Journal of Phytology 2010, 2(7): 53-69
An Open Access Journal
ISSN: 2075-6240
Available Online: www.journal-phytology.com

REGULAR ARTICLE

ARBUSCULAR MYCORRHIZAL FUNGI-INDUCED SIGNALLING IN PLANT DEFENCE AGAINST PHYTOPATHOGENS

Md. Haneef Khan[1], M.K. Meghvansi[1*], Vipin Panwar[2], H.K. Gogoi[1], Lokendra Singh[1]
[1]*Defence Research Laboratory, Post Bag No 2, Tezpur-784001, Assam, India*
[2]*Directorate of Wheat Research (ICAR), Karnal, Haryana, India*

SUMMARY

Arbuscular mycorrhizal fungi (AMF), the ancient mutualist and biotroph of plants, improve the supply of water and nutrients, such as phosphate and nitrogen to its host plant. In exchange of this, it takes a part of photosynthate sugar to complete its life cycle. Despite having its own immune system, the plant upon pathogen attack gets weaken and needs reinforcement to fight back and become stabilize in the battle ground. AMF fulfills the need of host plant and provides with support in many ways by induction of attenuated defence signaling for combating against phytopathogen. This elevation not only makes plant more tolerant towards the attack of phytopathogen but also, enhances the genetic, biochemical and signaling factors responsible for its defence purpose. In this article, we look forward to discuss the factors, mechanisms and pathways responsible for this back-up from AMF to plants with recent experimental proof. In addition, this meta-analysis will also try to focus on areas that have recently got attention or are less known, so that, lacunae and underestimated aspects should come in front for a further systematic research.

Md. Haneef Khan et al. Arbuscular Mycorrhizal Fungi-Induced Signalling in Plant Defence against Phytopathogens. J Phytol 2/7 (2010) 53-69.
*Corresponding Author, Email: mk_meghvansi@yahoo.co.in

1. Introduction

It is a well established fact that the plants deal with phytopathogens by means of their own immune system (IS). These include preformed physical and chemical barriers and several active mechanisms (Kachroo and kachroo, 2009). IS is further divided into primary immune system and secondary immune system. The primary immune system involves interaction of strain-specific avirulent (AVR) protein from the pathogen with a cognate plant resistance (R) protein (Dangl and Jones, 2001). This initiates systemic acquired resistance (SAR) in systemic tissues to provide with immunity against the secondary infections by related and unrelated pathogens (Durrant and Dong, 2004; Klessig et al., 2009). Another mode of secondary immunity, termed induced systemic resistance (ISR), is activated upon colonization of plant root by nonpathogenic rhizosphere microbes (Van Loon et al., 1998). Very often it has been observed that despite having their own defence system, plants require support to fight against phytopathogens. This may be due to slow response or low induction level of defense-related factors. AMF have long been known as a paramount among symbionts of plants. They belong to the phylum, Glomeromycota (Schübler et al., 2001) and colonize 70–90% of land plant species (Smith and Read, 2008). Though the colonization specificity does matter but not much, depending upon many factors including the genotype of the host plant (Koide and Schreiner, 1992; Meghvansi et al., 2008). There are several benefits of AMF colonization in plants, mainly the increase in nutrient uptake (Smith and Read, 2008). Despite this, still there is an ambiguity that the AMF has any direct involvement in the host's defence signaling against phytopathogens. Although, there are some indirect functions which contribute to intensify the plant defence responses

including augmentation of plant nutrition (Smith and Read, 2008) and damage compensation. Moreover, it includes anatomical alterations in the root system (Wehner et al., 2010), microbial changes in the rhizosphere and enhancing the attenuated plant defence responses by altering the host's signaling pathways (Pozo and Azcón-Aguilar, 2007). This is accomplished primarily through modulation in Jasmonic acid (JA) and salicylic acid (SA) dependent pathways (Pozo and Azcón-Aguilar, 2007). Furthermore, the AMF is likely to have role in induction of hydrolytic enzymes (Pozo et al., 1999), enhanced levels of Pathogenesis-related (PR) proteins, accrual of phytoalexins (Harrison and Dixon, 1993; Morandi, 1996; Larose et al., 2002), callose deposition (Cordier et al., 1998) and reactive oxygen species generation (Salzer et al., 1999). Hence, there are several reports exemplifying the potential of AMF in reducing the severity and incidence of phytopathogens for a long. But the knowledge of the mechanism behind it is scarce. In this review, we have attempted to discuss the essential keys responsible for plant defence signalling against phytopathogens in presence of AMF. Most importantly, we highlight the biochemical, molecular, ecological and signaling factors in charge of affecting the relationship and the interactions among them with possible mechanisms to understand the underlying pathways.

2. Genetic basis of AMF's contribution

During AMF's colonization, a strong genetic shift occurs which leads to the enhancement of signaling pathways of plant defence response against phytopathogen. However, AMF itself while colonization face an attack of different classes of chitinases (enzymes having antifungal property) especially of Class I chitinases. Interestingly, the Class I chitinases was found to be unable to inhibit AMF colonization (Arlorio et al., 1991; Salzer et al., 1997; Vierheilig et al., 1993). After having symbiotic relationship with its host, AMF possibly enhances genes-encoded products having antimicrobial activity. For instance, induction of *Medicago truncatula* genes TC104515 (6659-fold), TC101060 and TC98064 was observed in the roots colonized with *Glomus intraradices* (Liu et al., 2007). These genes were predicted to encode cysteine rich proteins that display antifungal activity (Terras et al., 1995). Their function is to elicit the hypersensitivity response with the matching resistance gene (de Wit et al., 1992). This response is mediated by reactive oxygen species (ROS) produced early in the plant-pathogen interaction (Levine et al., 1994). However, TC104515 transcripts were detected only in roots colonized with *G. intraradices* and not in roots colonized with *G. versiforme* or *Gigaspora gigantea*. This gene was also not expressed in *M. truncatula*/*G. mosseae* roots (Hohnjec et al., 2005). So, there is a considerable variation in the genetic shifts of different plant-related defence genes colonized with diverse AMF species, which needs exploration.

It has been reported that AMF's bioprotection strategy is more effective in the plant's root than the shoot. Even, within the AMF colonized roots, the complex differential gene expression pattern was observed (Liu et al., 2007) rendering AMF's bioprotection system more sensitive towards plant roots. In an experiment, a group of genes was identified through differential expression in shoots of AMF colonized plant, showing striking similarities with defence/stress signaling genes and ACRE genes (Liu et al., 2007). The ACRE genes were previously known to respond instantaneously in tomato upon infection of *Cladosporium fulvum* and suggested to be involved in the initial development of defense signaling (Durrant et al., 2000). Based on the split-root analyses, some of ACRE genes including two WRKY-type transcription factors and a TOLL-type protein showed a greater increase in transcripts in the noncolonized roots and shoots of the mycorrhizal plants (Liu et al., 2007). On the contrary, leaves of mycorrhizal plants infected with the phytopathogens *Botrytis cinerea* or tobacco mosaic virus showed a higher incidence and severity of necrotic lesions than those of nonmycorrhizal ones (Shaul et al., 1999). Further investigation revealed the induction of PR-1

