Induction and modulation of resistance in crop plants against disease by bioagent fungi (arbuscular mycorrhiza) and hormonal elicitors and Plant Growth Promoting Bacteria

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ABSTRACT: Arbuscular mycorrhizal (AM) fungi and bacteria and hormonal elicitors can interact synergistically to stimulate plant growth through a range of mechanisms that include improved nutrient acquisition and inhibition of fungal plant pathogens. These interactions may be of crucial importance within sustainable, low-input agricultural cropping systems that rely on biological processes rather than agrochemicals to maintain soil fertility and plant health. Although there are many studies concerning interactions between AM fungi and bacteria and hormonal elicitors the underlying mechanisms behind these associations are in general not very well understood, and their functional properties still require further experimental confirmation. Future mycorrhizal research in this context, the present article seeks to review and discuss the current knowledge concerning interactions between AM fungi and plant growth promoting rhizobacteria, and hormonal elicitors physical interactions between AM fungi and bacteria, and hormonal enhancement of phosphorus and nitrogen bioavailability through such interactions, and finally the associations between AM fungi and their bacterial endosymbionts. Overall, this review summarizes what is known to date within the present field, and attempts to identify promising lines of future research.

Keywords: Mycorrhizal fungi, interrelations, plant growth promoting rhizobacteria, hormonal elicitors

INTRODUCTION

The first clear indication of improved plant growth and biological control of root pathogens due to seed bacterization with rhizobacteria came from the works of (Burr et al., 1978) and (Kloepper et al., 1980) who reported the plant growth promoting effects of Pseudomonas strains which were antagonistic to a wide range of plant pathogens in vitro. Rhizobacteria have also been studied as plant growth promoters for increasing agricultural production and as biocontrol agents against plant diseases (Burris, 1998; Chen et al., 1996).

Plant growth promoting rhizobacteria (PGPR) exhibit direct and indirect mechanisms as plant growth promoters and biological control agents. Direct mechanisms by PGPR, include the provision of bioavailable phosphorus for plant uptake, nitrogen fixation for plant use, sequestration of iron for plant by siderophores, production of plant hormones like auxins, cytokinins and gibberellins and lowering plant ethylene levels using ACC deaminase that accumulate during biotic and abiotic stresses (Mayak et al., 2004). Indirect mechanisms of PGPR include production of antibiotics, viz. 2,4-Diacetyl phloroglucinol (DAPG), phenazine, pyoluteorin and pyrrolnitrin against pathogenic fungi and bacteria, reduction of iron available to phytopathogens in the rhizosphere, synthesis of fungal cell wall and insect-gut membrane lysing enzymes, chitinase enzyme for hydrolysis of chitin layer of the
eggshell of nematode and also competition with detrimental microorganisms for sites on plant roots and induction of systemic resistance against various pathogens and pests in plants (Ramamoorthy et al., 2001). These studies also provided the first evidence that the rhizosphere microbiota could be modified significantly with microorganisms introduced with the planting material. (Kloepper et al., 1989) coined the term plant growth promoting rhizobacteria (PGPR) to include bacteria inhabiting the root and rhizosphere soil which have the ability to increase plant growth. Plant Growth-Promoting Rhizobacteria (PGPR) have been reported to be key elements for plant establishment under nutrient-imbalance conditions (Egamberdiyeva and Höflich, 2004). PGPR may improve plant growth and yield by direct and indirect mechanisms (Noel et al., 1996). Indirect mechanisms of plant growth stimulation include a variety of mechanisms by which the bacteria prevent phytopathogens from inhibiting plant growth and development (Glick and Bashan, 1997). Direct mechanisms may act on the plant itself and affect growth by providing plants with fixed nitrogen, phytohormones, iron and soluble phosphate (Kloepper and Schroth, 1978).

