus semipenetrans*-infected and uninfected *Citrus limon* seedlings. J Nematol 11:247–250

Olah B, Briere C, Becard G, Denarie J, Gough C (2005) Nod factors and a diffusible factor from arbuscular mycorrhizal fungi stimulate lateral root formation in *Medicago truncatula* via the DMI1/DMI2 signalling pathway. Plant J 44:195–207

Ozgonen H, Erkilic A (2007) Growth enhancement and Phytophthora blight (*Phytophthora capsici* L.) control by arbuscular mycorrhizal fungal inoculation in pepper. Crop Prot 26:1682–1688

Pandey R (2005) Field application of bio-organics in the management of *Meloidogyn incognita* in *Mentha arvensis*. Nematol Mediterr 33:51–54

Paszkowski U, Boller T (2002) The growth defect of *lrt1*, a maize mutant lacking lateral roots, can be complemented by symbiotic fungi or high phosphate nutrition. Planta 214:584–590

Pereira JAP, Vieira IJC, Freitas MSM, Prins CL, Martins MA, Rodrigues R (2016) Effects of arbuscular mycorrhizal fungi on *Capsicum* spp. J Agric Sci 154:828–849

Perry RN, Moens M (2011) Introduction to plant-parasitic nematodes; modes of parasitism. In: Jones JT, Gheysen L, Fenoll C (eds) Genomics and molecular genetics of plant–nematode interactions. Springer, Heidelberg, pp 3–20

Pettigrew WT, Meredith WR, Young LD (2005) Potassium fertilization effects on cotton lint yield, yield components, and reniform nematode populations. Agron J 97:1245–1251

Pineda A, Zheng SJ, van Loon JJA, Pieterse CMJ, Dicke M (2010) Helping plants to deal with insects: the role of beneficial soil-borne microbes. Trends Plant Sci 15:507–514

Pinochet J, Calvet C, Camprubí A, Fernández C (1996) Interactions between migratory endoparasitic nematodes and arbuscular mycorrhizal fungi in perennial crops: a review. Plant Soil 185:183–190

Pinochet J, Fernandez C, de Jaimez M, Tenoury P (1997) Micropropagated banana infected with *Meloidogyne javanica* responds to *Glomus intraradices* and phosphorus. Hortic Sci 32:35–49

Pozo MJ, Azcon-Aguilar C (2007) Unraveling mycorrhiza-induced resistance. Curr Opin Plant Biol 10:393–398

Pozo MJ, Azcón-Aguilar C, Dumas-Gaudot E, Barea JM (1999) ß-1,3-glucanase activities in tomato roots inoculated witharbuscular mycorrhizal fungi and/or *Phytophthora parasitica* and their possible involvement in bioprotection. Plant Sci 141:149–157

Pozo MJ, Cordier C, Dumas-Gaudot E, Gianinazzi S, Barea JM, Azcon-Aguilar C (2002) Localized verses systemic effect of arbuscular mycorrhizal fungi on defence responses to *Phytophthora* infection in tomato plants. J Exp Bot 53:525–534

Pozo MJ, Jung SC, Lopez-Raez JA, Azcon-Aguilar C (2010) Impact of arbuscular mycorrhizal symbiosis on plant response to biotic stress: the role of plant defence mechanisms. In: Koltai H, Kapulnik Y (eds) Arbuscular mycorrhizas: physiology and function. Springer, Dordrecht, pp 193–207

Prasad R, Bhola D, Akdi K, Cruz C, Sairam KVSS, Tuteja N, Varma A (2017) Introduction to mycorrhiza: historical development. In: Varma A, Prasad R, Tuteja N (eds) Mycorrhiza. Springer, Dordrecht, pp 1–7

Rao MS, Kerry BR, Gowen SR, Bourne JM, Reddy PP (1997) Management of *Meloidogyne incognita* in tomato nurseries by integration of *Glomus deserticola* with *Verticillium chlamydosporium*. J Plant Dis Prot 104:419–422

Rao MS, Reddy PP, Mohandas MS (1998) Bio-intensive management of *Meloidogyne incognita* on eggplant by integrating *Paecilomyces lilacinus* and *Glomus mosseae*. Nematol Mediterr 26:213–216

