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Review Article

Interaction and symbiosis of AM fungi, Actinomycetes and Plant Growth Promoting Rhizobacteria with plants: Strategies for the improvement of plants health and defense system

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A B S T R A C T

Every year several crops affected by various diseases (biotic stresses), these could be pathogenic fungi or bacteria the most important factor worldwide for low agriculture output. The use of fungicides, bactericides and chemicals can control crop diseases up to some extent however, it can pollute environment and hence it is not a sustainable product to overcome the disease control without harm to environment. The alternative methods of disease control to be sought, including the use of microorganisms as biological control agents. Arbuscular Mycorrhizal Fungi (AMF), Plant Growth Promoting Rhizobacteria (PGPR) and Actinomycetes, as a rhizospheric microorganisms play an important role in promoting plant growth and protection against plant pathogen. These could participate direct or indirect in enhancement of root colonization by developing their individual effects on plant growth promotion, however the detrimental effect of the entire three groups with each other depends upon the species involved. These groups of fungi and bacteria may have their own mechanism and strategies to protect plant against pathogen (in terms of induction of ISR), their interaction with each other for the protection of plants yet to be elucidated conspicuously. So far, the research works towards the interaction among the three groups for the betterment of plant health and protection extensive in some level, but not systematic and deep. With the advancement of techniques in molecular biology and testing methods the new breakthrough will increase the study area as well as our understanding on the interactions among three groups for the improvement of plant health.

Keywords

Arbuscular Mycorrhiza Fungi (AMF), ISR, Rhizosphere, Root Colonization, Biological Control Agents (BCAs)

Introduction

Arbuscular Mycorrhizal (AM) fungi are ubiquitous fungi distributed widely in soil ecosystems. It has been showed that AM fungi play an important role in improving

soil nutrition and enhancing crop disease resistance, which have great application potentials in overcoming crop replant problems. Many microorganisms live in the portion of soil modified or influenced by plant roots, the portion of that soil called 'rhizosphere'. Among these microorganisms, some have positive effects on plant growth, able to stimulate plant growth through direct or indirect interactions with plant roots and these have been classified as plant growth promoting rhizobacteria (PGPR).

Glomus is the largest genus of Arbuscular mycorrhizal (AM) fungi, and all species form symbiotic relationship (mycorrhizas) with plant roots. As with other AM fungi, all Glomus species are thought to be obligate symbionts, dependent on their mycorrhizal association with plant roots to complete their life cycle. They cannot be cultured in the laboratory in the absence of a plant host. Glomus species are found in nearly all terrestrial habitats, including arable land, deserts, grasslands, tropical forests and tundra's.

Arbuscular mycorrhizal fungi can provide numerous benefits to their plant hosts, including improved nutrient uptake, drought resistance, and disease resistance. Two main groups of bacteria interact with AM fungi in the mycorrhizosphere: saprophytes and symbionts, both groups potentially consisting of detrimental, neutral and beneficial bacteria (Barea et al., 2002; Johansson et al., 2004).

Some PGPR may have properties that support both mycorrhizal establishment and function. In addition, Sanchez and colleagues (2004) showed that a fluorescent pseudomonad and an AM fungus (*G. mosseae*) had similar impacts on plant gene induction, supporting the hypothesis that some plant cell programs may be shared during root colonization by these beneficial microorganisms. Specific interactions between AM fungi and PGPR most likely occur, and certain groups of bacteria have been shown to be established to a much higher extent in the mycorrhizosphere compared with other groups.

In addition, most plant roots are colonized by mycorrhizal fungi and their presence also generally stimulates plant growth. Constituting the PGPR such as Azospirillum, Agrobacteria, Pseudomonas, several Gram positive Bacillus etc. Their role was recognized more recently than for mycorrhizae or nodules, many rhizospheric microorganisms also contribute to plant protection. Actinomycetes are one of the major components of the microbial populations present in soil. They belong to an extensive and diverse group of Gram-positive, aerobic, mycelial bacteria that play important ecological roles in soil nutrient cycling (Ames et al., 1984). In addition, these bacteria are known for their economic importance as producers of biologically active substances, such as antibiotics, vitamins and enzymes (de Boer et al., 2005). Actinomycetes are also an important source of diverse antimicrobial metabolites (Lazzarini et al., 2000; Terkina et al., 2006).

Interactions between AM fungi and bacteria

Plant root symbiosis with fungi occur in several different forms and are referred to as mycorrhiza (from the Greek 'mycos', meaning fungus and 'rhiza', meaning root). Arbuscular mycorrhizal fungi belong to phylum Glomeromycota, which are main component of the soil microbiota in most agro-ecosystems and form symbiotic association with most of the plants. By forming an extended, intricate hyphal

network, AM fungi can efficiently absorb mineral nutrients from the soil and deliver them to their host plants in exchange for carbohydrates. They facilitate nutrient uptake, particularly with respect to immobile nutrients, such as phosphorus and enhance tolerance to drought, disease resistance, building up a macroporous structure of soil that allows penetration of water and air and prevents erosion, enhance photosynthesis and reduce stresses during micropropagation.

Arbuscular mycorrhizal fungi (AMF) play a key role in facilitating nutrient uptake by crops in low-input farming systems. AMF spores provide a long-term reservoir of inoculum and are the only AMF propagules that can be identified to the species level. Several PGPR have been shown to be excellent root colonizers (Lugtenberg and Dekkers, 1999; Barea et al., 2002) and a number of surface components have been demonstrated to play a role in the physical interactions between such bacteria and plant roots (Bianciotto and Bonfante, 2002). However, little information is available concerning the extent to which PGPR colonize AM fungal hyphae.

