

REVIEW

AMF-MEDIATED DEFENSE RESPONSES IN CROP PLANTS AGAINST PHYTOPATHOGENIC FUNGI

Sreechithra M.S., Sherin A. Salam*, Krishnapriya P.J., Anu Rajan S. and Heera G.

College of Agriculture, Vellayani, (Kerala Agricultural University), Thiruvananthapuram, Kerala 695 522

Email: sherin.salam@kau.in

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Abstract: In a symbiotic relationship, Arbuscular Mycorrhizal Fungi (AMF) enhance the host's absorption of nutrients such as phosphate and nitrate while the heterotrophic fungal partner is provided with photosynthates from the host plant. Mycorrhiza-induced resistance, or MIR, is a trait of AMF-colonized plants that is attributed to a variety of mechanisms, including enhanced plant nutrition, altered root morphology and rhizosphere environment, controlled synthesis of secondary metabolites, competition for invasion sites and nutrients, stimulation of the plant defense system to elicit defense responses that include morphological, biochemical, and molecular ones, thus effectively managing fungal diseases. Therefore, in sustainable agriculture, AMF can be employed as an important tool in integrated crop disease management.

Keywords: AMF, defense responses, mechanisms, phyto pathogenic fungi

INTRODUCTION

In most of the plant species' roots and some types of fungi have a mutualistic relationship known as mycorrhiza (Harley, 1989). A. B. Frank coined the term "mycorrhiza" in 1885. It comes from the Greek words "myco" or "mykes" which indicate "fungi" and "rhiza" which means "roots." There are different types of mycorrhizal associations such as 1) Ecto mycorrhiza 2) Endo mycorrhiza 3) Ectendo mycorrhiza 4) Ericoid mycorrhiza 5) Mono tropoid mycorrhiza 6) Orchid mycorrhiza and 7) Arbutoid mycorrhiza (Smith and Read, 1997). A phenomenon known as arbuscular mycorrhizal symbiosis develops between fungi belonging to the phylum Glomeromycota and the roots of roughly 80% of terrestrial plant species (Schübler *et al.*, 2001).

The Arbuscular Mycorrhizal Fungi (AMF) forms internal structures known as arbuscules, by infiltrating into the root cortex and facilitating the nutrient exchange between the partners. The host provides photosynthates to the heterotrophic fungal partner in exchange for the extracellular hyphal network's extensive spread into the surrounding soil, which allows it to go beyond the nutrient depletion zone and improve the supply of inorganic nutrient like phosphate and nitrate (Smith *et al.*, 2011). According to Kapoor and Bhatnagar (2007), AM symbiosis is crucial for boosting plant growth and development as well as enhancing plant tolerance to biotic and abiotic stresses.

TAXONOMIC CLASSIFICATION

Fungi belong to:

Phylum-*Glomeromycota*

Class-*Glomeromycetes*

The phylum *Glomeromycota* is divided into 4 orders and 9 families. Order *Glomerales*: 1

family *Glomeraceae* (*Glomus*)

Order *Diversisporales*: 4 families: *Acaulosporaceae* (*Acaulospora*, *Entrophospora*), *Diversisporaceae* (*Diversispora*), *Gigasporaceae* (*Gigaspora*, *Scutellospora*), *Pacisporaceae* (*Pacispora*)

Order *Archaeosporales*: 3 families: *Archaeosporaceae* (*Archaeospora*), *Ambisporaceae* (*Ambispora*), *Geosiphonaceae* (*Geosiphon*)

Order *Paraglomerales*: 1 family *Paraglomeraceae* (*Paraglomus*) (Kirk *et al.*, 2008).

SIGNIFICANCE OF AMF-PLANT SYMBIOSIS

By use of a "common mycorrhizal network" (CMN), which facilitates the movement of nutrients to plants, mycorrhizal symbiosis brings its benefits from the level of individual symbiotic plants to that of communities. When a plant experiences biotic or abiotic stress, it also uses CMN to convey alarm signals, alerting other plants that share CMN to the same stress (Leake *et al.*, 2004).

AMF AS BIOCONTROL AGENT

AMF-colonized plants exhibit higher levels of resilience to several biotic and abiotic stresses.