PGPR can also protect plants from the deleterious effects of some environmental stresses including flooding (Grichko and Glick, 2001), drought (Mayak et al., 2004a), salt (Mayak et al., 2004b) and phytopathogens (Harman and Björkman, 1998). Bacillus subtilis can induce plant resistance to stress and produces various plant hormones for growth improvement (Han and Lee, 2005). Many workers have showed that inoculation of plants with B. subtilis increased plant growth, yield and nutrient uptake, especially under salt stress conditions (Ashraf et al., 2004; Saleh et al., 2005), by influencing phytohormone production (auxin, cytokinin, or gibberellin), and/or by enzymatic lowering of plant ethylene levels (Glick, 2001). Arbuscular Mycorrhizal Fungi (AMF) form symbiotic associations with the roots of most plant species (Al-Karaki and Al-Raddad, 1997). These symbiotic associations can enhance plant growth and nutrient uptake under various environmental stress conditions such as salinity, drought and low fertility (Zuccarini and Okurowska, 2008). Also under conditions of low nutrient availability the hyphae of AMF can absorb nutrient from soil beyond the zone depleted by roots so they increase the effectiveness with which the soil volume is exploded (Smith and Read, 1997). The beneficial effect of mycorrhizal fungi on plant growth was attributed to enhanced phosphorus uptake (Al-Karaki et al., 2001). Some authors also point out how AM fungi can increase plant resistance to salt stress by influencing the hormonal balance of the host plant (Danneberg et al., 1992) or by increasing water uptake (Ruiz-Lozano and Azcón, 1995).

It has been suggested that microorganisms isolated from the root or rhizosphere of a specific crop adopted better to that crop and provide effective control of diseases than organisms originally isolated from other plant species. Such plant associated microorganisms serve as better biocontrol agents because they are already closely associated and adopted to the plant or plant part as well as to the particular environmental condition in which they are supposed to function. The screening of such locally adopted strains has yielded improved biocontrol strains in some cases (Cook and Baker, 1983). However, now-a-days microbial biodiversity studies have enhanced the identification of potential bioagents suited to varied environmental conditions.

Finally to use antibiotic production, growth promotion, biocontrol potential and induced responses of PGPR as an effective pathogens management tool, we should evaluate their effects on plant performance and yield under agricultural settings. Although induction of disease resistance using arbuscular mycorrhiza fungi or hormonal inducers separately is well documented, there is little information about the mechanism of defense when used together. Thus, the objective of the present work was carried out to study the possible actions of the interaction between AM fungi and hormonal elicitors and PGPR in the induced defense mechanisms in plants against diseases.

1.1 RHIZOBACTERIA AS BIOCONTROL AGENTS

Rhizobacteria are ideal for use as biocontrol agents since they inhabit the rhizosphere that provides the front line defense for roots against attack by pathogens. Pathogens encounter antagonism from rhizobacteria before and during their primary infection of roots. Rhizobacteria are reported to provide protection against diverse plant pathogens.

(Sedra and Malouhy, 1994) studied six antagonists from 420 samples obtained from conducive and suppressive soils, for their inhibitory activity against F. oxysporum f.sp. albedinis. These antagonists suppressed the growth of F. oxysporum f.sp. albedinis in vitro by 24-47 per cent and its sporulation by 70-99 per cent. (Gupta et al., 1999) isolated P. aeruginosa from potato rhizosphere that displayed a strong antagonistic activity against important fungal pathogens, viz. Macrophomina phaseolina and Fusarium oxysporum.

(Tripathi and Johri, 2002) studied the biocontrol potential of fluorescent pseudomonas isolated from rhizosphere of pea and wheat in vitro and in vivo against maize sheath blight caused by Rhizoctonia solani. They found some isolates to possess multiple disease control potential, while some others exhibited biocontrol potential.
against specific pathogens, which indicated that fluorescent pseudomonads are diverse with respect to their biocontrol potential. (Ahmadzadeh et al., 2004) reported that antagonistic rhizobacteria, more specifically fluorescent pseudomonads and certain Bacillus species possessed the ability to inhibit fungal and bacterial root diseases of agricultural crops.

Plant growth-promoting rhizobacterial strain belonging to fluorescent pseudomonads was isolated from the rhizosphere of rice and sugarcane. Among 40 strains that were confirmed as fluorescent psuedomonads, 18 exhibited strong antifungal activity against Fusarium oxysporum and Rhizoctonia bataticola, mainly through production of antifungal metabolites (Ramesh Kumar et al., 2002).

(Tiwari and Thrimurthy, 2007) reported that twenty-one isolates of Pseudomonas fluorescens were isolated from the rhizosphere of rice, maize, wheat, chickpea, mung, urd, soybean and sunflower from Raipur and Bastar regions. Among these seven isolates which showed bright fluorescence under UV light were further tested. The isolates showed positive response of siderophore production and plant growth promoting activity on rice cv. Bamleshwari. Among the isolates PFR 1 and PFR 2 were found significantly superior to control in increasing the shoot length and root length. In vitro evaluation of the P. fluorescens isolates also confirmed their antagonistic ability against both Pyricularia oryzae and Rhizoctonia solani in dual culture tests.