Actinomycetes are quantitatively and qualitatively important in the rhizosphere, where they may influence plant growth and protect plant roots against invasion by root pathogenic fungi (Lechevalier 1988). However root-microorganism interactions have been extensively studied only for the nitrogen fixing Frankia species (Sardi et al., 1992) and a few species of the genus Streptomyces that are phytopathogens (Loria et al., 1997).

Actinobacteria were often found to be associated with AMF spores. Mugnier and Mosse in (1987) were reported that *G. mosseae* spores germinated in vitro only in the presence of microorganisms, including *Streptomyces orientalis*. Ames and coworkers (1989) found that out of 190 spores examined, 100 were colonized by one or more chitin-decomposing microorganisms; 82% were colonized by Actinomycetes, 17% by bacteria, and 1% by fungi. Carpenter-Boggs et al., (1995) demonstrated a positive correlation between higher germination rate and the amount of production of geosmin, CO2, and 2-methylisoborneol by the Actinomycetes.

Bianciotto and colleagues (1996a) reported that some Rhizobium and Pseudomonas species attached to germinated AM fungal spores and hyphae under sterile conditions, and that the degree of attachment varied with the bacterial strain. However, no specificity for either fungal or inorganic surfaces could be detected among the bacteria tested. Based on their results, these authors suggested that interactions between rhizobacteria and AM fungi were mediated by soluble factors or physical contact. Bianciotto and colleagues (2001) studied bacterial mutants inhibited in extracellular polysaccharide production and found that they were less able to attach to AM fungal hyphal surfaces compared with the wild-type strain. Several bacteria reported to be good root colonizers was from Pseudomonas spp., are also capable of adhering to AM fungal hyphal surfaces, suggesting that the mechanisms involved could be fairly similar.

Symbiosis of AM and soil bacteria to plant roots

An optimal colonization of plant roots, particularly in disturbed habitats such as agricultural fields, depends not only on the presence of extraradical hyphae or mycorrhizal root debris but, mainly, on the survival and well-timed germination of

AMF spores in the soil. This process can be altered by various abiotic and biotic factors, in particular by the association with soil microorganisms. Indeed, some bacterial populations, called mycorrhiza helper bacteria, have beneficial effects on AMF growth not only by improving mycorrhizal root colonization and stimulating extraradical hyphal growth but also by facilitating AMF spore germination. The latter effect has been shown for Actinomycetes, Pseudomonas, Corynebacterium and Bacillus spp.

Garbaye (1994) proposed the term 'mycorrhiza helper bacteria' for rhizobacteria that increased the ability of the root to establish symbiotic interactions with ectomycorrhizal fungi. He suggested a number of possible mechanisms for the helper effect, including stimulation of root development, enhanced susceptibility of the root to ectomycorrhizal fungal colonization, or enhancement of the recognition process between root and fungus. Several reports have also demonstrated enhanced AM fungal colonization levels in roots in the presence of PGPR. For example, association of *Pseudomonas putida* with indigenous AM fungi resulted in a clear growth enhancement of clover plants (Meyer and Linderman, 1986), suggesting that some PGPR may have properties that support both mycorrhizal establishment and function.

Juhnke et al., (1987) tested the root colonization ability of bacteria on wheat in fields and found that compared to other rhizobacteria, Streptomyces species were poor colonizers. In contrast, studies of Petrolini et al., (1996) and Sardi et al., (1992) provided evidence that streptomycetes are constantly present in cortical tissues of roots and that, despite heterogeneity in individual features; they can be regarded as a population that is reasonably consistent, having some common, well defined physiological peculiarities. Plant growth-promoting rhizobacteria are usually in contact with the root surface, or rhizoplane, and increase plant yield by one or more mechanisms such as improved mineral nutrition, disease suppression, or phytohormone production (Weller, 1988; Broek and Vanderleyden, 1995; Défago and Keel, 1995). An additional possibility is that the beneficial effects of some PGPR bacteria are due to their interactions with AM fungi.

Sanchez and colleagues (2004) showed that a fluorescent pseudomonad and an AM fungus (*G. mosseae*) had similar impacts on plant gene induction, supporting the hypothesis that some plant cell programmes may be shared during root colonization by these beneficial microorganisms. Specific interactions between AM fungi and PGPR most likely occur, and certain groups of bacteria have been shown to be established to a much higher extent in the mycorrhizosphere compared with other groups. Artursson et al., (2005) used molecular tools to bypass the problems commonly encountered with culture-based approaches to visualize changes in actively growing bacterial community compositions as a result of *G. mosseae* inoculation or plant species. He found that mostly 'uncultured bacteria' and *Paenibacillus* sp. were active in the *G. mosseae* inoculated soil, suggesting that many species of interest may be missed if relying on culturing alone.

Improvement of soil heath by AM and bacteria

An increasing demand for low-input agriculture has resulted in a greater interest in soil microorganisms which are able to enhance plant nutrition and health, and to improve soil quality (Jeffries et al., 2003).

Among the microbial groups, Actinomycetes bacteria and arbuscular mycorrhizal (AM) fungi are known to promote activities which can improve agricultural developments, thus these microorganisms appear as a research target with regard to sustainability purposes (Johansson et al., 2004).

Mycorrhizal fungi have received considerable interest from researchers, particularly for the past 40 years or so when their role as modulators of plant growth began to be universally recognized. It is only more recently that their interactions with other soil organisms have been studied in more detail. Difficulties in the commercial scale culture of some mycorrhizal fungi have limited their use in microbial inoculant products, yet they remain extremely promising candidates for this approach. Vesicular Arbuscular Mycorrhizas (VAM) and ectomycorrhizas (EM) are associated with about 95% of plant species world-wide. In fact, VAM form the largest component of all fungal material in the soil. Mycorrhizal fungi form mutualistic symbioses with the roots of host plants, which are beneficial to the plant. The complex infection procedure culminates in the formation of the mycorrhiza: an entity with distinct structure and function. Mycorrhizal hyphae extending from the roots of the host plant enhance the ability of the root to take up water and minerals. This contributes to the frequent observation of improved plant nutrition and drought tolerance of mycorrhizal plants.