Remy W, Taylor TN, Hass H, Kerp H (1994) Four hundred million year old vesicular arbuscular mycorrhizae. Proc Natl Acad Sci USA 91:11841–11843

Rodriguez A, Sanders IR (2015) The role of community and population ecology in applying mycorrhizal fungi for improved food security. ISME J 9:1053–1061

Ronsheim ML (2016) Plant genotype influences mycorrhiza benefits and susceptibility to a soil pathogen. Am Midl Nat 175(1):103–112

Rosendahl CN, Rosendahl S (1990) The role of vesicular arbuscular mycorrhizal fungi in controlling damping-off and growth reduction in cucumber caused by *Pythium ultimum*. Symbiosis 9:363–366

Sankaranarayanan C, Sundarababu R (1997) Effect of oil cakes and nematicides on the growth of blackgram (*Vigna mungo*) inoculate with VAM fungus (*Glomus fasciculatum*) and root-knot nematode (*Meloidogyne incognita*). Ind J Nematol 27:128–130

Sankaranarayanan C, Sundarababu R (2010) Influence of application methods of arbuscular mycorrhiza *Glomus mosseae* in the bio-management of root knot nematode, *Meloidogyne incognita* on black gram (*Vigna mungo* L.) Hepper. J Biol Control 24:51–57

Scannerini S, Fusconi A, Mucciarelli M, Seckback J (2001) The effect of endophytic fungi on host plant morphogenesis. In: Seckback J (ed) Symbiosis: organisms and model systems. Kluwer, Dordrecht, pp 427–447

Scheffknecht S, Mammerler R, Steinkellner S, Vierheilig H (2006) Root exudates of mycorrhizal tomato plants exhibit a different effect on microconidia germination of *Fusarium oxysporum* f. sp. *lycopersici* than root exudates from non-mycorrhizal tomato plants. Mycorrhiza 16:365–370

Scheffknecht S, St-Arnaud M, Khaosaad T, Steinkellner S, Vierheilig H (2007) An altered root exudation pattern through mycorrhization affecting microconidia germination of the highly specialized tomato pathogen *Fusarium oxysporum* f.sp *lycopersici* (Fol) is not tomato specific but also occurs in *Fol* nonhost plants. Can J Bot 85:347–352

Schellenbaum L, Berta G, Raviolanirina F, Tisserant B, Gianinazzi S, Fitter AH (1991) Influence of endomycorrhizal infection on root morphology in a micropropagated woody plant species (*Vitis vinifera* L.) Ann Bot 68:135–141

Schouteden N, De Waele D, Panis B, Vos CM (2015) Arbuscular mycorrhizal fungi for the biocontrol of plant-parasitic nematodes: a review of the mechanisms involved. Front Microbiol 6:1280

Schüßler AH, Gehrig H, Schwarzott D, Walker C (2001) Analysis of partial Glomales SSU rRNA gene sequences: implications for primer design and phylogeny. Mycol Res 105:5–15

Shakoor S, Inam-ul-Haq M, Bibi S, Ahmed R (2015) Influence of root inoculations with vasicular arbuscular mycorrhizae and rhizomyx for the management of root rot of chickpea. Pak J Phytopathol 27:153–158

Sharma HKP, Mishra SD (2003) Effect of plant growth promoter microbes on root knot nematode *Meloidogyne incognita* on okra. Curr Nematol 14:57–60

Sharma IP, Sharma AK (2016) Physiological and biochemical changes in tomato cultivar PT-3 with dual inoculation of mycorrhiza and PGPR against root-knot nematode. Symbiosis 69. https://doi.org/10.1007/s13199-016-0423-x

Shaul O, Galili S, Volpin H, Ginzberg I, Elad Y, Chet I, Kapulnik Y (1999) Mycorrhiza-induced changes in disease severity and PR protein expression in tobacco leaves. Mol Plant Microbe Interact 12:1000–1007

Siasou E, Standing D, Killham K, Johnson D (2009) Mycorrhizal fungi increase biocontrol potential of *Pseudomonas fluorescens*. Soil Biol Biochem 41:1341–1343

Siddiqui ZA, Akhtar MS (2006) Biological control of root-rot disease complex of chickpea by AM fungi. Archiv Phytopathol Plant Prot 39:389–395