Pure culture of P. aeruginosa was obtained from the soil and studied for siderophore production. The antifungal activity of the strain against three phytopathogenic fungi, viz. F. moniliforme, Altenaria solani and Helminthosporum heribrosus was assayed by poison food technique. Inhibition of these fungal pathogens appeared to be due to production of antifungal secondary metabolites by P. aeruginosa (Kanika Sharma et al., 2007).

Various antagonistic rhizobacteria have been reported to be active in the rhizosphere and shown to play a significant role in suppressing the population and activity of R. solanacearum. The mechanisms by which they bring about the beneficial effect vary. (Jagadeesh, 2000) reported that bacterial wilt of tomato caused by R. solanacearum was controlled by the rhizobacteria, by an extent of 16.66 to 83.33 per cent. Inoculation of three strains (fluorescent pseudomonas strain RJA112 and RBG 114 and Arthrobacter RBE 201) and the reference strain (P. fluorescens CHAO) resulted in 83.33 per cent disease control.

(Anith et al., 2004) reported that when PGPR (Pseudomonas putida, Bacillus pumilus) and Actigard (acibenzolar-S-methyl) application were combined, the bacterial wilt incidence caused by R. solanacearum was reduced when compared to the untreated control.

(Sikora, 1990) found that P. fluorescens exhibited an in vitro repellent effect towards R. similis and Meloidogyne spp.

(Johnathan et al., 2000) studied the efficacy of plant growth promoting uncharacterized actinomycetes (strain 29 and 45) and the nematode parasitic bacterium Pasteuria penetrans (isolate 100) against M. incognita race 1 on tomato and banana. Seed treatment with P. fluorescens and P. chlororaphis significantly reduced the root of M. incognita race 1 in tomato cv. Rutgers (Johnathan et al., 2000).

Pseudomonas fluorescens, Bacillus spp. and arbuscular mycorrhizae were tested against M. incognita and Tylechulus semipenetrans in horticultural crops such as citrus, tomato, potato and chilli. The results showed that these organisms could be used as successful biocontrol agents for the management of plant parasitic nematode (Rajendran et al., 2001). (Seenivasan and Lakshmanan, 2001) studied the nemotoxic effects of culture filtrates of P. fluorescens strain Pf1 on Hirschmanniella gracilis at 25, 50, 75 and 100 per cent concentration in vitro. Application of P. fluorescens or B. subtillis increased the growth and yield of chickpea and reduced the infection by M. incognita by minimizing the number of galls/root system, egg mass production and soil population (Khan et al., 2001). Mortality of M. incognita juveniles was observed to be similar both in unheated and heated culture filtrates of P. fluorescens and the mortality increased with increase in concentration (Sirohi et al., 2000).

(Devi and Dutta, 2002) reported that bhendi seeds treated with P. fluorescens for 12 hours exhibited significant increase in growth and reduced root galling of M. incognita. Culture filtrates of Pseudomonas fluorescens caused significant reduction in egg hatching of M. incognita and resulted in considerable reduction in nematode population densities in soil and subsequent root knot development in tomato (Khan and Akram, 2000).

(Johnathan et al., 2006) reported that there was highest reduction in nematode egg hatch and the greatest mortality of M. incognita juveniles in the culture filtrate of P. fluorescens strain Pf22 at 100 per cent concentration. The nematode infestation was reduced both in soil and roots, with the least number of adult females, number of egg masses, number of eggs per egg mass and gall index of M. incognita in banana plants treated with the local isolate of P. fluorescens Pf22 under glasshouse conditions. Cultures and cell free culture filtrates (CFC) of 133 bacterial strains at three different dilutions (S-4, S-16, S-64) were tested in vitro against Meloidogyne javanica J2 mortality. Sixteen isolates showing 50 per cent or more mortality at lowest dilution were short listed. Four isolates,
identified as Providencia rettgeri, Vibrios sp. and Pseudomonas putida reduced egg hatching of M. javanica from 20 to 30 per cent (Ashima Kapoor et al., 2007).