Bioactive metabolites production by actinomycetes and PGPR

Actinomycetes produced branching mycelium which may be of two kinds viz., substrate mycelium and aerial mycelium. Among Actinomycetes, the Streptomyces are the dominant. The non-streptomycetes are called rare Actinomycetes, comprising approximately 100 genera. Members of the Actinomycetes, which live in marine environment, are poorly understood and only few reports are available pertaining to Actinomycetes from mangroves (Siva Kumar, 2001; Lakshmanaperumalsamy, 1978). Actinomycetes can also degrade adverse compounds, such as xenobiotics and aromatic molecules, and constitute a major factor for life in extreme soil conditions. The Actinomycetes, particularly Streptomyces species, are well-known saprophytic bacteria that decompose organic matter, especially polymers such as lignocellulose, starch and chitin in soil. Many of the work has done on Actinomycetes for its importance and useful products had extracted and used in agriculture and other area.

The most commonly described Actinomycetes genera have been Streptomyces and Micromonospora. The genus Streptomyces is in fact known as one of the major sources of bioactive natural products (Figure 1) (Bull et al., 1992; Basilio et al., 2003; Terkina et al., 2006). Particularly, it has been estimated that approximately two-thirds of natural antibiotics have been isolated from Actinomycetes, and about 75% of them are produced by members of the genus Streptomyces (Newman et al., 2003; Jimenez-Esquilin and Roane, 2005). In the last decade research has focused on minor groups of Actinomycetes, including species that are difficult to isolate and cultivate, and those that grow under extreme conditions, i.e. alkaline and acidic conditions (Lazzarini et al., 2000). However, most soil Actinomycetes show their optimum growth in neutral and slightly alkaline conditions.

Indole-3-acetic acid (IAA) is the principal form of auxin, which regulates several

fundamental cellular processes, including cell division, elongation and differentiation. It also leads to decrease in root length and increase in root hair formation, thus enhancing the capability of the plant to absorb soil nutrients. Besides, there are many developmental processes in which auxin plays a role, including embryo and fruit development, organogenesis, vascular tissue differentiation, root patterning, elongation and tropistic growth, apical hook formation and apical dominance.

Streptomyces occur in the rhizosphere of plants and can enhance plant growth by producing plant growth promoter substances e.g. auxin or gibberellin (Kaunat 1969, Brown 1972, Merckx et al., 1987). The auxins are a group of indole ring compounds which have the ability to improve plant growth by stimulating cell elongation, root initiation, seed germination and seedling growth (El- Tarabily 2008). Indole acetic acid (IAA) is a common natural auxin and is a product of L-tryptophan metabolism in microorganisms.

Manulis et al., (1994) described the production of the plant hormone indole-3-acetic acid (IAA) and the pathways of its synthesis by various Streptomyces spp. including, *S. violaceus*, *S. scabies*, *S. griseus*, *S. exfoliatus*, *S. coelicolor*, and *S. lividans*. While prior works had reported IAA synthesis in Streptomyces spp. (El-Sayed et al., 1987), this was the first confirmation of its production using modem analytical methods such as HPLC and GC-MS, and Manulis et al., (1994) provided a detailed description of the IAA biosynthetic pathways in Streptomyces. This study lent further credence to the possibility that certain rhizobacteria, including the actinomycetes, may act as plant growth enhancers. This activity may be due to, at least in part, an increase in bioavailable phytohormones that are PGPR produced since all PGPR strains produced substantial amounts of exogenous auxins (IAA), as well as gibberellins and cytokinins.

Wheeler et al., (1984), Kravchenko et al., (1991), studied the rich supply of substrates available in root exudates creates the potential for the streptomycetes to synthesize and release IAA. Several Streptomyces species, such as *S. olivaceoviridis, S. rimosus*, *S. rochei* and Streptomyces spp. from the tomato rhizosphere, have the ability to produce IAA and improve plant growth by increased seed germination, root elongation and root dry weight (Aldesuquy et al., 1998, El-Tarabily 2008).

Bhavdish et al., (2003) reported that approximately 80% of rhizosphere bacteria can secrete IAA. Streptomyces spp., inhabiting the rhizospheres of various plants, also serves as good source of IAA. Nowadays, some rhizosphere Actinomycetes are studied and developed as a commercial product.

Biological control agents (BCAs)

The VAM fungus *Glomus mosseae* stimulated localized and induced systemic resistance to Phytophthora parasitica in tomato using mycorrhizal and non-mycorrhizal roots in a split root experimental system demonstrated by Condier et al., (1998). In this scheme, decreased pathogen development in mycorrhizal and non-mycorrhizal parts of mycorrhizal root systems was associated with the accumulation of phenolic compounds, and with typical plant cell defence responses. Mycorrhizal cortical cells were immune to *P. parasitica* and showed callus development at sites of parasite infection. The systemic component of resistance was characterized by host cell

wall thickenings of pectins and proteins in non-mycorrhizal root parts, as well as callus deposition at infection sites. None of these observations were apparent in non-mycorrhizal pathogen-infected root systems. Filion et al., (1999) demonstrated that the Crude extracts of the growth medium of the AM fungus Glomus intraradices fungi reduced the incidence and severity of the fungal pathogen *Fusarium oxysporum* in carrot whilst, at the same time, stimulating the growth of rhizosphere bacteria *Pseudomonas chlororaphis* and *Clavibacter michiganensis*. Jeannine et al., (2009) reported the fungal diversity to protect the plant pathogen by AM. AM fungi can confer protection to host plants against some root pathogens, and several mechanisms for these phenomena have been proposed. If AM fungal taxa vary in the ways that they limit the negative effects of pathogens on host plants, additive and/or synergistic interactions among members of diverse AM fungal assemblages and communities may result in a greater pathogen protection. Jeannine et al., also proposed that functional complementarity of AM fungal taxa in interactions with pathogens could mimic, or even be the cause of, previously observed relationships between AM fungal diversity and plant productivity.