and PR-3 expression was observed in the leaves of both nonmycorrhizal and mycorrhizal plants (Shaul et al., 1999). Although, accretion and mRNA steady-state levels of these proteins were lower, and their appearance were delayed in the leaves of the mycorrhizal plants (Shaul et al., 1999). They concluded that prior infection of AMF than pathogen attack is required. In support of this, Cartieaux et al., (2003) found that photosynthesis-associated gene expression was downregulated in *Arabidopsis* leaves in mycorrhizal plants specifically of the small subunit of Rubisco (Liu et al., 2007). So, it is evident that there must be some regulatory processes which get initiated in the roots of mycorrhizal plants, that modified the disease-symptom development and gene expression in the tobacco leaves. Another common feature of the resistance responses induced by AMF is priming. Priming is a plausible strategy which includes preconditioning of plant tissues for a more effective activation of defenses (Conrath et al., 2006). For example, colonization of mycorrhizal fungi in tomato roots systemically protects the plant against *Phytophthora parasitica* infection without direct accumulation of PR proteins (Conrath et al., 2006). However, Conrath et al., (2006) found that upon pathogen attack, mycorrhized plants accumulate considerable amount of PR-1a, which confers SAR and basic β-1,3 GLUCANASE (BGL) proteins than non-mycorrhized plants. AMF-colonized rice was found to have induced lipid transfer protein (encoded from *Ltp* gene) (Blilou et al., 2000b.) which is accountable for plant defence response for its antimicrobial property (Molina and García-Olmedo, 1993; García-Olmedo, 1995). Phenylalanine ammonia lyase (PAL) enzyme (encoded from *Pal* gene), which leads to the production of phytoalexins and phenolic compounds, was also persuaded in the rice infected with AMF (Blilou et al., 2000b.). In addition to this, *VCH3* gene-encoded chitinase enzyme was observed in the primed expression of AMF-colonized grapevine roots against *Meloidogyne incognita* (Li et al., 2006). These evidences are strongly in favour of AMF triggered localized and systemic priming of plants. But, above stated studies lack the observation of induction of these constitutive genes on the plant's health which is a costly affair for the host. Moreover, these findings are based on only observations of few defence-related genes. So, these limited findings need to be extended and the mechanism behind the stimulatory effect of AMF in plant's defence response against phytopathogens should come in front. More effective and in depth studies are required to make a link between AMF and plant defence signaling.

Table 1. List of genes induced after AMF colonization in host plant and are responsible for the plant's defence against phytopathogen.

Sl. No.	Gene	Product	Function	Source	Reference
1.	*TC104515*	Cysteine rich protein	Antifungal property	*M. truncatula*	Liu et al., 2007
2.	*TC101060*	Cysteine rich protein	Antifungal property	*M. truncatula*	Liu et al., 2007
3.	*TC98064*	Cysteine rich protein	Antifungal property	*Medicago truncatula*	Liu et al., 2007
4.	*PR-1a*	PR-1a protein	Pathogenesis-related (Antimicrobial)	Tomato	Conrath et al., 2006
5.	*BGL*	β-1,3 Glucanase (PR protein family)	Antifungal property	Tomato	Conrath et al., 2006
6.	*VCH3*	Chitinase protein (PR protein family)	Antifungal property against *Meloidogyne incognita*	*Vitis amurensis* Rupr. (Grapevine)	Li et al., 2006
7.	*Pal*	Phenylalanine ammonia lyase (PAL) enzyme	leads to production of phytoalexins and phenolic substances	Rice	Blilou et al., 2000b.

8.	*Ltp*	Lipid transfer protein	Antimicrobial	Rice	Blilou et al., 2000b.
9.	*PR10*	PR 10	Pathogenesis-related protein (have RNases activity)	Pea; Parsely	Ruiz-Lozano, 1999; Moieyev et al., 1994; Walter et al., 1996
10.	*pI 49*	pI 49	Member of multigene family PR 10 (have Ribonuclease activity)	Pea	Ruiz-Lozano, 1999; Hadwiger et al., 1992
11.	*pI 176*	pI 176	Member of multigene family PR 10 (have Ribonuclease activity)	Pea	Ruiz-Lozano, 1999; Hadwiger et al., 1992
12.	*pI 206*	pI 206	Linked to appressorium formation in *G. mosseae*-inoculated pea plant and plant-pathogen interaction as well	Pea	Ruiz-Lozano, 1999
13.	Unknown	Chalcone isomerase	Requires for the production of phytolexins	Pea	Ruiz-Lozano, 1999; Harrison and Dixon, 1993, 1994
14.	Unknown	Transcinnamic acid 4-hydroxylase	Requires for the production of phytolexins	Pea	Ruiz-Lozano, 1999; Harrison and Dixon, 1993, 1994
15.	Unknown	Basic A1-chitinase	Antifungal property having vacuolar compartmentation	Pea	Ruiz-Lozano, 1999

3. Biochemical basis of AMF's involvement

The recognition of potential invader by the plant, a prerequisite for an effective response, is accomplished through the recognition of specific signal molecules known as elicitors (Garcia-Garrído and Ocampo, 2002). These elicitors are secreted either by pathogens (exogenous elicitors) or through damage in the plant's cell wall caused by the pathogens. Upon perception of which, a cascade of biochemical reactions occurs in response of host's defence. These include changes in the ion permeability of the plasma membrane bound enzymes, the activation of kinases, phosphatases, phospholipases and the production of signal molecules, including active oxygen species (Somssich and Hahlbrock, 1998). Similar events like signal perception, signal transduction and activation of defence genes have been encountered during AMF-plant interaction. Salzer and Boller, (2000) suggested that AMF and other mycorrhizal fungi secrete similar chitin elicitors like that of phytopathogen, which could induce plant-defence related gene. For example, *G. intraradices* induces the expression of chalcone synthase (an antimicrobial compound), the first enzyme in flavonoid compound, such as phytoalexin, in *M. truncatula* (Bonanomi et al., 2001). On the contrary, RNA blot analysis revealed slightly higher accumulation of chalcone synthase in *G. intraradices*-colonized roots of dark red kidney bean (*Phaseolus vulgaris* L. cv Moncalm) when compared with the non-colonized ones. This may be due to the fact that different plants may have their specific requirements. With the plausible induction of the genes by AMF in plants, it may play an implicate role in the biochemical reactions with proteins, secondary metabolites and other chemicals involved in plant defence response. It has been well reported that, with the AMF-colonized roots, the above ground effect against phytopathogen is quite apparent (Cimen et al., 2009; Sensoy et al.,

2007; Ozgonen et al., 2010; Al-Askar and Rashad, 2010; Kapoor, 2008).

The most studied phytohormone in the AMF-plant interactions is JA which has been exploited for a long. Both, the accommodation of AMF and the nutrient provided by it within the plant root cells are regulated by JA. It is also involved in the regulation of wound response and resistance against necrotrophs (Ton et al., 2002; Glazebrook, 2005). Moreover, it has been suggested that JA plays a pivotal role in systemic resistance (Van der Ent et al., 2009) in *Arabidopsis* (Truman et al., 2007). JA biosynthesis requires substrate level availability (Stenzel et al., 2003; Wasterneck, 2007) and for that, lipases are the enzymes which generate its precursors (eg. Linolenic acid) from plastid lipids (Hyon et al., 2008; Ishiguro et al., 2001). Upon pathogen attack, how this lipase gets activated or some exogenous elicitors do this job is yet to explored fully. There are several studies which show the increase in the endogenous JA levels in arbusculated cells of plant (Hause et al., 2002; Vierheilig and Piché, 2002; Stumpe et al., 2005; Meixner et al., 2005) upon phytopathogens attack. More evidences from experimental analysis suggest that JA pathway has some links with the primed deposition of callose in grapevine (Hamiduzzaman et al., 2005). In support of this, Cordier et al., in 1998, also found that in *P. parasitica* infected AMF tissues of tomato roots; arbusculated cells form wall appositions, suggesting a possible presence of callose. Nevertheless, whether AMF-induced JA biosynthesis is only a localized effect or extended up to systemic level also is a question unanswered.

Other phytohormones like SA and Ethylene, which have a crucial role in SAR and ISR respectively (Van Loon et al., 2006; Van der Ent et al., 2009), get activated upon pathogen perception by the plant. They show broad-spectrum effectiveness against several phytopathogen like fungal root pathogen *Fusarium oxysporum*, downy mildew pathogen *Hyaloperonospora arabidopsis* (Pieterse et al., 1996; Ton et al., 2002), necrtotrophic pathogens *Alternaria brassicicola* (Ton et al., 2002), *Botrytis cinerea* (Van der Ent et al., 2008), *Plectosphaerella cucumerina* (Segarra et al., 2009). Like other pathogens, SA also recognizes AMF as pathogen and acts against it by delaying its colonization or in some cases suppresses its growth. But, in mycorrhizal defective (myc^-) mutants, it has been found that in response to AMF, SA levels are enhanced (Garcia-Garrído and Ocampo, 2002).