2. BIOCHEMICAL CHARACTERIZATION OF PGPR

Various phenotypic and biochemical methods have been developed and used for characterizing fluorescent pseudomonad isolates. The genus Pseudomonas is characterized by gram-negative rod shaped aerobic cells and are associated with plants. The important species include P. fluorescens, P. putida, P. aeruginosa and P. aureofaciens. Most of the tests conducted for identification of fluorescent pseudomonads have been based on physiological and nutritional tests (Krieg and Holt, 1984). Among the Pseudomonads group, P. aeruginosa forms a light cluster and grows above 41°C (Hildebrand et al., 1992). Most of the associated Pseudomonas sp. belong to P. fluorescens and P. putida complex.

There was no clear distinction between P. fluorescens and P. putida (Sheath et al., 1981). However, these two species are identified based on trehalose utilization and gelatin liquefaction. In this, P. fluorescens exhibits positive for both the tests whereas P. putida show negative response (Hildebrand et al., 1992). The species of fluorescent pseudomonas are again grouped in different biovars and subgroups based on similarity in biochemical tests. Thus, rapid identification of potentially and economically viable bioagents is possible through various methods of biochemical characterization (Zehnder et al., 2000; Singh et al., 2000).

2.1 BIOCONTROL MECHANISMS OF PGPR

PGPR exhibit multiple numbers of mechanisms to promote plant growth and to serve as potential biocontrol agents. Generally, PGPR traits associated with the biocontrol of plant pathogens include:

1. Atmospheric nitrogen fixation and its supply to plants
2. Synthesizing various phytohormones including auxins and cytokinins
3. Providing mechanisms for the solubilization of minerals such as phosphorus
4. Antibiotic synthesis (Haas and Defago, 2005),
5. Production of low molecular weight metabolites such as hydrogen cyanide with antifungal activity (Dowling and O’Gara, 1994).
6. Production of enzymes including chitinase, b-1,3-glucanase, protease and lipase which can lyse some fungal cells (Chet and Inbar, 1994).
7. Production of oxidative stress enzymes such as catalases, superoxide dismutases, peroxidase and polyphenol oxidases for scavenging active oxygen species.
9. Lowering the production of stress ethylene in plants with the enzyme ACC deaminase (Penrose et al., 2001).

1.2. PLANT GROWTH PROMOTION

Rhizobacterial strains were found to increase plant growth after inoculation in seeds and therefore called “Plant growth promoting rhizobacteria” (Kloepper et al., 1980). The mechanisms of growth promotion by these PGPR are complex and appear to comprise both changes in the microbial balance in the rhizosphere and alterations in host plant physiology (Glick et al., 1999). Plant growth promoting rhizobacteria, including fluorescent pseudomonads are capable of surviving and colonizing the rhizosphere of all field crops. They promote plant growth by secreting auxins gibberellins and cytokinins (Vidyasekaran, 1998).

PGPR has a significant impact on plant growth and development in both indirect or direct ways. Indirect promotion of plant growth occurs when bacteria or prevent some of the deleterious effects of a phytopathogenic organism by one or more mechanisms. On the other hand, the direct promotion of plant growth by PGPR generally entails providing the plant with compound that is synthesized by the bacterium or facilitating the uptake of nutrients from the environment (Glick et al., 1999). Plant growth benefits due to the addition of PGPR include increase in germination rates, root growth, yield including grain, leaf area, chlorophyll content, magnesium, nitrogen and protein content, hydraulic activity, tolerance to drought and salt stress, shoot and root weights and delayed leaf senescence (Lucy et al., 2004). Seed treatment with PGPR resulted in increased yield and growth in potato under field conditions (Kloepper et al., 1980). (Van Peer and Schippers, 1988) documented the increased root and shoot fresh weight of tomato, cucumber, lettuce and potato as a result of bacterization with Pseudomonas strains.
(Mashooda Begum et al., 2003) studied the effectiveness of plant growth promoting rhizobacterial isolates against some seed borne fungal diseases. Among them B. pumilus (SE-34), B. pasteurii (T4), B. subtilis (IN 937-6) and B. subtilis (GB-03) strains stood first in the improvement of crop, both in greenhouse and field condition. Potential strains increased the biomass of plants, total number of leaves, fruits, length, girth, biomass of the fruit. The colonization of these bacterial strains reduced the incidence of seed mycoflora which indirectly enhanced the per cent seed germination and vigour index of seedlings. (Minakshi et al., 2005) isolated a total of 113 rhizobacteria from different rhizotic zones of pigeonpea. Seed treatment using four isolates, viz. RS29, RS39, RS41 and RP3 resulted in 90 per cent seed germination in contrast with 50 per cent obtained in untreated control after 72 h of incubation and the isolates RS34, ER17, RP7 and RS41 increased shoot height and shoot dry biomass as compared to uninoculated control whereas isolates RS45, RS36, RS37, ER23, RP24 influenced root dry biomass significantly.