Siddiqui ZA, Mahmood I (1996) Biological control of *Heterodera cajani* and *Fusarium udum* on pigeonpea by *Glomus mosseae*, *Trichoderma harzianum* and *Verticillium chlamydosporium*. Isr J Plant Sci 44:49–56

Siddiqui ZA, Singh LP (2005) Effects of fly ash and soil micro-organisms on plant growth, photosynthetic pigments and leaf blight of wheat. J Plant Dis Protect 112:146–155

Sikes BA (2010) When do arbuscular mycorrhizal fungi protect plant roots from pathogens? Plant Signal Behav 5:763–765

Singh M (2015) Interactions among arbuscular mycorrhizal fungi, *Trichoderma harzianum*, *Aspergillus niger* and biocontrol of wilt of tomato. Arch Phytopathol Plant Protect 48:205–211

Singh I (2017) Antimicrobials in higher plants: classification, mode of action and bioactivities. Chem Biol Lett 4:48–62

Singh R, Adholeya A, Mukerji KG (2000) Mycorrhiza incontrol of soil borne pathogens. In: Mukerji KG, Chamola BP, Singh J (eds) Mycorrhizal biology. Kluwer Academic/Plenum Publishers, New York, pp 173–196

Singh R, Soni SK, Kalra A (2013) Synergy between *Glomus fasciculatum* and a beneficial Pseudomonas in reducing root diseases and improving yield and forskolin content in *Coleus forskohlii* Briq. under organic field conditions. Mycorrhiza 23:35–44

Sipahioglu MH, Demir S, Usta M, Akkopru A (2009) Biological relationship of Potato virus Y and arbuscular mycorrhizal fungus *Glomus intraradices* in potato. Pest Tech 3:63–66

Sitaramaiah K, Sikora RA (1982) Effect of mycorrhizal fungus *Glomus fasciculatum* on the host parasite relationship of *Rotylenchulus reniformis* in tomato. Nematologica 28:412–419

Smith GS, Kaplan DT (1988) Influence of mycorrhizal fungus, phosphorus and burrowing nematode interactions on growth of rough lemon citrus seedlings. J Nematol 20:539–544

Smith SE, Read DJ (1997) Mycorrhizal symbiosis, 2nd edn. Academic Press, London

Smith SE, Read DJ (2008) Mineral nutrition, toxic element accumulation and water relations of arbuscular mycorrhizal plants. In: Smith SE, Read DJ (eds) Mycorrhizal symbiosis. Academic Press, London, pp 145–148

Smith SE, Smith FA (2011) Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystems scales. Annu Rev Plant Biol 63:227–250

Sood GS (2003) Chemotactic response of plant-growth-promoting bacteria towards roots of vesicular-arbuscular mycorrhizal tomato plants. FEMS Microbiol Ecol 45:219–227

St-Arnaud M, Vujanovic V (2007) Effect of the arbuscular mycorrhizal symbiosis on plant diseases andpests. In: Hamel C, Plenchette C (eds) Mycorrhizaein crop production. Haworth Press, Binghamton, pp 67–122

Steinkellner S, Lendzemo V, Langer I, Schweiger P, Khaosaad T, Toussaint JP, Vierheilig H (2007) Flavonoids and strigolactones in root exudates as signals in symbiotic and pathogenic plant-fungus interactions. Molecules 12:1290–1306

Stoffelen R, Verlinden R, Xuyen NT, De Waele D, Swennen R (2000) Host plant response of Eumusa and *Australimusa bananas* (*Musa* spp.) to migratory endoparasitic and root-knot nematodes. Nematol 2:907–916

Strobel N, Hussey R, Roncadori R (1982) Interactions of vesicular-arbuscular mycorrhizal fungi, *Meloidogyne incognita*, and soil fertility on peach. Phytopathol 72:690–694

Tahat MM, Kamaruzaman Sijam K, Othman R (2012) The potential of endomycorrhizal fungi in controlling tomato bacterial wilt *Ralstonia solanacearum* under glasshouse conditions. Afr J Biotechnol 11:13085–13094

Torres-Barragan A, Zavaleta-Mejia E, Gonzalez-Chavez C, Ferrera-Cerrato R (1996) The use of arbuscular mycorrhizae to control onion white rot (*Sclerotium cepivorum* Berk.) under field conditions. Mycorrhiza 6:253–257