AMF was also found to induce several phytoalexins such as Phenylalanine Ammonia Lyase (PAL), Rishitin and solavetivone (Engström et al., 1999), hydroxyproline-rich glycoproteins (Lambais, 2000; Garcia-Garrído and Ocampo, 2002), isoflavonoid (-)-medicarpin, medicarpin-3-0-glycoside and formononetin in alfalfa (Volpin et al., 1995; Harrison and Dixon, 1993), glyceollin and coumestrol (Morandi and Le Querre, 1991). They are low molecular weight, anti-microbial compounds that are both synthesized by and accumulated in plants after encountering pathogens (Paxton, 1981). AMF colonization in roots stimulates the phenylpropanoid pathway (Morandi, 1996), which can be due to the induction of PAL activity as observed by Kapoor (2008). Cordier et al., (1998) found that decreased colonization by *P. parasitica* in mycorrhizal parts of the plants was associated with an elevated accumulation of phenolics and than Ortho-dihydric phenol non-mycorrhizal (Kapoor, 2008). This increase in concentration of phenols and O-dihydric phenols in mycorrhizal tomato plants can be due to the induction of PAL enzyme activity (Kapoor, 2008). However, many of these Phytoalexins and hydroxyproline-rich glycoproteins were found to induce either temporarily or the level of accumulation of these molecules was moderate when compared with the non-colonized plants (Yao et al., 2002, 2003; Lambais, 2000; Garcia- Garrído and Ocampo, 2002).

AMF is also reported to stimulate defence related other enzymes such as polyphenol oxidase and peroxidase (Al-Askar and Rashad, 2010), specific isoforms of hydrolytic enzymes like chitinases and glucanases (Pozo and Azcón-Aguilar, 2007), catalase and ascorbate peroxidase (Blilou et

al., 2000a) upto a significant level. Accumulation of reactive oxygen species (ROS) in the mycorrhized plants has also been observed (Pozo and Azcón-Aguilar, 2007). Although its accumulation was not so significant and was generally localized (Pozo and Azcón-Aguilar, 2007). It is evident that AMF-colonized plants stand in better position than the non-colonized ones. However, some studies don't comply with this statement because it depends on many other factors such as soil community dynamics and its nutrient status in combination with several other environmental factors. Therefore, these areas of intra-disciplines of biology need more emphasis as there are still huge lacunae remain which need more detailed investigations.

4. Signal transduction between AMF and plant upon pathogen attack

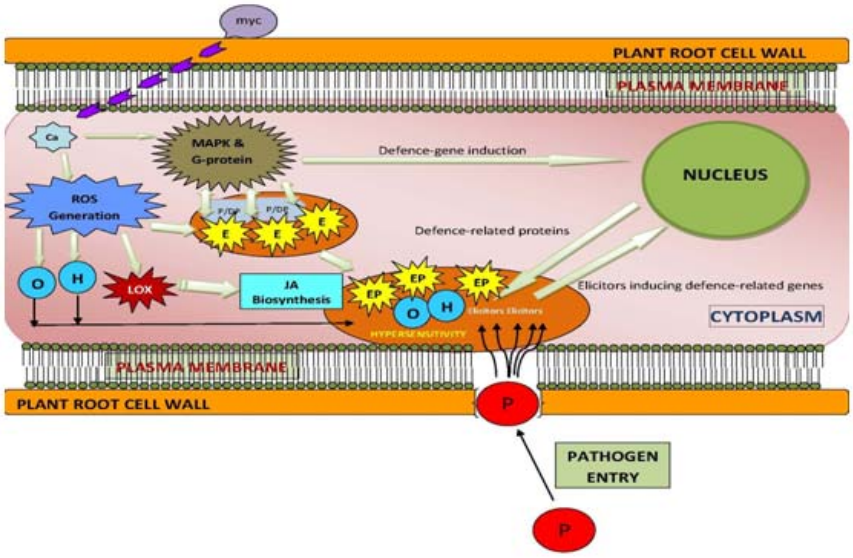
During plant-microbe interactions, an extensive exchange of molecular messages in form of signal transduction befalls. These signaling pathways are an integrated system of diverse defence-related compounds. It includes cytosolic calcium, reactive oxygen species (ROS), fatty acids, jasmonic acid, salicylic acid and Ethylene which get activated through a cascade of reactions. Cytosolic free Ca^{2+} concentration ($[Ca^{2+}]_{cyt}$) is an illustrious component of signal transduction pathways involved in plant-pathogen interactions (Scheel, 1998; Sanders et al., 2002). Upon receiving signals from plant, AMF replies through yet an unidentified small molecule known as Myc factor which is responsible for triggering downstream responses including Ca responses (Müller et al., 2000), thereby leading to form a symbiotic relationship with the host plant. A Ca–calmodulin-dependent protein kinase (ccaMK) is essential for AMF symbiosis (Lévy et al., 2004; Mitra et al., 2004). The calmodulin-binding domain and Ca-binding EF hand motifs of ccaMK allow the protein to sense calcium, making it a prime candidate for the response to calcium signatures that are induced by AM fungi (Kosuta et al., 2008). These promptly induce the cytosolic calcium ($[Ca^{2+}]_{cyt}$) elevation (Navazio et al., 2007), which is an initial step of active defence, making increment in the ROS generation (Strange, 2003). ROS includes superoxide anion (O_2^{-}) and hydrogen peroxide (H_2O_2) which are associated with normal plant biochemical processes (Zhu et al., 2004). They are also responsible for the lipid peroxidation with membrane destruction, protein inactivation, DNA mutation (Torres et al., 2006), oxidative burst and probably hypersensitive response (HR) or systemic acquired resistance (Bolwell, 2004) at the pathogen infected site of plants. Generation of H_2O_2 exhibit antimicrobial activity which inhibit spore germination of fungal pathogens and participates in the formation of phenoxyl-radicals during phenol-polymerization within the plant cell wall (Lamb & Dixon, 1997). In addition, lipid peroxidation through ROS generation leads to membrane integrity, tissue necrosis and induction of phytoalexins, which is synthesized by the action of lipoxygenases (LOXs) (El- Khallal, 2007). LOX metabolites possibly exert antimicrobial activity and induce or alter wound/pathogen defense gene expression (Künke et al., 2002) through an octadecanoid pathway (Hause et al., 2007) which leads to Jasmonate biosynthesis. Jasmonates serve as a putative endogenous signal in mycorrhiza-induced systemic resistance (El- Khallal, 2007), which still requires elucidation. Furthermore, Several antioxidant enzymes such as peroxidase (POX), superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) take part in the ROS metabolism during the pathogen attack (El- Khallal, 2007). POXs are one among the defence compounds that are stimulated in plants in response to pathogen infection like *Fusarium oxysporum* (Morkunas & Gmerek, 2007). Augmentation in SOD activity has been implicated in inducing pathogen-related HR development in plants, however, catalase activity gets reduced during microorganism induced HRs (Delledonne et al., 2002). In bean roots, it was found that catalase activity was regulated according to AMF infectivity and the availability of phosphorus (Lambais, 2000). In another experiment, it was observed that *G. intraradices* regulates the catalase and

peroxidase in bean and wheat (Blee and Anderson, 2000).

The induced cytosolic calcium ($[Ca^{2+}]_{cyt}$) elevation also induces Mitogen activated protein kinase (MAPK) and alterations in G-protein after or parallel with ROS generation. MAPKs and G-protein modifications regulate activity of several enzymes responsible for defence mechanisms through phosphorylation or dephosphorylation (Strange, 2003). Their role to transduce the external stimuli to the cell's machinery, leads to bringing about a response (Strange, 2003) against phytopathogen.