2.4. HYDROGEN CYANIDE (HCN) PRODUCTION

The cyanide ion is exhaled as HCN and metabolized to a lesser degree in to other compounds. HCN first inhibits the electron transport and the energy supply to the cell is disrupted leading to the death of the organisms. It inhibits proper functioning of enzymes and natural receptors reversible mechanism of inhibition (Corbett, 1974) and it also known to inhibit the action of cytochrome oxidase (Gehring et al., 1993). HCN is produced by many rhizobacteria and is postulated to lay a role in biological control of pathogens (Defago et al., 1990). Production of HCN by certain strains of fluorescent pseudomonads has been involved in the suppression of soil borne pathogens (Voisard et al., 1989). Suppression of black root rot of tobacco (Stutz et al., 1986) and take-all of wheat (Defago et al., 1990) by P.fluorescens strain CHAO was attributed to the production of HCN. Pseudomonas fluorescens HCN inhibited the mycelial growth of Pythium in vitro (Westeijn, 1990).

The cyanide producing strain CHAO stimulated root hair formation, indicating that the strain induced and altered plant physiological activities (Voisard et al., 1989). Four of the six PGPR strains that induced systemic resistance in cucumber against Colletotrichum orbiculare produced HCN (Wei et al., 1991). Fluorescent pseudomonas strain RRS1 isolated from Rajanigandha (tuberose) produced HCN and the strain improved seed germination and root length (Saxena et al., 1996). (Pessi and Haas, 2000) reported that low oxygen concentrations are a prerequisite for the activity of the transcription factor ANR which positively regulates HCN biosynthesis.

HCN from P. fluorescens strain CHAO not repressed by fusaric acid played a significant role in disease suppression of F. oxysporum f.sp. radicis- lycopersici in tomato (Duffy et al., 2003). (Ramettee et al., 2003) reported that hydrogen cyanide is a broadspectrum antimicrobial compound involved in biological control of root disease by many plant associated fluorescent pseudomonads. Further, they noted that the enzyme HCN synthase is encoded by three biosynthetic genes (henA, henB and henC).

2.2. INDOLE-3-ACETIC ACID (IAA) PRODUCTION

IAA is phytohormone which is known to be involved in root initiation, cell division and cell enlargement (Salisbury, 1994). This horne is very commonly produced by PGPR (Barazani and Friedman, 1999). (Vessey, 2003) has reviewed the production of this hormone and implicated it in the growth promotion by PGPR. However, the effect of IAA on plants depends on the plant sensitivity to IAA and the amount of IAA produced from plant associated bacteria and induction of other phytohormones (Peck and Kende, 1995). Patten and Glick (2002) demonstrated that bacterial IAA from P. putida played a major role in the development of host plant root system. Similarly, IAA production in P. fluorescens HP 72 correlated with suppressing of creeping bent grass brown patch (Suzuki et al., 2003).

2.3. ANTIBIOSIS

Antibiotics are generally considered to be organic compounds of low molecular weight produced by microbes. Antibiosis plays an active role in the biocontrol of plant disease and it often acts in concert with competition and parasitism. Antibiosis has been postulated to play an important role in disease suppression by rhizobacteria (Gutterson et al., 1986).

Fluorescent pseudomonad strains are known to reduce fungal growth in vitro by the production of one or more antifungal antibiotics that may also have activity in vivo (Whippes, 2001). Several strains of Pseudomonas spp. have been shown to produce wide array of antibiotics which include 2,4-diacyl phloroglucinol; hydrogen cyanide, kanosamine, phenazine-1-carboxylic acid, pyoluteorin, oomycin A, pyrrolnitrin, pyocyanin and viscosinamidase as well as several other uncharacterized moieties (Tharne et al., 1999). Phloroglucinols phenazines, pyoluteorin,
pyrrolnitrin and cyclic lipopeptides all of which are diffusible and hydrogen cyanide is volatile in nature (Haas and Defago, 2005).