*Corresponding Author

"Mycorrhiza-induced resistance" (MIR) is the term for this type of induced resistance that is seen against different pathogens, such as bacteria, viruses, and fungi (Bennett *et al.*, 2006). It is accomplished by enhancing plant nutrition, altering the morphological structure of plant roots, enhancing the micro environment of the rhizosphere, controlling the synthesis of secondary metabolites, or directly competing with plant pathogenic microorganisms for nutrients as well as invasion sites, triggering plant defense system activation and thus improving disease resistance which are the main mechanisms that contribute to MIR (Chen *et al.*, 2021, Jaiti *et al.*, 2007, Song *et al.*, 2011).

PLANT DEFENSE RESPONSES INDUCED BY AMF

AMF, when it colonizes plant roots activates plant defense mechanisms by triggering specific relay processes. Microbe associated molecular patterns (MAMP) are tiny compounds found on the surface of most of the plant pathogenic as well as defense-activating microbes, including AMF. Additionally, these microbes produce effector proteins into or out of plant cells. Plant receptor protein complexes, or pattern recognition receptors (PRR), can then recognize the MAMP and effector molecules, activating either MAMP-triggered immunity (MTI) or Effector-triggered immunity (ETI) in turn (Mc Dowell, 2019). These plant resistance (R) proteins will identify some effect or molecules, while others will target host proteins to decrease MTI (Chisholm *et al.*, 2006). Effect or-triggered immunity (ETI) is a defense response that is initiated when effect or chemicals are recognized by R proteins (Dangl *et al.*, 2013). Although the two responses qualitatively resemble each other in many ways, but ETI is quicker and stronger than MTI (Dodds and Rathjen, 2010). Hypersensitive reaction (HR) is one type of programmed cell death triggered by ETI responses.

It is characterized by rapid, localized necrosis at the site of the first pathogen entry (Mur *et al.*, 2008). During the first phase, the level of salicylic acid (SA) increases. Later on, an antagonistic effect is caused by higher levels of hormones such as abscisic acid (ABA) and jasmonic acid (JA) which suppresses this reaction. Although its involvement in MIR is debatable, ABA is thought to transmit the long-distance signals of MIR throughout the plant, whereas JA promotes the development of induced systemic resistance (ISR). Early stage SA induction causes systemic acquired resistance (SAR) to develop (Kadam *et al.*, 2020). By inhibiting the plant immune mechanism and promoting the development of AMF symbiosis, one of the effector molecules such as SP7 (secreted protein 7), secreted by *Glomus intraradices*, helps to develop a biotrophic status of AMF in roots (Kloppholz *et al.*, 2011). Later on, the linked AMF's myc factor causes cytosolic Ca²⁺ to rise, which in turn causes the production of Reactive Oxygen Species (ROS), Mitogen-Activated Protein Kinase (MAPK), and G-proteins alteration. The induction of lipoxygenase (LOX) by ROS also facilitates the production of JA. Several anti oxidant enzymes are produced, including catalases (CAT), peroxidases (POX), ascorbate peroxidase (APX), and superoxide dismutase (SOD). These enzymes are important in the metabolism of ROS and are phosphorylated by G-protein and MAPK. When a pathogen penetrates host tissues, MAPK and G-protein also activate genes involved in plant defense. The proteins that are produced by these defense related genes target and attempt to kill the invasive microorganisms. The antioxidant enzymes and ROS produced at the site of pathogen infection, however, function constitutively and initiate HR leading to the suppression of the diseases causing pathogen (Maharshietal.,2019).

Important fungal pathogens controlled by AMF (Table.1)

AMF species	Fungal pathogen	Host	Reference
<i>Glomus intraradices</i>	<i>Phytophthora sojae</i>	Soybean	Marquez <i>et al.</i> (2018)
<i>Rhizoglomus intraradices</i>	<i>Magnaporthe oryzae</i>	Rice	Tian <i>et al.</i> (2019)
<i>Glomus claroideum</i>	<i>Fusarium oxysporum</i>	Cucumber	Ahamed <i>et al.</i> (2020)
<i>Rhizophagus irregularis</i>	<i>Magnaporthe oryzae</i>	Rice	Campo <i>et al.</i> (2020)
<i>Rhizoglomus irregularis</i>	<i>Botrytis cinerea</i>	Tomato	Sanmartin <i>et al.</i> (2020)
<i>Funneliformis mosseae</i> <i>Rhizophagus irregularis</i>	<i>Fusarium oxysporum</i>	Tomato	Singh <i>et al.</i> (2020)

MORPHOLOGICAL RESPONSES INDUCED BY AMF

AMF primarily induces lignification, deposition of callose and non-esterified pectins, the creation of structures resembling papillae against phytopathogenic fungi (Ahamed *et al.*, 2020, Chen *et al.*, 2021).