Taking consideration of the above facts, it could be stated that AMF has the potential and is to be involved in plant defence signaling through activation of certain precursors from a course of reactions which lead to their respective end products, responsible for combating with harmful invaders. But, there are many other aspects that are unknown like the exact reaction or pathway in the AMF induction, potent factors responsible for this activation, the changes in plant before and after the activation through these factors and finally, how plant react and up to which extent it come up with these changes. This necessitates further exploration with the help of advanced phytochemical studies coupled with genomics and proteomics approach.

Fig 1. Schematic representation of AMF-induced defence signaling in plant cell



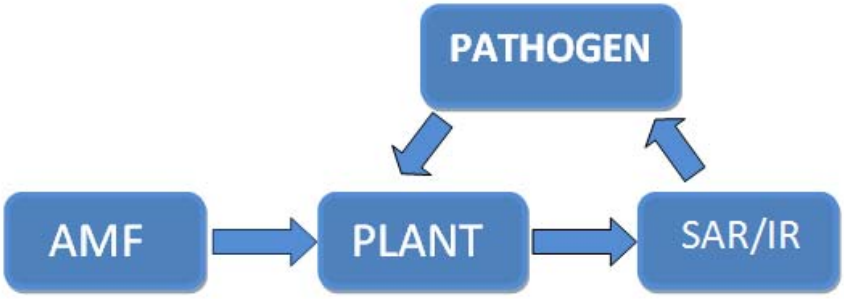
The myc (myc factor) from AMF, triggers ($[Ca^{2+}]_{cyt}$; abbreviated as Ca) which further induces ROS generation, and MAPK & G-protein alterations. ROS includes O_2^- (abbreviated as O) and H_2O_2 (abbreviated as H). ROS also induces LOX, which leads to JA biosynthesis. Antioxidant enzymes (E) such as SOD, POD, catalase and APX which plays an important role in ROS metabolism gets phosphorylated (EP) through MAPK & G-protein. MAPK & G-protein also triggers plant's defence genes. As pathogen enters, it either secretes some elicitors or by damaging cell wall caused by the pathogen triggers plant's defence genes. These defence related genes encoding proteins attack on pathogen and try to neutralize them. Whereas, antioxidant enzymes and ROS act constitutively on the pathogen infected site and initiate hypersensitivity reaction leading to apoptosis of the infective cells.

5. Plant's response with AMF towards phytopathogen

The phrase SAR explains the induction of local defence related pathways which incite the intercellular signal that produces a general response (Slater et al., 2006). In 1966, Ross demonstrated this phenomenon in tobacco inoculated with tobacco mosaic virus. In 1979, White also observed decrease in the symptoms of Tobacco Mosaic virus when treating with aspirin (acetyl salicylic acid). SAR responses include lignification (Dean and Kuć, 1987), PR proteins (Strange, 2003; Van Loon et al., 2006), callose containing papillae and oscillation of Ca^{2+} (Stumm and Gessler, 1986). This resistance is broad-spectrum and long lasting (Durrant and Dong, 2004; Ross, 1966) and to large extent is dedicated to SA. However, the relation

between AMF and SAR is not very positive and still in ambiguity. The reports related to their relationship are also very limited. It has been suggested that SA regulates the enteric endophytic colonization (Iniguez et al., 2005) like that of AMF. Application of SA exogenously, delays mycorrhizal colonization thus; it is plausible that for a compatible interaction, AM fungi repress SA-dependent defence responses (Dumas-Gaudot et al., 2000). This may leads to delay in systemic accumulation of PR-proteins (Shaul et al., 1999). SA levels increases while colonization of AMF in plants but decreases when colonization is over (Pozo and Azcón-Aguilar, 2007). This makes researchers to ponder and deduce some unexplored aspects of this relationship like what happens to SA level when AMF-colonized plants are being attacked by the pathogen? If SA level increases then, does it affects the AMF colonized within the same host or there also exist some kind of genetic shift which makes SA to recognize AMF as a friend of plant? Likewise, there are several queries regarding SAR and AMF affiliation in respect of plant defence which is vague and waiting for a reply.

Fig 2. Interaction of AMF induced plant defence responses (SAR/IR) with the pathogen



Other forms of disease resistance such as ISR, a SA-independent pathway, is also induced by avirulent phytopahtogens (Slater et al., 2006) like AMF (Pozo and Azcón-Aguilar, 2007). These are mainly attributed to the jasmonates and its family with several other volatile chemicals such as methyl jasmonates and Ethylene (Slater et al., 2006; Van der Ent et al., 2009). Jamonates have been implicated in plant disease resistance from pathogen attack (Strange, 2003). They activate and modulate the genes encoding protease inhibitors and expression of cell wall proteins that provide protection against insect attack (Strange, 2003; Yen et al., 2001). Its biosynthetic precursors are volatile aldehydes and alcohols that are inhibitory to the pathogens such as 2-hexanol is an effective inhibitor of *Pseudomonas syringae* (Strange, 2003). Another potent ISR component is Ethylene whose role is still perplexing (Boller, 1991; Strange, 2003; Knoester et al., 1998) in AMF-colonized plants. Several reports stating that AMF-colonized plants show low level of Ethylene production or increased level of Ethylene thereby repressing growth of AMF (Geil and Guinel, 2002; Geil et al., 2001; McArthur and Knowles, 1992; Barker and Tagu, 2000; Vierheilig et al., 1994). However, there are very few reports suggesting the increased level of Ethylene formation in plants. Dugassa et al., (1996) observed the enhanced Ethylene formation in *Linum usitatissimum* roots inoculated with *G. intraradices*. So, there is an uncertainty in the knowledge of AMF-induced SAR and IR corresponding to the plant's defence response which needs a detailed investigation.

6. Factors affecting AMF colonization leading to plant defence response

Plant defense responses not only depend on gene induction, SAR and ISR, but also rely on other factors regulating AMF colonization. These include host genotype, competition for colonization from soil-borne pathogens and within themselves, degree of mycorrhization and mycorrhizal autoregulation. It has been well documented that AMF colonization depends on the host genotype and hence, its development and effect within host is partially under genetic control of host (Lackie et al., 1987; Hetrick et al., 1993; Vierheilig and Ocampo, 1990, 1991).

In an experiment, mycorrhizal strawberry showed a different susceptibility to *Phytophthora fragariae* depending upon the host genotype (Mark and Cassels, 1996). However, there are very few studies supporting this fact.

Direct (interference competition, including chemical interactions) and indirect (via exploitation competition) interactions have been suggested as strategies of AM fungi for the reduction of pathogenic fungi in roots (Wehner et al., 2010). Most likely, there is a great similarity between the soil-borne pathogens and AMF in their resources like infection sites, space and photosynthate within the root (Whipps, 2004). Once AMF has colonized the host plant's root, less carbon will be available for the root fungal pathogen (Singh et al., 2000; Azcon-Aguilar et al., 2002; Xavier and Boyetchko, 2004). This is in the case between AMF and other pathogens. Interestingly, there is very limited number of reports suggesting the competition within AMF species. In an experiment, inoculation of multi-species AM fungal assemblage (*Glomus monosporus*, *G. clarum* or *G. deserticola*) increased the colonization intensity in date palm roots but did not result in refraining of *F. oxysporum* f. sp. *albedinis* infection on plant growth (Jaiti et al., 2007). So, it was deduced that competition within AMF doesn't affect the total level of colonization (Abbott and Robson, 1981; Davis and Menge, 1981; White, 1984; Jansa et al., 2008).

In several studies, a high degree of AM root colonization shows high localized bioprotective effect, whereas intermediate and low levels of AM root colonization showed very less bioprotective effect (Vierheilig, 2008). In mycorrhizal tomato plants, a bioprotective effect against *P. parasitica* (Cordier et al., 1998) and *F. oxysporum* (Caron et al., 1986a, b) was observed. In addition, wheat plants against *Gaeumannomyces graminis* (Graham and Menge, 1982), could be observed only when AMF colonized heavily into the roots. Recently, it has been found out that not only the local, but also the general bioprotective effect of mycorrhization depends on the degree of AM root colonization (Khaosaad et al., 2007).