Root associated fluorescent pseudomonads produce and excrete secondary metabolites which are inhibitory to plant pathogenic organisms including fungi, bacteria and nematodes (Haas and Keel, 2003). Among these metabolites the polyketide compound. DAPG has received particular attention because of its broad spectrum antifungal, antibacterial and antihelminthic activity (Keel and Defago, 1997). Phenazines (PHZ) are N containing heterocyclic pigments synthesized by species of Pseudomonas, Streptomyces, Burkholderia and Brevibacterium (Steves et al., 1994). Pyrrolnitrin (PRN) is a broad spectrum antifungal metabolite produced by many fluorescent and non-fluorescent strains of the genus Pseudomonas(Howell and Stipanovic, 1979). A phenyl pyrrol derivative of PRN has been developed as an agricultural fungicide. Pyrrolnitrin persists actively in the soil for at least 30 days.

Pyloluteorin (PLT) is an aromatic polyketide antibiotic consisting of a resorcinol ring derived through polyketide biosynthesis. PLT is produced by several Pseudomonas sp. including strains that suppress plant diseases caused by phytopathogenic fungi (Murhofer et al., 1994). PLT mainly inhibits the oomycetous fungi including Phytophthora ultimum against which it is strongly active when applied to seeds. PLT-producing Pseudomonads decrease the severity of Pythium damping off (Nowak-Thompson et al., 1999). Pseudomonas fluorescens strain CHAO/PM 3424, repeatedly reduced M. incognita galling in tomato, brinjal, mung and soybean in early growth stage. A strong negative correlation existed between rhizobacteria colonization and nematode invasion (Siddiqui and Shaukat, 2003).

2.5.INDUCED SYSTEMIC RESISTANCE (ISR)

Induced resistance is defined as an enhancement of the plants defensive capacity against a broad spectrum of pathogens and pests that is acquired after appropriate stimulation. The resulting elevated resistance due to an inducing agent upon infection by pathogen is called induced systemic resistance (ISR) or systemic acquired resistance (SAR) (Hammerschmidt and Kuc, 1995). The induction of systemic resistance by rhizobacteria is referred to as ISR, whereas that by other agencies is called SAR (Van Loon et al., 1998). Once resistance is induced, it will afford non-specific protection against pathogenic fungi, bacteria, nematodes and viruses as well as against insect pests.

A large number of defense enzymes that have been associated with ISR include phenylalanine ammonia lyase (PAL), chitinase, b-1,3-glucanase, peroxidase (PO), polyphenol oxidase (PPO), superoxide dismutase (SOD), catalase (CAT), lipoygenase (LOX), ascorate peroxidase (APX) and proteinase inhibitors (Van Loon, 1997). These enzymes also bring about liberation of molecules that elicit the initial steps in induction of resistance, phytoalexins and phenolic compounds (Van Loon et al., 1998).

Induced systemic resistance by PGPR has been achieved in large number of crops including Arabidopsis (Pieterse et al., 1996), cucumber (Wei et al., 1996), tomato (Duijff et al., 1997), potato (Doke et al., 1987), radish (Leeman et al., 1996), carnation (Van Peer et al., 1991), sugarcane (Viswanathan and Samiyappan, 1999), chilli brinjal (Bharathi et al., 2004), rice (Nandakumar et al., 2001) and mango (Vivekananthan et al., 2004) against broad spectrum of pathogens including fungi (Leeman et al., 1995), bacteria (Liu et al., 1995), nematodes (Paul and Kumar, 2003) and viruses (Kandan et al., 2005).

Seed treatment and seedling root dipping induced early and enhanced levels of PO in rice plants (Nayar, 1996). Two peroxidase isoforms were induced in the PGPR-treated rice plants inoculated with the sheath blight pathogen, R. solani (Nandakumar et al., 2001). High level expression of PO was reported in P. fluorescens P11 treated chilli plants challenged with C. capsici (Bharathi et al., 2004). Similarly, increased activity of PPO was observed in PGPR treated tomato plants challenged with F. oxysporum f.sp. lycopersici (Ramamoorthy et al., 2002).

Plants treated with Pseudomonas strains initially showed higher level of PAL compared to control (Chen et al., 2000). (Radjacommare et al., 2004) reported that seedling dip with talc based formulation of P. fluorescens induced the activity of PAL in finger millet leaves against blast disease. The inoculation of PGPR strains P. putida 89B-27 and Serratia marcescens 90-166 and the pathogen, F. oxysporum f.sp. cucumerium on separate halves of roots of cucumber seedlings exhibited that both PGPR strains induced systemic resistance against the Fusarium wilt as expressed by delayed disease symptom development and reduced number of dead plants (Liu et al., 1995). The same PGPR strains also induced systemic resistance in cucumber against bacterial angular leaf spot caused by Pseudomonas syringae pv. lachrymans (Liu et al., 1995).