The induction of resistance against *Colletotrichum orbiculare* in cucumber leaves by *Glomus intraradices* was studied by Lee *et al.*, 2005. When comparing the leaves of AMF infested plants to those of untreated control plants, there was a noticeable deterioration in the disease severity. Pre-treatment with DL-3 amino butyric acid (BABA) was employed as a positive control and it was shown that

this verity of disease was significantly reduced. On the plants leaves treated with *G. intraradices*, however, the frequency of callose development was noticeably high five days after inoculation. Consequently, they proposed that, resistance caused by *G. intraradices* colonization may be linked to an increase in callose development at the site of penetration by pathogen in the infected leaves.

Jalaludeen *et al.*, 2020 assessed the relationship between *Glomus mosseae* and particular Act in oomycetes on chilli peppers in relation to *F. oxysporum* in a green house setting. They also looked in to the possibility of Act in oomycetes and *G. mosseae* working together to induce resistance against *Fusarium* wilt. The AMF inoculum was 10 g of dry soil and 100 mature spores. They discovered that there was a decrease in root mortality and an induction of lignification in the dual-treated chilli pepper root. The lignin content was measured using lignothioglycolic acid derivatives (LTGA). The highest total lignin content was found in the roots of dual-treated chilli peppers on days 10 and 18, with 2.592 and 2.922 LTGA $\mu\text{g g}^{-1}$ tissue, respectively, compared to the control samples, which had 1.259 to 1.212 LTGA $\mu\text{g g}^{-1}$ tissue.

BIOCHEMICAL RESPONSES INDUCED BY AMF

The biochemical responses that are triggered by AMF against plant pathogenic fungi include altered composition of root exudate (Sarathambal *et al.*, 2023), the synthesis of phenolic compounds, phytoalexins and defense enzymes (Eke *et al.*, 2016), the induction of signaling molecules (Nair *et al.*, 2015), and more. Nair *et al.* (2015) measured the following items to investigate the role of jasmonic acid (JA) and salicylic (SA) acid in the expression of MIR against *A. alternate* such as

- (i) levels of methyl jasmonate (MeJA) and jasmonic acid (JA); and
 - (ii) activity of enzymes reported to be involved in their biosynthesis, namely lipoxygenase (LOX) and
 - (iii) phenyl alanine ammonia lyase (PAL).
- Compared to control plants, AM-colonized plants exhibited three times increased LOX activity; however, in contrast to controls, this did not rise further in response to pathogen application. In AM colonized plants, there was a four-fold increase in MeJA in the leaves when compared to controls, which was correlated with higher LOX activity in those plants. The findings imply that in response to AM colonization, the expression of MIR against *A. alternata* is significantly influenced by the systemic rise in JA.

A study was conducted by Eke *et al.* (2016) to assess the efficacy of four AMF formulations such as *Glomus intraradices*, *Glomus hoi*, *Gigaspora margarita*, and *Scutellospora gigantea* in improving