Several properties associated with Actinomycetes might explain the ability of several of them to act as biocontrol tools. Those properties are the ability to colonize plant surface, the antibiosis against plant pathogens, the synthesis of particular extracellular proteins, and the degradation of phytotoxins.

Tahvonen (1982a), (1982b) reported a prime example of Streptomyces biocontrol agent is *Streptomyces griseoviridis* Anderson et al., (1988) strain K61. This strain, originally isolated from light coloured Sphagnum peat, has been reported to be antagonistic to a variety of plant pathogens including *Alternaria brassicola, Botrytis cinerea, Fusarium avenaceum, F. culmorum, F. oxysporum, Pythium debaryanum, Phomopsis sclerotioides, Rhizoctonia solani* and *Sclerotinia clerotiorum* (Tahvonen and Avikainen 1987). Weller (1988) reported that the microorganism that colonizes roots is ideal for use as a biocontrol agent against soil-borne diseases. *Streptomyces griseoviridis* is a good example for colonization of plant rhizosphere by Actinomycetes. *S. griseoviridis* is an antagonistic microorganism effective in biocontrol of plant diseases such as the Fusarium wilt of carnation, the damping-off of Brassica and the root rot disease of cucumber (Tahvonen and Lahdenpera 1988).

Endophytic streptomycetes (Gurney and Mantle 1993) colonize an ecological niche similar to that of pathogens, especially vascular wilt pathogens, which might favour them as candidates for biocontrol agents. Some intensive work on rhizosphere biocontrol agents has shown that five of six rhizobacteria, which induced systemic resistance in cucumber, exhibited both external and internal root colonization (Kloepper and Beauchamp 1992). Streptomyces species have also been implicated in the biological control of a number of other pathogens. *S. ambofaciens* inhibited Pythium damping-off in tomato plants and Fusarium wilt in cotton plants. *S. hygroscopius* var. geldanus was able to control Rhizoctonia root rot in pea plants and the inhibition was due to the production of the antibiotic geldanamycin. *Streptomyces lydicus* WYEC108 inhibited *Pythium ultimum* and *R. solani* in vitro by the production of antifungal metabolites (Yuan and Crawford, 1995). There are several biocontrol agents has been isolated

which produced a range of antibiotics for disease resistance against particular phytopathogenic fungi. (Table 1)

Streptomyces lydicus WYEC108, a root-colonizing actinobacterium capable of mycoparasitism of fungal root pathogens and excretion of anti-fungal metabolites in the rhizosphere is capable of incr easing root nodulation frequency in pea (*Pisum sativum*) (Tokala et al., 2001). Actinoplanes missouriensis, isolated from surface sterilised lupin roots, was f ound to be an antagonist of *Plectosporium tabacinum*, the causal agent of lupin root rot in Egypt (El-Tarabily, 2003). The inhibition of *P. tabacinum* appears to be through the production of chitinase and the ability of *A. missouriensis* to degrade the hyphae of *P. tabacinum* in vitro (El-Tarabily, 2003).

Activation of Plant Defence Mechanisms through BCAs

Studies of the interaction between mycorrhizal fungi and sedentary parasitic nematodes have provided evidence that resistance to soil pathogens can be related to factors other than improved plant nutrition. Investigations of the interactions between root knot nematode (*Meloidogyne hapla*) and VAM fungi on susceptible cultivars of tomato and white clover revealed that phosphorus nutrition was negatively correlated with nematode numbers in mycorrhizal roots (Cooper & Grandison,1986). Furthermore, nematode numbers per gram of root were consistently less in mycorrhizal soils, and plants pre-infected with mycorrhizal fungi showed improved growth compared to un-inoculated controls. Mycorrhizal fungi and other soil microorganisms are known to confer resistance, tolerance, or other forms of bioprotection to host plants, the actual mechanisms involved are not clear.

ISR and SAR through bacteria Systemic resistance to a wide range of pathogens can be induced by two different methods, systemic acquired resistance (SAR) and induced systemic resistance (ISR).

Systemic Acquired Resistance (SAR)

Systemic Acquired Resistance (SAR) is induced by prior inoculation with a necrotizing pathogen or the application of chemical agents such as salicylic acid (SA), 2-6-dichloro isonicotinic acid (INA) and benzo (1,2,3) thiadiazole-7-carbothioic acid S-methyl ester (BTH) (Uknes et al., 1992). Once the SAR pathway has been activated resistance can be conferred to a number of pathogens. SAR has been extensively studied in the dicots, tobacco (*Nicotiana tabacum*) and *Arabidopsis thaliana* . SAR was first characterised in tobacco plants that expressed increased resistance systemically after infection by tobacco mosaic virus (Ross, 1961).

SAR is characterized by an early increase of endogenously synthesized SA and the enhanced production of pathogenesis-related (PR) proteins. Eleven different PR families are recognized in tomato and tobacco (van Loon and van Stein, 1999). The PR-1 family is the main group of PRs induced by pathogens or SA and is commonly used as a marker for SAR. PR-1, though, is the only family for which no function or relationship is known (van Loon and van Stein, 1999).