Maize plants raised from P. fluorescens treated seeds showed higher activity of peroxidase, polyphenol oxidase and PAL, when leaf sheaths were inoculated with the pathogen, R. solani. The bacterized seeds with P. fluorescens lead to accumulation of higher phenolic compounds and higher activity of PO, PPO and PAL that may
play a role in defense mechanism in plants against pathogen (Sivakumar and Sharma, 2003). (Kloepper et al., 2004) also observed, control of nematode diseases in tomato and bell pepper by treatments with PGPR strains through induction of systemic resistance. (Siddiqui and Shaukat, 2002) observed that the application of PGPR strains to one half of the split root system of tomato caused a significant reduction (42%) in nematode penetration in the other half of the split root system and this was attributed to ISR activity of the strain.

(Hariprasad and Umesh, 2007) reported that PGPR application were made by seed, root and foliar spray treatments separately in combinations in field. Among the PGPR strains Bacillus subtilis strain GB3 was the most effective in providing significant suppression of bacterial spot and was well correlated with increased activity of defense related enzymes, viz. peroxidase and PAL. PGPR that were effective in greenhouse were also able to induce resistance in tomato against bacterial spot under field conditions.

3.1. BIOFORMULATIONS OF PGPR STRAINS

An important area of biological control is the development of formulations that would case for viable microbial activity for long period of time. Mass multiplication of PGPR in a suitable medium and development of a powder formulation was first carried out in 1980. A dried powder formulation of PGPR, especially is important for seed treatment and soil application. The survival of PGPR in a dried formulation and the effectiveness of methyl cellulose in a powder formulation for coating sugarbeet seed has been well documented (Suslow, 1980). A talc-based formulation of PGPR has been developed for inoculation of potato seed pieces (Kloepper and Schroth, 1981). Talc based formulation of P. fluorescens isolated from the rhizosphere of different crops has been developed (Vidhyasekaran and Muthamilan, 1995).

Root dip with P. fluorescens formulated in talc was found to be effective in reducing M. incognita and caused 40 per cent reduction in root galls under glasshouse conditions in grape vine (Mani, 1996). Glasshouse and microplot experiment with P. fluorescens strain Pf1 at 1, 2 or 4 g/plant in grape vine reduced the severity of infection by M. incognita (race 3) and enhanced root colonization by the rhizobacterium. Colonization was observed in the roots produced during second season (Shanthi et al., 1998). Biopriming of plants with some PGPB can also provide systemic resistance against a broad spectrum of plant pathogens. Diseases of fungal bacterial and viral origin and in some instances, even damage caused by insects and nematodes can be reduced after application of PGPB (Compant et al., 2005).

3. RHIZOBACTERIA IN THE MANAGEMENT OF PLANT DISEASES

PGPR are having the ability to protect above ground plant parts against fungal, bacterial and viral diseases by induced systemic resistance (ISR). (Kloepper et al., 1992) reported that among the PGPR, fluorescent pseudomonads are the most exploited bacteria for biological control of soil borne and foliar plant pathogens. In the past three decades numerous strains of fluorescent pseudomonads have been isolated from the soil and plant roots by several workers and their biocontrol activity against soil borne and foliar pathogens have been reported (Ramamoorthy et al., 2002).

Pseudomonas fluorescens isolates are effective bacterial antagonists for the management of soil borne and foliar diseases. Among the various isolates tested, P. fluorescens isolate Pf1 effectively inhibited mycelial growth of the pathogen in vitro conditions and decreased the fruit rot incidence under greenhouse conditions (Ramamoorthy and Samiyappan, 2001).

The application of biocontrol PGPR strains has given promising results in cereals, vegetables, fruit and ornamental plant production under glass house and field conditions (Raupach and Kloepper, 1998). In greenhouse and field experiments, PGPR strain B. pumilus INR-7 effectively protected pearl millet against downy mildew (Niranjan Raj et al., 2003).

PGPR mediated resistance in mango trees infected with Colletotrichum gloeosporioides significantly reduced the anthracnose infection besides enhancing fruit yield under field conditions (Vivekananthan et al., 2004). These studies clearly indicate the PGPR have diverse mechanism to operate to combat the pests and pathogens and work efficiently in both greenhouse and field conditions.