growth of common bean (*Phaseolus vulgaris* L.) and biocontrol against *Fusarium solani* in green house conditions. The findings showed that all of the mycorrhizal preparations considerably decreased the incidence and severity of the *Fusarium* infection in bean plants that were affected. After being inoculated with *F. solani*, the mycorrhizal rhizospheric competency (root colonization and spore density) was affected. Furthermore, following mycorrhizal colonization, there was an increase in the amount of flavonoids and total soluble phenols as well as the specific activity of phenyl alanine ammonia lyase (PAL), suggesting that the defense mechanism of the plant had strengthened against the pathogen. The potential function of the AMF consortium in promoting plant systemic defense against *Fusarium oxysporum* f. sp. *lycopersici* (FOL) in tomato plants was investigated by Hashem *et al.* (2021). The wilt disease and fusaric acid production within vascular tissue was lessened by AMF inoculation which may have contributed to the decreased wilting. FOL had an antagonistic effect on AMF by inhibiting its colonization in the host, reduced the production of spores, arbuscules, and vesicles. AMF also reduced the harm caused by *Fusarium* wilt by raising chlorophyll levels and phosphate- metabolizing enzyme activity (acid and alkaline phosphatases). Furthermore, mycorrhizal-inoculated tomato plants exhibited elevated levels of antioxidant enzymes such as catalase, glutathione reductase, and others, which ultimately impacted the removal of reactive oxygen species. Furthermore, increased photosynthetic efficiency, an increase in phosphatase, and antioxidant enzymatic systems all led to tomato plants developing induced resistance to FOL. Sarathambal *et al.* (2023) studied the impact of mycorrhizal colonization on the constituents of root exudates in blackpepper plants infected with *Phytophthora capsici*. This is the first study to assess the root exudation profiles of *P. capsici* infection and/or AM colonization in blackpepper. In comparison to *P. capsici* inoculated plants, the root exudates of AM colonized plants exhibited higher levels of fatty acid/fatty acyl compounds, such as tetradecanoic acid, n-hexadecanoic acid, octadecanoic acid, and nonacos-1-ene. On the other hand, the root exudates of *P. capsici*-inoculated plants, the majority of alkane hydrocarbons mostly found included (z)-3-tetradecene, octylcyclohexane, 4-cyclohexylundecane, and decylcyclohexane. According to multivariate analysis of the root exudate data, the content of root exudates during *Phytophthora* infection was normalized by AM colonization in black pepper roots and was comparable to control plants. According to the study, an AM- infected root modifies its metabolism and aids in the management of biotic stress in plants.

Other biochemical responses induced by AMF (Table.2)

Fungal pathogen	Host	AMF species	Response	Reference
<i>Magnaporthe oryzae</i>	Rice	<i>Rhizoglo mus intraradices</i>	Regulation of auxin and SA metabolism, increased α -linolenic acid production, improved JA synthesis, induce the shikimate pathway, syntheses of terpenoids and phenol, biosynthesis of brassino steroids	Tian <i>et al.</i> , 2019
<i>Fusarium oxysporum</i>	Chilli Pepper	<i>Glomus mosseae</i>	Increased PO and PPO activities	Jalaluldeen <i>et al.</i> , 2020
<i>Fusarium oxysporum</i>	Alfalfa	<i>Funneliformis mosseae</i>	Accumulation of antioxidant enzymes, plant hydrolase and plant hormones, such as superoxide dismutase, β -1, 3-glucanase, chitinase, PAL, ABA, Ethylene and H ₂ O ₂	Wang <i>et al.</i> , 2020
<i>P.parasitica</i>	Trifoliatorange	<i>Funneliformis mosseae</i>	Activities of root chitinase, PAL and β -1, 3-glucanase	Tian <i>et al.</i> , 2021
<i>Verticillium dahliae</i>	Artichoke	<i>Glomus viscosum</i>	Significant increase in APX, SOD activities, higher content of ascorbate and glutathione, decrease in the levels of lipid Peroxidation and H ₂ O ₂	Villani <i>et al.</i> , 2021
<i>R.solani</i>	<i>Vicia faba</i>	<i>Funneliformis mosseae</i> <i>Gigasporagigantea</i>	Increased phenolic content, PPO and PO Content	Gazzar <i>et al.</i> , 2023
<i>Phytophthora nicotianae</i> (Blackshank)	Tobacco	<i>Paraglomus occultum</i>	Accumulation of GSH, proline, total phenols, and flavonoids	Li <i>et al.</i> , 2023

MOLECULAR RESPONSES INDUCED BY AMF

AMF invasion triggers several molecular changes at the genetic level that result in the activation of the plant defense system and different genes are triggered in the host plant that are in charge of the defense mechanism against phytopathogens. Rashad *et al.* (2020) examined the potential of endophytic *Bacillus amyloliquefaciens* GGA and/or AMF to control *Sclerotium cepivorum* causing white rot disease in garlic. The use of the combined therapy of *B. amyloliquefaciens* GGA and AMF decreased disease severity and incidence more than the individual treatments, as demonstrated by the results from pot studies. Using qRT-PCR, the transcript levels of the defensin gene in garlic plants were measured in response to the various applied treatments. All treatments significantly increased the expression of defensin in the two harvests taken as compared to the control treatment. Compared to 60 days post inoculation (dpi), the induction effect was largest at 30 dpi. The highest levels of gene expression were seen in the two harvests in *S. cepivorum* inoculated plants treated with AMF and *B. amyloliquefaciens* GGA (13.2-fold increase at 30dpi, and 9.5-fold at 60 dpi). Additionally, there

were variable degrees of impact on chitinase gene expression. Expression was higher at 30 dpi than it was at 60 dpi. When compared to the untreated control, the plants that were inoculated with *S. cepivorum* and treated with *B. amyloliquefaciens* GGA and AMF exhibited the highest levels of gene expression (8.9-times increase at 30 dpi). Garlic plant growth and yield metrics improved as a result of this treatment.