The second stage, the establishment phase, involves perception of the mobile signal (Cameron et al., 1999). The final stage of SAR requires the plant to be challenged with a second normally virulent pathogen and the plant responds to this pathogen as if it was a virulent (Cameron et al., 1999). In Arabidopsis the SAR pathway confers resistance to *Pseudomonas syringae* (P.v)

maculicola ES 4326 and Peronospora parasitica (Ryals et al., 1996). SAR has been reported in rice with *Pseudomonas syringae* pv. syringae as the inducing pathogen. Although SAR has not been conclusively demonstrated in wheat, it has been reported that Erysiphe graminis infection appears to induce SAR as does treatment with BTH leading to induced resistance against Septoria spp., *P. recondita* and *E. graminis* (Gorlach et al., 1996).

In contrast to dicots, the orthologous PR-1 proteins in wheat do not correlate to SAR induction (Molina et al., 1999). Pathogen-induced resistance has been correlated with the expression of Wheat Induced Resistance (WIR) genes and chemically induced resistance with Wheat Chemical Induced (WCI) genes (Kmcel et al., 1995). The behaviour of the WIR and WCI genes has been postulated to be different fr om genes in the Arabdiopsis SAR pathway (Schaffrath et al., 1997). Bacterial determinants and types of host resistance induced by microbes (Table 2).

Mycorrhiza-induced resistance (MIR)

Mycorrhizal symbiosis is mutual symbiosis between plants and mycorrhizal fungi during which photosynthetic products are exchanged for soil-derived mineral nutrients (Smith and Read, 2008), illustrating the importance of this mutualism to both partners. Research on plant–mycorrhiza interactions has mostly focused on the physiology of nutrient for carbon exchange and plant signal transduction pathways controlling the interaction. Comparatively little is known about the mechanisms conferring non nutritional benefits by mycorrhiza such as suppression of soil-borne diseases and enhancing plant resistance to pests and diseases (Cameron, 2010). Plants routinely signal to conspecific organisms in the rhizosphere by re-leasing primary and secondary metabolites from their roots. Some of these metabolites recruit beneficial microbes, including AMF. Furthermore, AMF infection is known to stimulate biological activity in the rhizosphere, a phenomenon commonly referred to as the 'mycorrhizosphere effect' (Linderman, 1988). This effect includes the attraction and selection of specific bacterial strains, such as plant growth-promoting rhizobacteria (PGPR) that possess the capacity to enhance plant growth and suppress pests and diseases. Some of these mycorrhizosphere inhabiting bacteria can act as 'mycorrhiza helper bacteria' and promote the efficiency of mycorrhizal symbiosis (Frey-Klett et al., 2007).

AMF can suppress plant pests and diseases through induction of systemic resistance (Jung et al. 2012, Pozo et. al 2007, Pineda et al. 2010). The induced resistance shares characteristics with both pathogen-induced SAR and rhizobacterial ISR; MIR has been associated with SAR-like priming of salicylic acid (SA)-dependent genes, but more often coincides with priming of jasmonic acid (JA)-dependent defences and cell wall defences MIR confers protection against a wide range of attackers, including biotrophic pathogens, necrotrophic pathogens, nematodes, and herbivorous arthropods (Table 3). It has been proposed that MIR is the result of active suppression of components in the SA-dependent defence pathway, causing systemic priming of JA-dependent defences (Pozo et. al 2007).

However, the exact contribution of jasmonates in MIR remains unclear (Hause et al. 2007) and the long distance signals controlling MIR remain to be resolved. It is plausible that initial induction of plant

immunity is based on host recognition of microbe-associated molecular patterns (MAMPs) from the AMF. Recognition of MAMPs by pattern-recognition receptors elicits a series of signalling cascades resulting in enhanced production of the plant defence hormone SA and expression of MAMP-trig-gered immunity (Zhang et. al., 2010). Localised MAMP recognition and SA production can lead to production of long distance SAR signals and cause systemic priming of SA-dependent defences (Conrath 2011, Heil et. al., 2008, Mishina et. al., 2007). Because most SAR studies have been conducted with AMF-incompatible Arabidopsis, it is difficult to draw direct comparisons between SAR and MIR. However, like SAR, MIR has been associated with systemic priming of SA-dependent defences and protection against (hemi)biotrophic pathogens. We therefore propose that SAR-related signals during the early stages of plant–AMF interactions contribute to MIR.

Most MIR studies have quantified the level of resistance when the plant–AMF symbiosis and the mycorrhizosphere are fully established (Jung et al., 2012). It is therefore possible that MIR involves an ISR component elicited by bacteria in the mycorrhizosphere. Like AMF, rhizobacteria possess MAMPs, which can trigger MAMP-induced immune responses (Berendsen et al., 2012). Well-known examples of defence eliciting MAMPs from bacteria are rhamnolipids, the elongation factor Tu, flagellin, and cell-wall lipopolysaccharides (Boller et. al., 2009). The spatially confined structure of the mycorrhizosphere allows rhizobacterial strains to reach exceptionally high cell densities (Linderman, 1988). Under these conditions, bacterial gene expression can be controlled by small diffusible signal molecules from members of the population themselves. This autoinduction process, known as quorum sensing (QS), allows bacteria to adjust community gene expression in accordance with their environment (Waters et. al., 2005). Many rhizosphere-colonizing bacteria, including Pseudomonas and Burkholderia strains, employ QS to control gene expression (Lugtenberg et. al., 2009). Some QS autoinducer molecules, like N-3-oxo-tetradecanoyl- L-homoserine lactone, can elicit resistance in Arabidopsis to *Pseudomonas syringae* and *Golovinomyces orontii* and in barley (*Hordeum vulgare*) to *Blumeria graminis* f. sp. *hordei* (Schikora et. al., 2011).