In recent years, a new term has been introduced "autoregulation of mycorrhization" which means once the plant is colonized with AMF; it suppresses the further colonization in order to limit the energy costs of this symbiotic relationship (Vierheilig, 2004; Garcia-Garrido and Vierheilig, 2007). Number of split-root systems of plants were inoculated on one side with an AMF and, when after establishing symbiosis, the other side was inoculated with the same or another AMF. In these experiments, with different AMF host plants such as barley (Vierheilig et al., 2000a, b), alfalfa (Catford et al. 2003, 2006) and soybean (Meixner et al., 2005, 2007), it was undoubtedly revealed that AM pre-colonization on one side of a split-root system systemically stifled AM root colonization on the other side of the root system. This is a very interesting fact that is recently gaining attention. The factors and mechanisms beneath this autoregulatory function of plant, is still unknown.

7. Conclusion

Over the past few years, AMF have proven to be potent and reliable candidate for the mutual collaboration and nutrient trading. This symbiont has an important impact on plant interactions with phytopathogens. From colonization to induction of defence signaling, the above discussed genetic, biochemical and signaling factors, their mechanisms and pathways involved, are less known to us or whose link has been missing. Knowing these factors, unraveling the mechanisms and elucidating their pathways in combination with the findings of regulatory ecological factors involved, will represent the next logical step in this line of research. Further research efforts should be directed to know the direct or indirect relationship of AMF with below-ground and above-ground community via plants. Advance studies like mutational analysis, metabolomic and proteomic studies coupled with transcript profiling are warranted to understand AMF-Plant-Phytopathogen interactions. Conclusively, efforts should be made in such a way to

make AMF as a complete commercial supplement for crops in agriculture system.

References

Abbott, L. K. and A. D. Robson, 1981. Infectivity and effectiveness of five endomycorrhizal fungi: competition with indigenous fungi in field soils. Australian Journal of Agricultural Research, 32: 621-630.

Al-Askar, A. A. and Y. M. Rashad, 2010. Arbuscular Mycorrhizal Fungi: A Biocontrol Agent against common Bean *Fusarium* Root Rot Disease. Plant Pathol. J., 9: 31-38.

Arlorio, M., A. Ludwig, T. Boller, P. Mischiati and P. Bonfante, 1991. Effects of chitinase and β-1,3 glucanase from pea on the growth of saprophytic, pathogenic and mycorrhizal fungi. Giorn. Bot. Ital., 125: 956-959.

Azcon-Aguilar, C., M. C. Jaizme-Vega and C. Calvet, 2002. The contribution of arbuscular mycorrhizal fungi to the control of soil-borne plant pathogens. In: S. Gianinazzi, H. Schuepp, J. M. Barea and K. Haselwandter, (eds). Mycorrhizal technology in agriculture. Birkhauser, Switzerland, pp. 187–197.

Barker, S. and D. Tagu, 2000. The roles of auxins and cytokinins in mycorrhizal symbioses. J. Plant Growth Regul., 19: 144-154.

Blee, K. A, and A .J. Anderson, 2000. Defence responses in plants to arbuscular mycorrhizal fungi. In: G. K. Podilla, D. D. Douds, (eds.) Current advances in Mycorrhizae research. Minnesota, USA: The American Phytopathological society, 45-59.

Blilou, I., P. Bueno, J. A. Ocampo, J. M. Garcia-Garrido, 2000a. Induction of catalase and ascorbate peroxidase activities in tobacco roots inoculated with the arbuscular mycorrhizal fungus *Glomus mosseae*. Mycol Res., 104: 722-725.

Blilou, I., J. A. Ocampo, J. M. Garcia-Garrido, 2000b. Induction of Ltp (Lipid transfer protein) and Pal (Phenylalanine ammonia-lyase) gene expression in rice roots colonized by the arbuscular mycorrhizal fungus *Glomus mosseae*. Journal of Experimental Botany, 51: 1969-1977.

Bolwell, G.P. 2004. Role of active oxygen species and NO in plant defence responses. Current Opinion in Plant Biology, 2: 287-294.

Bonanomi, A., J. H. Oetiker, R. Guggenheim, T. Bollet, A. Wiemken and R. Vogeli-Lange, 2001. Arbuscular mycorrhizas in mini-mycorrhizotrons: first contact of *Medicago truncatula* roots with *Glomus intraradices* induces chalcone synthase. New phytologist, 150: 573-582.

Caron, M., J. A. Fortin and C. Richard, 1986a. 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.

Caron, M., J. A. Fortin and C. Richard, 1986b. Effect of phosphorus concentration and *Glomus intraradices* on *Fusarium* crown and root rot of tomatoes. Phytopathology, 76: 942–946.

Cartieaux, F., M. C. Thibaud, L. Zimmerli, P. Lessard, C. Sarrobert, P. David, A. Gerbaud, C. Robaglia, S. Somerville and L. Nussaume, 2003. Transcriptome analysis of Arabidopsis colonized by a plant-growth promoting rhizobacterium reveals a general effect on disease resistance. Plant J., 36: 177–188.

Catford, J. G., C. Staehelin, G. Larose, Y. Piché and H. Vierheilig, 2006. Systemically suppressed isoflavonoids and their stimulating effects on nodulation and mycorrhization in alfalfa split-root systems. Plant Soil, 285: 257–266.

Catford, J. G., C. Staehelin, S. Lerat, Y. Piché, and H. Vierheilig, 2003. Suppression of arbuscular mycorrhizal colonization and nodulation in split-root systems of alfalfa after pre-inoculation and treatment with Nod factors. J Exp Bot., 54: 1481–1487.

Conrath, U., G. J. M. Beckers, V. Flors, P. García-Agustín, G. Jakab, F. Mauch, M-A. Newman, C. M. J. Pieterse, B. Poinssot, M. J. Pozo, A. Pugin, U. Schaffrath, J. Ton, D. Wendehenne, L. Zimmerli and B. Mauch-Mani, 2006. Priming: Getting

Ready for Battle. Mol. Plant-Microbe Interact., 19: 1062–1071.

Cordier, C., M. J. Pozo, J. M. Barea, S. Gianinazzi and V. Gianinazzi-Pearson, 1998. Cell Defense responses Associated with Localized and Systemic Resistance to *Phytophthora parasitica* Induced in Tomato by an Arbuscular Mycorrhizal Fungus. Molecular Plant Microbe Interaction, 11: 1017-1028.

Dangl, J. and J. Jones, 2001. Plant pathogens and integrated defence responses to infection. Nature, 411: 826–833.

Davis, R. M. and J. A. Menge, 1981. *Phytophthora parasitica* inoculation and intensity of vesicular-arbuscular mycorrhizae in citrus. New Phytologist, 87: 705-715.

de Wit, P. J. G. M., 1992. Molecular characterization of gene-for-gene systems in plant-fungus interactions and the application of avirulence genes in control of plant pathogens. Annu. Rev. Phytopathol., 30: 391-418.

Dean, R. A. and J. Kuć, 1987. Rapid lignification in response to wounding and infection as a mechanism for induced systemic protection in cucumber. Physiological and Molecular Plant Physiology, 31: 69-81.

Delledonne, M., I. Murgia, D. Ederle, P. F. Sbicego, A. Biondian, A. Polverari and C. Lamb, 2002. Reactive oxygen intermediates modulates nitric oxide signaling in the plant hypersensitive disease-resistance response. Plant Physiol Biochem., 40: 605-610.

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

Dumas-Gaudot, E., A. Gollotte, C. ordier, S. Gianinazzi and V. Gianinazzi-Pearson, 2000. Modulation of host defence systems. In Arbuscular Mycorrhizas: Physiology and Function. Kluwer Academic Publishers, pp 173-200.

Durrant, W.E. and X. Dong, 2004. Systemic acquired resistance. Annu. Rev. Phytopathol., 42: 185-209.

Durrant, W. E., O. Rowland, P. Piedras, K. E. Hammond-Kosack and J. D. G. Jones, 2000. cDNA-AFLP reveals a striking overlap in race specific resistance and wound response gene expression profiles. Plant Cell, 12: 963–977.