Zhang *et al.* (2018) assessed *Rhizophagus irregularis* CD1's impact on resistance of cotton to *Verticillium* wilt and plant growth promotion. In comparison to the control, AMF colonization significantly increased the amount of inorganic phosphate (Pi) in the roots and leaves. It also prevented *Verticillium dahlia* from developing symptoms and significantly increased the expression of genes linked to pathogenesis, such as GhHSR203J, GhHIN1, GhPR1, GhPR3, GhPR4, GhPR5, and GhPR9, as well as genes related to lignin synthesis. Cotton treated with mycorrhiza also showed up-regulation of the genes that encode for important enzymes associated with the JA production pathway, including GhLOX1, GhACO1, and GhOPR3. Tests were conducted on the antimicrobial properties of AMF against *Verticillium*

dahliae *in vitro*. The nonvolatile solutes were kept from diffusing between the two compartments by utilizing divided Petri plates. They discovered that the mycelial growth of *V. dahliae* was inhibited by AMF symbionts, in contrast to AMF hyphae or spores.

Based on *in vitro* investigations, it was determined that the AMF endosymbiont might impede the growth of phytopathogenic fungi, such as *V. dahliae*, by emitting volatile compounds.

Other molecular responses induced by AMF (Table.3)

Fungal Pathogen	Host	AMF species	Response	Reference
<i>Fusarium oxysporum</i>	Cucumber	<i>Glomus claroideum</i>	Increased the activity and transcripts of SOD, APX and the content of glutathione and proline	Ahmed <i>et al.</i> , 2020
<i>Botrytis cinerea</i>	Tomato	<i>Rhizoglyphus irregularis</i>	JA defense-related genes were upregulated	Sanmartín <i>et al.</i> , 2020
<i>P. parasitica</i>	Trifoliate orange	<i>Funneliformis mosseae</i>	Up-regulation of SA synthesis genes (PtPAL1 and PtEPS1) Higher expression of pathogenesis-related protein gene1 (PtPR1), PtPR4, and PtPR5	Tian <i>et al.</i> , 2021
<i>Fusarium oxysporum</i>	Tomato	<i>Rhizophagus irregularis</i>	Induced expression of the JA synthesis genes including AOC and LOX and increased activities of PPO and PAL	Wang <i>et al.</i> , 2022
<i>P. capsici</i>	Black pepper	<i>Rhizophagus irregularis</i>	Up-regulation of pathogenesis related genes viz., APX, osmotin and β -1, 3-glucanase, PAL and NPR1 in black pepper leaves and roots	Sarathambal <i>et al.</i> , 2023

CHALLENGES TO THE USE OF AMF AS A BIO CONTROL AGENT

Due to its obligatory biotrophicity, it is not possible to produce AMF inoculum on a large scale. After field introduction, there can be some unfavorable interactions between the native AMF and the residing microbial community. The compatibility of the AMF association with the host plant is crucial because it influences both the AMF colonization and the favorable or unfavorable effects on the host plant that result from it. It is exceedingly difficult to maintain the diversity of AMF in soil because a variety of factors that may indirectly change soil AMF diversity viz., the host's genotype, the amount of fertilizer and pesticide applied, tillage, crop rotation, the impact of related microbes, etc.

CONCLUSION

Plant diseases are on the rise due to plant pathogens in the farming environment becoming more resistant as a result of the extensive use of chemicals. Hence, environmentally friendly methods of controlling plant diseases are therefore crucial. Within the mycorrhizae, AMFs are the most prevalent, biomass-rich, and important beneficial fungal group. They have a particular antagonistic or inhibitory effect on plant pathogens. AMF can activate the plant defense system and induce defense responses including

morphological, biochemical, and molecular ones. It can also effectively manage crop diseases by competing with pathogens for space and photosynthates, regulating secondary metabolite formation in plants by altering the morphological structures of plant roots. Therefore, AMF can be utilized as an important candidate in integrated crop disease management in sustainable agriculture.

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