Both ISR and MIR have frequently been associated with systemic priming of JA and ethylene-inducible defences (Jung et. al., 2012, Van der Ent et. al., 2009, Van Wees et. al., 2008). Jasmonates also accumulate during mycorrhizal symbiosis (Hause et. al., 2007, Lopez-Raez et al., 2010). It is thus possible that jasmonates function as complementary long-distance signals of MIR, which may be the result of systemic signaling processes similar to autoregulation of nodulation during rhizobia-legume interactions (Zamioudis et. al., 2012). Although the exact contribution of jasmonates to MIR has yet to be demonstrated, we propose that priming of JA-dependent defences during MIR is partially determined by ISR-eliciting rhizobacteria in the mycorrhizosphere.

Induced Systemic Resistance

Induced Systemic Resistance (ISR) is phenotypically similar to SAR; however, the resistance is induced by non-pathogenic biotic agents. It is believed that ISR is distinct from the SAR pathway, but mediated by a JA/ET pathway and it has

been reported that there is no up-regulation of PR proteins (Hammerschmidt, 1999; van Wees et al., 2000; Pieterse, 2002). There are some conflicting reports on this matter. Park and Kloepper (2000) investigated the effect of ten PGPR strains on the induction of the PR-1a gene promoter in regards to systemic resistance in tobacco against *Pseudomonas syringae* pv. tabaci. The results of this study indicated that PR-1a promoter activity and PGPR-mediated induced systemic resistance are linked events but this finding contradicts the model for PGPR mediated ISR proposed by Pieterse et al. (1998). However, the architecture of the SAR and ISR pathways may vary among different plant species.

Pieterse et al. (1998) investigated ISR in Arabidopsis, using the non-pathogenic, root-colonising *Pseudomonas fluorescens* WCS417r as the inducing agent. *P. fluorescens* WCS417r triggers ISR in carnation (van Peer et al., 1991), radish (Leeman et al., 1995), tomato (Duijff, 1997) and Arabidopsis (Pieterse et al., 1996). *P. fluorescens* WCS417r induced systemic resistance independent of SA accumulation and PR gene activation in Arabidopsis. Using the Arabidopsis mutants jar1, etr1 and npr1, ISR was blocked indicating the ISR pathway triggered by *P. fluorescens* requires JA and ET perception and NPR1 function. Pieterse et al. (1998) found that there was no induction of PDF1.2, PR-1, and Hel genes, suggesting the final ISR defensive compounds are different to the compounds up-regulated in the SAR and JA/ET pathways. The defence compounds induced by *P. fluorescens* WCS417r confer resistance to *Fusarium oxysporum* f.sp. raphani, the oomycetous leaf pathogen *Peronospora parasitica*, and the bacterial leaf pathogens *Xanthomonas campetris* pv. campetris and *Pseudomonas syringae* pv. tomato indicating ISR is effective against different types of pathogens (van Wees et al., 2000). Rhizobacteria-mediated ISR signaling pathway and the systemic or pathogen-derived signal pathway could be understand following the model proposed by (Wang et. al., 2002) Figure 2.

Conrath et al. (2002) believe that the non-pathogenic bacteria prime the plant for accelerated and enhanced response when the plant is challenged by a second stress stimulus such as a pathogen. Verhagen et al. (2004) used the microarray technique to identify ISR-related genes in Arabidopsis. Over 8000 genes were surveyed and it was found, when using the ISR-inducing bacterium *P. fluorescens* WCS417r, there was a substantial change in the expression of 97 genes in the roots but no changes in expression could be detected in the leaves. However, after subsequent challenge with *Pseudomonas syringae* pv. tomato DC3000 there was a change in the expression of 81 genes in the leaves. This indicates the role of rhizobacteria in priming the plant for ISR.

In the past few years, research has been directed more toward the induced systemic resistance (ISR), a process by which PGPR stimulate the defense mechanisms of host plants without causing apparent harm to the host. More recently, Choudhary and Johri (2008) have reviewed ISR by Bacillus spp. in relation to crop plants and emphasized on the mechanisms and possible applications of ISR in the biological control of pathogenic microbes. Various strains of species *B. amyloliquefaciens*, *B. subtilis*, *B. pasteurii*, *B. cereus*, *B. pumilus*, *B. mycoides*, and *B. sphaericus* are know n as potential elicitors of ISR and exhibit significant reduction in the incidence or severity of various diseases on diverse hosts (Choudhary and Johri 2008; Kloepper et al. 2004). It is believed that plants have the ability to acquire enhanced level of resistance to pathogens after getting exposed to biotic stimulation provided by

many PGPR's and this is known as rhizobacteria mediated ISR (Choudhary et al. 2007).

It is not certain if plants actively select beneficial soil microbial communities in their rhizosphere through rhizodeposition, though earlier studies showed that plants select for taxonomic functional groups in the rhizosphere (Grayston et al. 2001; 1998). Although some field studies with mixed plant com munities did not find such selection s in the rhizosphere, there are reports that suggest a strong correlation between plant and soil microbial communities (Duineveld et al. 2001; Smalla et al.2001). The root exudation is believed to be plant specific and this specificity may reflect the evolution or specific physiological adaptation to conditions of a particular soil habitat (Crowley and Rengel 1999). The type of root exudates is crucial for the ecosystem distribution and niche specificity of certain plants. Composition of root exudates was shown to vary with plant species and stage of plant growth (Jaeger et al. 1999).