El- Khallal, S. M. 2007. Induction and modulation of resistance in tomato plants against *Fusarium* wilt disease by bioagent fungi (arbuscular mycorrhiza) and/or hormonal elicitors (Jasmonic acid & Salicylic acid): 2-Changes in the antioxidant enzymes, phenolic compounds and pathogen related-proteins. Australian Journal of Basic and Applied Sciences, 1: 717-732.

Engström, K., A. K. Widmark, S. Brishammar and S. Helmersoon, 1999. Antifungal activity to *Phytophthora infestans* of sesquiterpendoids from infectd potato tyubers. Potato Res., 42: 43-50.

Garcia-Garrído, J. M. and J. A. Ocampo, 2002. Regulation of the plant defence response in arbuscular mycorrhizal symbiosis. Journal of Experimental Botany, 53: 1377-1386.

García-Olmedo, F., A. Molina, A. Segura and M. Moreno, 1995. The defensive role of non-specific Lipid-transfer proteins in plant. Trends in Microbiology, 3: 72-74.

Geil, R. and F. Guinel, 2002. Effects of elevated substrate-ethylene on colonization of leek (*Allium porrum*) by the arbuscular mycorrhizal fungus *Glomus aggregatum*. Can. J. Bot., 80: 114-119.

Geil, R., R. Peterson and F. Guinel, 2001. Morphological alterations of pea (*Pisum sativum* cv. Sparkle) arbuscular mycorrhizas as a result of exogenous ethylene treatment. Mycorrhiza, 11: 137-143.

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

Graham, J. H. and J. A. Menge, 1982. Influence of vesicular-arbuscular mycorrhizae and soil phosphorous on take-all disease of wheat. Phytopathology, 72: 95–98.

Hadwiger, L. A., C. C. Chiang and D. Horovitz, 1992. Expression of disease resistance response genes in near-isogenic pea cultivars following challenge by *Fusarium oxysporum* race 1. Physiol. Mol. Plant Pathol., 40: 259-270.

Hamiduzzaman, M. M., G. Jakab, L. Barnavon, J. M. Neuhaus, B. Mauch-Mani, 2005. β-Aminobutyric acid-induced resistance against downy mildew in grapevine acts through the potentiation of callose formation and jasmonic acid signalling. Mol Plant Microbe Interact., 18: 819-829.

Harrison, M. and R. Dixon 1993. Isoflavonoid accumulation and expression of defense gene transcripts during the establishment of vesicular arbuscular mycorrhizal associations in roots of *Medicago truncatula*. Mol Plant-Microbe Interact., 6: 643–659.

Harrison, M. J. and R. A. Dixon, 1994. Spatial patterns of expression of flavonoid/isoflavonoid pathway genes during interactions between roots of *Medicago truncatula* and the mycorrhizal fungus *Glomus versiforme*. Plant J., 6: 9-20.

Hause, B., W. Maier, O. Miersch, R. Kramell and D. Strack, 2002. Induction of jasmonate biosynthesis in arbuscular mycorrhizal barley roots. Plant Physiol., 130: 1213–1220.

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

Hetrick, B. A. D., G. W. T. Wilson and T. S. Cox, 1993 Mycorrhizal dependence of modern wheat cultivars and ancestors: a synthesis. Can J Bot., 71: 512–518.

Hohnjec, N., M. F. Vieweg, A. Puhler, A. Becker and H. Kuster, 2005. Overlaps in the transcriptional profiles of *Medicago truncatula* roots inoculated with two different *Glomus* fungi provide insights into the genetic program activated during arbuscular mycorrhiza. Plant Physiol., 137: 1283–1301.

Hyun, Y., S. Choi, H. J. Hwang, J. Yu, S. J. Nam, J. Ko, J. Y. Park, Y. S. Seo, E.Y. Kim, S.B. Ryu, W.T. Kim, Y.H. Lee, H. Kang and I. Lee, 2008. Cooperation and functional diversification of two closely related galactolipase genes for Jasmonate biosynthesis. Dev. Cell., 14: 183-192.

Iniguez, A. L., Y. Dong, H. D. Carter, B. M. Ahmer, J. M. Stone and E. W. Triplett, 2005. Regulation of enteric endophytic bacterial colonization by plant defense. Mol. Plant- Microbe Interact., 18: 169-178.

Ishiguro, S., A. kawai-Oda, J. Ueda, I. Nishida and K. Okada, 2001. The defective in anther dehiscience gene encodes a novel phospholipase A1 catalyzing the initial step of jasmonic acid biosynthesis, which synchronizes pollen maturation, anther dehiscence, and flower opening in *Arabidopsis*. Plant Cell, 13: 2191-2209.

Jaiti, F., A. Meddich and I. Haddrami, 2007. Effectiveness in arbuscular mycorrhizal fungi in the protection of date palm (*Phoenix dactylifera* L.) against bayoud disease. Physiological and Molecular Plant Pathology, 71: 166-173.

Jansa, J., F. A. Smith, and E. S. Sally, 2008. Are there benefits of simultaneous root colonization by different arbuscular mycorrhizal fungi? New Phytologist, 177: 779-789.

Kachroo, A. and P. Kachroo, 2009. Fatty Acid–Derived Signals in Plant Defense. Annu. Rev. Phytopathol., 47: 153–76.

Kapoor, R., 2008. Induced resistance in Mycorrhizal Tomato is correlated to concentration of Jasmonic Acid. OnLine Journal of Biological Sciences, 8: 49-56.

Khaosaad, T., J. M. García-Garrido, S. Steinkellner and H. Vierheilig, 2007. Talk-all disease is systemically reduced in roots of mycorrhizal barley plants. Soil Biol and Biochem., 39: 727-734.

Klessig, D. F., C. A. Vlot and D. A. Dempsey, 2009. Salicylic acid, a multifaceted hormone to combat disease. Annu. Rev. Phytopath., 47: 177–206.

Koide, R. T. and R. P. Schreiner, 1992. Regulation of the vesicular arbuscular mycorrhizal symbiosis. Annual review of plant physiology plant molecular biology, 43: 557-581.

Kosuta, S., S. Hazledine, J. Sun, H. Miwa, R. J. Morris, J. A. Downie and G. E. D. Oldroyd, 2008. Differential and chaotic

calcium signatures in the symbiosis signaling pathway of legumes. Proc. Natl Acad. Sci. USA., 105: 9823–9828.

Künke, B. N. and D. M. Brooks, 2002. Cross talk between signaling pathway in pathogen defense. Curr. Opin. Plant Biol., 5: 325-331.

Lackie, S. M., M. L. Garriock, R. L. Peterson and S. R. Bowley, 1987. Influence of host plant on the morphology of the vesicular-arbuscular mycorrhizal fungus *Glomus versiforme* (Daniels and Trappe) Berch. Symbiosis, 3: 147–158.

Lamb, C. and R. A. Dixon, 1997. The oxidative burst in plant disease resistance. Annu Rev Plant Physiol Plant Mol Biol., 48: 251-257.

Lambais, M. R. 2000. Regulation of plant defence-related genes in arbuscular mycorrhizae. In: G. K. Podilla, D. D. Douds, eds. Current advances in Mycorrhizae research. Minnesota, USA: The American Phytopathological society, pp 45-59.

Larose, G, Chenevert, Moutoglis P, Gagne, S and Piche, Vierheilig H. 2002. Flavonoid levels in roots of *Medicago sativa* are modulated by the developmental stage of the symbiosis and the root colonizing arbuscular mycorrhizal fungus. J Plant Physiol., 159: 1329–1339

Levine, A., R. Tenhaken, R. Dixon and C. J. Lamb, 1994. H_20_2 from the oxidative burst orchestrates the plant hypersensitive disease resistance response. Cell, 79: 583-593.

Lévy, J., C. Bres, R. Geurts, B. Chalhoub, O. Kulikova, G. Duc, E-P. Journet, J-M. Ané, E. Lauber, T. Bisseling, J. Dénarié, C. Rosenberg and F. Debellé, 2004. A putative Ca^{2+} and calmodulin dependent protein kinase required for bacterial and fungal symbioses. Science, 303: 1361–1364.