Trotta A, Varese GC, Gnavi E, Fusconi A, Sampo S, Berta G (1996) Interactions between the soil borne pathogen *Phytophthoranicotianae* var. *parasitica* and the arbuscular mycorrhizal fungus *Glomus mosseae* in tomato plants. Plant Soil 185:199–209

Tylka GL, Hussey RS, Roncadori RW (1991) Interactions of vesicular-arbuscular mycorrhizal fungi, phosphorus and *Heterodera glyciens* on soybean. J Nematol 23:122–123

Van Wees SC, Van der Ent S, Pieterse CM (2008) Plant immune responses triggered by beneficial microbes. Curr Opin Plant Biol 11:443–448

Veresoglou SD, Rillig MC (2012) Suppression of fungal and nematode plant pathogens through arbuscular mycorrhizal fungi. Biol Lett 8:214–217

Vierheilig H, Steinkellner S, Khaosaad T (2008) The biocontrol effect of mycorrhization on soilborne fungal pathogens and the autoregulation of the AM symbiosis: one mechanism, two effects? In: Varma A (ed) Mycorrhiza. Springer, Berlin, pp 307–320

Vigo C, Norman JR, Hooker JE (2000) Biocontrol of the pathogen *Phytophthora* parasitica by arbuscular mycorrhizal fungi is a consequence of effects on infection loci. Plant Physiol 49:509–514

Vos C (2012) Arbusculaire Mycorrhizenschimmels in De Biocontrole Van Plantenparasitaire Nematoden. University of Leuven (KU Leuven), Leuven

Vos C, Schouteden N, Tuinen D, Chatagnier O, Elsen A, De Waele D, Panis B, Gianinazzi-Pearson V (2013) Mycorrhiza-induced resistance against the root-knot nematode *Meloidogyne incognita* involves priming of defense gene responses in tomato. Soil Biol Biochem 60:45–54

Vos CM, Yang Y, De Coninck B, Cammue BPA (2014) Fungal (-like) biocontrol organisms in tomato disease control. Biol Control 74:65–81

Waceke JW, Waudo SW, Sikora R (2001) Suppression of *Meloidogyne hapla* by arbuscular mycorrhiza fungi (AMF) on pyrethrum in Kenya. Int J Pest Manag 47:135–140

Wehner J, Antunes PM, Powell JR, Mazukatow J, Rillig MC (2010) Plant pathogen protection by arbuscular mycorrhizas: a role for fungal diversity? Pedobiologia 53:197–201

Wesemael W, Viaene N, Moens M (2011) Root-knot nematodes (*Meloidogyne* spp.) in Europe. Nematol 13:3–16. https://doi.org/10.1163/138855410X526831

Whipps JM (2004) Prospects and limitations for mycorrhizas in biocontrol of root pathogens. Can J Bot 82:1198–1227

Wyss U (2002) Feeding behaviour of plant-parasitic nematodes. In: Lee DL (ed) Biology of nematodes. Taylor and Francis, London, pp 233–259

Xavier LJC, Boyetchko SM (2004) Arbuscular mycorrhizal fungi in plant disease control. In: Arora D, Bridge P, Bhatnagar D (eds) Fungal biotechnology in agricultural, food, and environmental applications. Marcel Dekker, New York, pp 183–194

Yang H, Zhang Q, Dai Y, Liu Q, Tang J, Bian X (2014) Effects of arbuscular mycorrhizal fungi on plant growth depend on root system: a meta-analysis. Plant Soil 389:361–374

Yao M, Tweddell R, Désilets H (2002) Effect of two vesicular-arbuscular mycorrhizal fungi on the growth of micropropagated potato plantlets and on the extent of disease caused by *Rhizoctonia solani*. Mycorrhiza 12:235–242

Yuanjing L, Zhilei L, Hongyan H, Hong L, Xiancan Z, Xuhui L, Chunjie T (2013) Arbuscular mycorrhizal fungi-enhanced resistance against *Phytophthora sojae* infection on soybean leaves is mediated by a network involving hydrogen peroxide, jasmonic acid, and the metabolism of carbon and nitrogen. Acta Physiol Plant 35:3465–3475

Zhu HH, Yao Q (2004) Localized and systemic increase of phenols in tomato roots induced by *Glomus versiforme* inhibits *Ralstonia solanacearum*. J Phytopathol 152:537–542