Table.1 Some of antibiotics produced by BCAs

Antibiotic	Source	Target pathogen	Disease	Reference
2, 4-diacetyl-phloroglucinol	*Pseudomonas fluorescens* F113	*Pythium* spp.	Damping off	Shanahan et al. (1992)
Agrocin 84	*Agrobacterium radiobacter*	*Agrobacterium tumefaciens*	Crown gall	Kerr (1980)
Bacillomycin D	*Bacillus subtilis*AU195	*Aspergillus flavus*	Aflatoxin contamination	Moyne et al. (2001)
Bacillomycin, fengycin	*Bacillus amyloliquefaciens*FZB42	*Fusarium oxysporum*	Wilt	Koumoutsi et al. (2004)
Xanthobaccin A	*Lysobacter* sp. strain SB-K88	*Aphanomyces cochlioides*	Damping off	Islam et al. (2005)
Gliotoxin	*Trichoderma virens*	*Rhizoctonia solani*	Root rots	Wilhite et al. (2001)
Herbicolin	*Pantoea agglomerans* C9-1	*Erwinia amylovora*	Fire blight	Sandra et al. (2001)
Iturin A	*B. subtilis*QST713	*Botrytis cinerea* and*R. solani*	Damping off	Paulitz and Belanger (2001), Kloepper et al. (2004)
Mycosubtilin	*B. subtilis*BBG100	*Pythium aphanidermatum*	Damping off	Leclere et al. (2005)
Phenazines	*P. fluorescens* 2-79 and 30-84	*Gaeumannomyces graminis* var. *tritici*	Take-all	Thomashow et al. (1990)
Pyoluteorin, pyrrolnitrin	*P. fluorescens*Pf-5	*Pythium ultimum*and *R. solani*	Damping off	Howell and Stipanovic (1980)
Pyrrolnitrin, pseudane	*Burkholderia cepacia*	*R. solani* and *Pyricularia oryzae*	Damping off and rice blast	Homma et al. (1989)
Zwittermicin A	*Bacillus cereus*UW85	*Phytophthora medicaginis* and *P. aphanidermatum*	Damping off	Smith et al. (1993)

Table.2 Bacterial determinants and types of host resistance induced by biocontrol agents (BCAs)

Bacterial strain	Plant species	Bacterial determinant	Type	Reference
*Bacillus mycoides*strain Bac J	Sugar beet	Peroxidase, chitinase and β-1,3-glucanase	ISR	Bargabus et al. (2002)
Bacillus subtilis GB03 and IN937a	*Arabidopsis*	2,3-butanediol	ISR	Ryu et al. (2004)
Pseudomonas fluorescens strains				
CHA0	Tobacco	Siderophore	SAR	Maurhofer et al. (1994)
	Arabidopsis	Antibiotics (DAPG)	ISR	Iavicoli et al. (2003)
WCS374	Radish	Lipopolysaccharide	ISR	Leeman et al. (1995)
		Siderophore		Leeman et al. (1995)
		Iron regulated factor		Leeman et al. (1995)
WCS417	Carnation	Lipopolysaccharide	ISR	Van Peer and Schipper (1992)
	Radish	Lipopolysaccharide	ISR	Leeman et al. (1995)
		Iron regulated factor		Leeman et al. (1995)
	Arabidopsis	Lipopolysaccharide	ISR	Van Wees et al. (1997)
	Tomato	Lipopolysaccharide	ISR	Duijff et al. (1997)
*Pseudomonas putida*strains	*Arabidopsis*	Lipopolysaccharide	ISR	Meziane et al. (2005)
WCS 358	*Arabidopsis*	Lipopolysaccharide	ISR	Meziane et al. (2005)
		Siderophore	ISR	Meziane et al. (2005)
BTP1	Bean	Z,3-hexenal	ISR	Ongena et al. (2004)
*Serratia marcescens*90-166	Cucumber	Siderophore	ISR	Press et al. (2001)

Figure.1 Bioactive secondary metabolites produced by actinobacteria **(Berdy, 1989)**

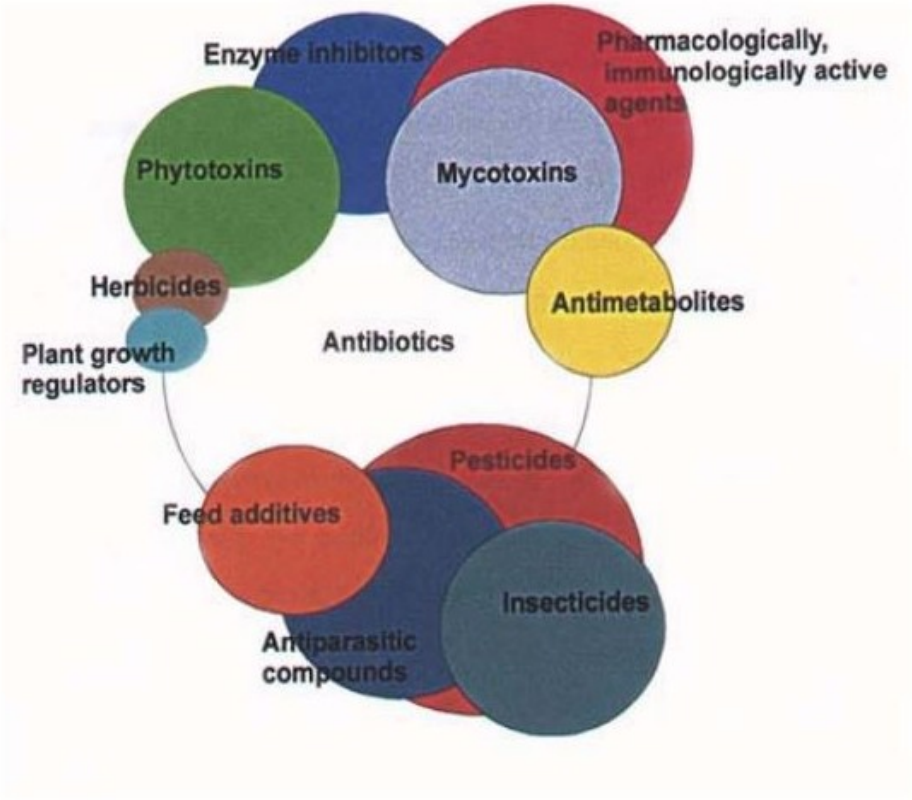
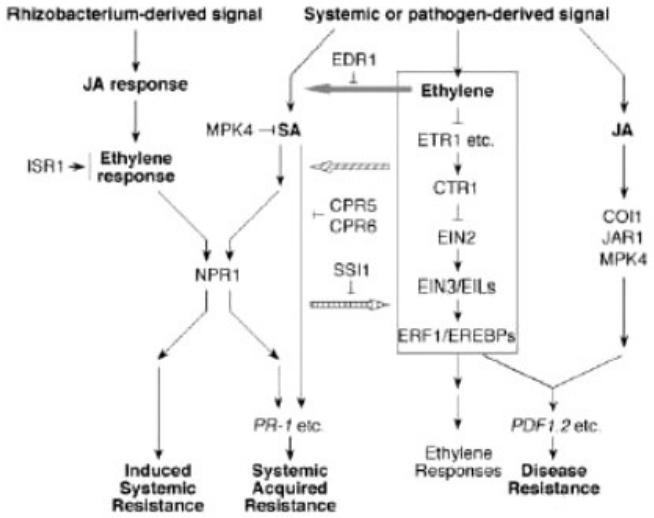