Li, H. Y., G. D. Yang, H. R. Shu, Y. T. Yang, B. X. Ye, I. Nishida and C. C. Zheng, 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.

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

Mark, G. L. and A. C. Cassells, 1996. Genotype-dependence in the interaction between *Glomus fistulosum*, *Phytophthora fragariae* and the wild strawberry (*Fragaria vesca*). Plant Soil, 185: 233–239.

McArthur, D. A. J. and N. R. Knowles, 1992. Resistance responses of potato to vesicular-arbuscular mycorrhizal fungi under varying abiotic phosphorus levels. Plant Physiol., 100: 341-351.

Meghvansi, M. K., K. Prasad, D. Harwani and S. K. Mahna, 2008. Response of soybean cultivars toward inoculation with three arbuscular mycorrhizal fungi and *Bradyrhizobium japonicum* in the alluvial soil. *European Journal of Soil Biology* 44: 316-323.

Meixner, C., J. Ludwig-Müller, O. Miersch, P. Gresshoff, C. Staehelin and H. Vierheilig, 2005. Lack of mycorrhizal autoregulation and phytohormonal changes in the supernodulating soybean mutant nts1007. Planta, 222: 709–715.

Meixner, C., G. Vegvari, J. Ludwig-Muller, H. Gagnon, S. Steinkellner, C. Staehelin, P. Gresshoff and H. Vierheilig, 2007. Two defined alleles of the lrr receptor kinase GmNARK in supernodulating soybean govern differing autoregulation of mycorrhization. Physiol Plant., 130: 261–270.

Mitra, R. M., C. A. Gleason, A. Edwards, J. Hadfield, J. A. Downie, G. E. D. Oldroyd and S. R. Long, 2004. A Ca^{2+}/calmodulin-dependent protein kinase required for symbiotic nodule development: gene identification by transcript-based cloning. Proc. Natl Acad. Sci., USA, 101: 4701–4705.

Moieyev, G. P., J. J. Beintema, L. Fedoreyeva and G. I. Yakovlev, 1994. High sequence similarity between a ribonuclease from

ginseng calluses and fungus-elicited proteins from parsley indicates that intracellular pathogenesis-related proteins are ribonucleases. Planta, 193: 470-472.

Molina, A. and F. García-Olmedo, 1993. Developmental and pathogen-induced expression of three barley genes encoding lipid-transfer protein. The Plant Journal, 4: 983-991.

Morandi, D. 1996. Occurence of phytoalexins and phenolic compounds on endomycorrhizal interactions, and their potential role in biological control. Plant Soil, 185: 241–251.

Morandi, D. and J. L. LeQuerre, 1991. Influence of nitrogen on accumulation of isosojagol (a new deterred coumestan in soybean) and associated isoflavonoids in roots and nodules of mycorrhizal and non-mycorrhizal soybean. New Phytol., 117: 75-79.

Morkunas, I. and J. Gemerek, 2007. The possible involvement of peroxidase in defense of yellow lupin embryo axes against *Fusarium oxysporum*. J. Plant Physiol., 164: 497-506.

Müller, J., C. Staehelin, Z. P. Xie, G. Neuhaus-Url and T. Boller, 2000. Nod factors and chitooligomers elicit an increase in cytosolic calcium in aequorin-expressing soybean cells. Plant Physiol., 124: 733–740.

Navazio, L., B. Baldan, R. Moscatiello, A. Zuppini, S. L. Woo, P. Mariani and M. Lorito 2007. Calcium-mediated perception and defense responses activated in plant cells by metabolite mixtures secreted by the biocontrol fungus *Trichoderma atroviride*. BMC Plant Biology 7: 41-49.

Ozgonen, H., D. S. Akgul and A. Erkilic, 2010. The effects of arbuscular mycorrhizal fungi on yield and stem rot caused by *Sclerotium rolfsii* Sacc. In peanut. African Journal of Agricultural Research, 5: 128-132.

Paxton, J. D. 1981. Phytoalexins-a working redefinition. Phytopathol., 101: 106-109.

Pieterse, C.M.J., Van Wees, S.C.M., Hoffland, E., Van Pelt, J.A. and Van Loon, L.C. 1996. Systemic resistance in *Arabidopsis* induced by biocontrol bacteria is independent of salicylic acid accumulation and pathogenesis-related gene expression. Plant Cell. 8: 1225-1237.

Pozo, M. J. and C. Azcón-Aguilar, 2007. Unraveling mycorrhiza-induced resistance. Current Opinion in Plant Biology, 10: 393-398.

Pozo, M. J., E. Dumas-Gaudot and J. M. Barea, 1999. β-1,3-glucanase activities in tomato roots inoculated with arbuscular mycorrhizal fungi and/or *Phytophthora parasitica* and their possible involvement in bioprotection. Plant Sci., 141: 149-157.

Ross, A., 1966. 'Systemic effects of local lesion formation'. In Viruses of Plants. A. Beemster, & S. Dykstra, (eds.) North Holland, Amsterdam, pp 127-150.

Ruiz-Lozano, J. M., H. Roussel, S. Gianinazzi and V. Gianinazzi-Pearson, 1999. Defense Genes Are Differentially Induced by a Mycorrhizal Fungus and *Rhizobium* sp. in Wild-Type and Symbiosis-Defective Pea Genotypes. Mol. Plant-Microbe Interact., 12: 976–984.

Salzer, P, H. Corbiere and T. Boller, 1999. Hydrogen peroxide accumulation in *Medicago truncatula* roots colonized by the arbuscular mycorrhiza-forming fungus *Glomus mosseae*. Planta, 208: 319–325.

Salzer, P. and T. Boller, 2000. Elicitor-induced reactions in mycorrhizae and their suppression. In: G. K. Podila, D. D. Douds, (eds). Current advances in mycorrhizae research. Minnesota, USA: The American Phytopathological Society, pp 1-10.

Salzer, P., B. Hübner, A. Sirrenberg and A. Hager, 1997. Differential effect of purified spruce chitinases and β-1,3-glucanases on the activity of elicitors from ectomycorrhizal fungi. Plant Physiol., 114: 957-968.

Sanders, D., J. Pelloux, C. Brownlee and J. F. Harper, 2002. Calcium at the crossroads of signaling. Plant Cell, 14: S401-S417.

Scheel, D. 1998. Resistance response physiology and signal transduction. Curr Opin Plant Biol., 1: 305-310.

Schübler, A., D. Schwarzott and C. Walker, 2001. A new fungal phylum, the

Glomeromycota: phylogeny and evolution. Mycol. Res., 105: 1413–1421.

Segarra, G., S. Van der Ent, I. Trillas and C. M. J. Pieterse, 2009. MYB72, a node of convergence in induced systemic resistance triggered by a fungal and a bacterial beneficial microbe. Plant Biol., 11: 90-96.

Sensoy, S., S. Demir, O. Turkmen, C. Erdinc, and O. B. Savur, 2007. Responses of some different pepper (*Capsicum annuum* L.) genotypes to inoculation with two different arbuscular mycorrhizal fungi. Scientia Horticulturae, 113: 92-95.

Shaul, O., S. Galili, H. Volpin, I. Ginzberg, Y. Elad, I. Chet and Y. Kapulnik, 1999. Mycorrhiza-Induced Changes in Disease Severity and PR Protein Expression in Tobacco Leaves. Mol. Plant-Microbe Interact., 12: 1000–1007.

Singh, .R, A. Adholeya and K. G. Mukerji, 2000. Mycorrhiza in control of soil-borne pathogens. In: K. G. Mukerji, B. P. Chamola and J. Singh, (eds.) Mycorrhizal biology. Kluwer, New York, pp 173–196.

Slater, A., N. W. Scott and M. R. Fowler, 2006. Plant Biotechnology: The Genetic Manipulation of Plants, Oxford University Press.

Smith, S. E. & D. J. Read, 2008. Mycorrhizal Symbiosis (Academic, London).

Somssich, I. E. and K. Hahlbrock, 1998. Pathogen defence in plants: a paradigm of biological complexity. Trends in plant Science, 3: 86-90.

Stenzel, I., B. Hause, O. Miersch, T. Kurz, H. Maucher, H. Weichert, J. Ziegler, I. Feussner and C. Wasterneck. 2003. Jasmonate biosynthesis and the allene oxide cyclase family of *Arabidopsis thaliana*. Plant Mol. Biol., 51: 895-911.

Strange, R. N. 2003. Introduction to Plant Pathology. John Wiley & Sons Ltd., England.

Stumm, D. and C. Gessler, 1986. Role of papillae in the induced systemic resistance of cucumbers against *Colletotrichum lagenarium*. Physiological and Molecular Plant Physiology, 29: 405-410.

Stumpe, M., J.-G. Carsjens, I. Stenzel, C. Gobel, I. Lang, K. Pawlowski, B. Hause and I. Feussner, 2005. Lipid metabolism in arbuscular mycorrhizal roots of *Medicago truncatula*. Phytochemistry, 66: 781–791.

Terras, F. R. G., K. Eggermont, V. Kovaleva, N. V. Raikhel, R. W. Osborn, A. Kester, S. B. Rees, S. Torrekens, F. V. Leuven, J. Vanderleyden, B. P. A. Cammue and W. F. Broekaert, 1995. Small Cysteine-Rich Antifungal Proteins from Radish: Their Role in Host Defense. The Plant Cell, 7: 573-588.

Ton, J., J. A. Van Pelt, L. C. Van Loon and C. M. J. Pieterse, 2002. Differential effectiveness of salicylate-dependent and jasmonate/ethylene-dependent induced resistance in *Arabidopsis*. Mol Plant Microbe Interact., 15: 27-34.

Torres, M. A., D. G. Jonathan and J. L. Dangl, 2006. Reactive oxygen species signaling in response to pathogen. Plant physiol., 141: 373-378.

Truman, W., M. H. Bennett, I. Kubigsteltig, C. Turnbull and M. Grant, 2007. Arabidopsis systemic immunity uses conserved defense signaling pathways and is mediated by jasmonates. Proc Natl Acad Sci, U S A., 104: 1075-1080.

Van der Ent, S., S. C .M. Van Wees, and C. M. J. Pieterse, 2009. Jasmonate signaling in plant interactions with resistance – inducing beneficial microbes. Phytochemisty, 70: 1581-1588.

Van der Ent, S., B. W. M. Verhagen, R. Van Doorn, D. Bakker, M. G. Verlaan, M. J. C. Pel, R. G. Joosten, M. C. G. Proveniers, L. C. Van Loon, J. Ton, and C. M. J. Pieterse, 2008. MYB72 is required in early signaling steps of rhizobacteria-induced systemic resistance in *Arabidopsis*. Plant Physiol., 146: 1293-1304.

Van Loon, L. C., P. A. Bakker and C. M. Pieterse, 1998. Systemic resistance induced by rhizosphere bacteria. Annu. Rev. Phytopathol., 36: 453–83.

Van Loon, L. C., M. Rep and C. M. J. Pieterse, 2006. Significance of inducible defence-related proteins in infected plants. Annv. Rev. Phytopathol., 44: 135-162.

Vierheilig, H. and J. A. Ocampo, 1990. Effect of isothiocyanates on germination of

spores of *G. mosseae*. Soil Biol Biochem., 22: 1161–1162.

Vierheilig, H. 2004. Further root colonization by arbuscular mycorrhizal fungi in already mycorrhizal plants is suppressed after a critical level of root colonization. J Plant Physiol., 161: 339–341.

Vierheilig, H. and J. A. Ocampo, 1991. Receptivity of various wheat cultivars to infection by VA-mycorrhizal fungi as influenced by inoculum potential and the relation of VAM effectiveness to succinic dehydrogenase activity of the mycelium in the roots. Plant Soil, 133: 291–296

Vierheilig, H. and Y. Piché, 2002. Signalling in arbuscular mycorrhiza: facts and hypothesis. In: B. Buslig and J. Manthey, (Eds.), Flavonoids in Cell Function. Kluwer Academic Publishers/PlenumPress, New York, pp. 23–39.

Vierheilig, H., M. Alt, U. Mohr, T. Boller and A. Wiemken, 1994. Ethylene biosynthesis and activities of chitinase and β-1,3-glucanase in the roots of host and non-host plants of vesicular-arbuscular mycorrhizal fungi after inoculation with *Glomus mosseae*. J. Plant Physiol., 143: 337-343.

Vierheilig, H., M. Alt, J.-M. Neuhaus, T. Boller and A. Wiemken, 1993. Colonization of transgenic *Nicotiana sylvestris* plants, expressing different forms of *Nicotiana tabacum* chitinase, by the root pathogen Rhizoctonia solani and by the mycorrhizal symbiont *Glomus mosseae*. Mol. Plant-Microbe Interact. 6: 261-264.

Vierheilig, H., H. Gagnon, D. Strack and W. Maier, 2000b. Accumulation of cyclohexenone derivatives in barley, wheat and maize roots in response to inoculation with different arbuscular mycorrhizal fungi. Mycorrhiza, 9: 291–293.

Vierheilig, H., M. J. Garcia-Garrido, U. Wyss and Y. Piché, 2000a. Systemic suppression of mycorrhizal colonization in barley roots already colonized by AM-fungi. Soil Biol Biochem., 32: 589–595.

Vierheilig, H., S. Steinkellner, T. Khaosaad and J. M. Garcia-Garrído, 2008. The Biocontrol effect of Mycorrhization on Soilborne Fungal Pathogens and the Autoregulation of the AM Symbiosis: One Mechanism, Two Effects? Varma, A. (ed.) Mycorrhiza. Springer-Verlag, Berlin, Heidelberg, pp 307-320.

Volpin, H., D. A. Phillips, Y. Okon and Y. Kapulnik, 1995. Suppression of an isoflavonoid phytoalexin defense response in myocrrhizal alfalfa roots. Plant Physiol., 108: 1449-1545.

Walter, M. H., J. W. Liu, J. Dünn and D. Hess, 1996. Bean ribonuclese-like pathogenesis-related protein genes (Ypr10) display complex patterns of developmental, dark-induced and exogenous-stimulus dependent expression. Eur. J. Biochem., 239: 281-293.

Wasterneck, C. 2007. Jasmonates : an update on biosysnthesis, signal transduction and action in plant stress response, growth and development. Ann. Bot. (Lond.)., 100: 681-697.

Wehner, J., P. M. Antunes, J. R. Powell, J. Mazukatow and M. C. Rillg, 2010. Plant pathogen protection by arbuscular mycorrhizas: A role of fungal diversity? Pedobiologia, 53: 197-201.

Whipps, J. M. 2004. Prospects and limitations for mycorrhizas in biocontrol of root pathogens. Canadian Journal of Botany, 82: 1198-1227.

White, J. M. 1984. Competition for infection between vesicular-arbuscular mycorrhizal fungi. New Phytologist, 97: 427-435.

White, R. F. 1979. Acetylsalicylic acid (aspirin) induces resistance to tobacco mosaic virus in tobacco. Virology, 99: 410-412.

Xavier, L. J. C. and S. M. Boyetchko, 2004. Arbuscular mycorrhizal fungi in plant disease control. In: D. K. Arora, (ed) Fungal biotechnology in agricultural, food, and environmental applications. Dekker, New York, pp 183–194.

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

Yao, M. K., H. Desilets, M. T. Charles, R. Boulanger and R. J. Tweddell, 2003. Effect of mycorrhization on the accumulation of rishitin and solavetivone in potato plantlets challenged with *Rhizoctonia solani*. Mycorrhiza., 13: 333-336.

Zhu, H. H. and Q. Yao, 2004. Localized and systemic increase of phenols in tomato roots induced by *Glomus versiforme* Inhibit *Ralstonia Solanacearum*. J. Phytopathology., 152: 537-546.