Table.3 Defence mechanisms associated with ISR by AMF

Proposed mode of action of systemic resistance	Resistance-inducing AMF strain	Host plant	Disease or pest	Refs
Priming of JA- and SA-inducible defence genes	*R. irragularis*[a] *G. vermiforme* *F. mosseae*[b]	Grapevine(vitis vinifera) Grapevine, tobbaco (Nicotiana tobacum) maize	*Xiphinema index* *Meloidogyne incognita* *Rhizoctonia solani*	Li, H.Y. et al. (2006) Hao, Z. et al. (2012) Song, Y. et al. (2011)
SA-independent resistace	*F. mosseae*[b]	Barley	*Gaeumannomyces graminis*	Khaosaad, T. et al. (2007)
Priming of SA- inducible PR genes	*Glomus sp*. MUCL 41833	Patato	*Phytopthora infastance*	Gallou, A. et al. (2011)
Amf specific modulation of herbivore leaf induce chemicals	*Gigaspora margarita* *Acaulospora longula*	Lotus japonicus	*Tetranycus urticeae*	Nishida, T. et al. (2010)
Priming of cell wall defence	*F. mosseae* *Glomus and Gigaspora sp.*	Tomato Common bean	*Phytopthora prasitica and Rhizoctonia solani*	Cordier, C. et al. (1998), Pozo, M.A .J. et al. (1999), (2002)
Priming of defence- related protein production	*F. mosseae*	Tomato	*Phytopthora prasitica*	Abdel-Fattah, G.M. et al. (2011)
Priming of defence- related enzymatic activity	*Glomus and Gigaspora sp.*	Common bean	*Rhizoctonia solani*	Abdel-Fattah, G.M. et al. (2011)
Enhance production of phenolics compound	*Glomus and Gigaspora sp. and G. vermiforme*	Common bean Tomato	*Rhizoctonia solani* *Ralstonia solanacearum*	Abdel-Fattah, G.M. et al. (2011) Zhu, H.H. and Yao, Q. (2004)
Enhance expression of stress-related genes	*R. irragularis*	Madicago truncatula	*Xanthomonas campestris*	Liu, J. et al. (2007)
Enhance production of benzoxazinoid	*F. mosseae*[b]	Maize	*Rhizoctonia solani*	Song , Y. et al. (2011)

[a]Syn. G. Intraradices [b]syn. G. mosseae

Figure.2 Proposed model of the rhizobacteria-mediated ISR signaling pathway and the systemic or pathogen-derived signal pathway (Wang et. al., 2002)



Induced resistance may be defined as a physiological "state of enhanced defensive capacity" elicited in response to specific environment al stimuli and consequently the plant's innate defenses are potentiated against subsequent biotic challenges (van Loon 2000). In addition, there is another defined form of induced resistance, popularly know n as systemic acquired resistance (SAR) which is different from ISR in cont ext to the nature of elicitor and regulatory path ways involved. While ISR relies on pathways regulated by jasmonic acid (JA) and ethylene (ET), SAR involves accumulation of salicylic acid (SA) and pathogenesis related (PR) proteins chitinase and cellulase. PGPRs are among the various groups of plant associated microorganisms that can elicit the plant defense systems resulting in reduction of disease severity or incidence of diseases caused by pathogens which are spatially different from the inducing agent (van Loon and Glick 2004).

Recently, Choudhary and Johri (2008) explicate d the mechanism s and role of Bacillus species as inducers of systemic resistance in relation to plant microbe interactions and demarketed the pathways involved in their regulation. Available reports suggest that specific strains of the species *B. amyloliquefaciens*, *B. subtilis*, *B. pasteurii*, *B. cereus*, *B. pumilus*, *B. mycoides*, and *B. sphaericus* elicit significant reductions in the incidence or severity of various diseases on a diversity of hosts including greenhouse studies or field trials on tomato, bell pepper, muskmelon, watermelon, sugar beet, tobacco, Arabidopsis species, cucumber, loblolly pine, and tropical crops (Kloepper et al. 2004).

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