Since 1987 in China, PGPR, called yield increasing bacteria (YIB) have been largely applied in 48 different crops over 3.35 millions of hectares. In that country, productivity gains as high as 23.1% and 22.5% were obtained, respectively, in sweet potatoes and tomatoes. Additionally, remarkable 85.5% and 80.3% reduction levels of diseases caused by Xanthomonas oryzae pv. oryzae and Glomerella cingulata, respectively, were recorded (Zhang et al., 1996).

Black rot caused by Xanthomonas campestris pv. campestris (Xcc) causes severe economic losses in all developmental crucifer stages (Mariano et al., 2001). Bacillus spp. isolated from healthy cabbage, kale, and radish...
had reduced black rot incidence in kale and cabbage in greenhouse and field experiments (Assis et al., 1996). (Monteiro et al., 2005) showed that four of these Bacillus strains produced lipopeptides active against Xcc during its late growth phase. These peptide antibiotics are amphipathic compounds with surfactant activity (Zuber et al. 1993). Recently, it was demonstrated that lipopeptides can stimulate ISR in plants, probably by interacting with plant cell membranes and inducing temporary alterations in the plasma membrane which could raise plant defenses (Ogema et al., 2009).

Fusarium wilt of banana caused by Fusarium oxysporum f. sp. cubense is a very destructive disease in Brazil and other parts of the world. The rhizomes and pseudostems of infected plants used for propagation are the principal sources of inoculums and disease dispersion. Therefore, micropropagated health plantlets are used to prevent or delay the introduction of this pathogen in soils. However, these plantlets are more susceptible to this and other soilborne pathogens and should be protected before transplanting. PGPR are an alternative for improving this system. In greenhouse studies, endophytic and epiphytic bacteria applied, isolated or in mixtures, as root and substrate treatments, significantly increased the growth of micropropagated banana plantlets and controlled fusarium wilt (Mariano et al., 2004). According to (Nowak and Shulaev, 2003), the production of high-quality propagules with disease resistance may be achieved among others methods by their “in vitro” and “ex vitro” biopriming (priming with beneficial microorganisms).

Commonly, control is based on the use of single biocontrol agents. This strategy must be changed because, from the ecological point of view, the disease is part of a complex agroecosystem. As reported by (Fravel, 2007), a holistic view of this system can help take correct decisions about management. Therefore, a special approach for improving the PGPR efficiency is the use of mixtures containing different genera or species that presents additive or synergistic effects such as nitrogen-fixing bacteria and mycorrhiza helper bacteria (MHB). Another strategy is to use PGPR, mixed or alternated with fungicides, integrating biological and chemical control.

MHB are those which either assist mycorrhiza formation or promote the functioning of their symbiosis. They exist in arbuscular and ectomycorrhizal systems. MHB present three significant functions: nutrient mobilization from soil minerals, fixation of atmospheric nitrogen, and plant protection against root pathogens (Frey-Klett et al., 2007). According to these authors, PGPR induced increases in mycorrhizal root colonization from 1.1 to 17.5 fold in different interactions. Some of the MHB cited were Pseudomonas fluorescens, P. monteilii, Bacillus coagulans, B. subtilis, Paenibacillus brasiliensis, Rhizobium leguminosarum, and Bradyrhizobium japonicum.

Wheat seeds treated with different mixtures of Paenibacillus macerans and difenoconazole showed significant reduced incidences of pathogens (Luz, 2003a), and in field all treatments promoted germination and grain yield except for difenoconazole alone that increased only yield. Similar results were obtained when corn seeds were bacterized with the same bioprotector + fludioxonil + metalaxyl M (Luz, 2003b). Also Bacillus-based treatments have been successfully combined with traditional chemical seed treatments (Bugg et al., 2009). Therefore, the use of such mixtures may lead to a substantial reduction of pesticide use in several crops. It is also important to focus on the critical stages of commercialization of biocontrol agents. Screening for new agents should consider the biology and ecology of the pathosystem, as well as agricultural practices associated with the crop (Fravel, 2007).

This knowledge will help prevent variation in field performance which is responsible for lack of wider adoption of biocontrol for disease management. The formulation stage aim is to deliver the biocontrol agent in a physiologically active state to provide the needed control. The formulation must be economical and present good shelf-life and a suitable form for shipping, storage, and application. Risk assessment to human health and to the environment are needed before releasing the new product, and early in the screening; even microorganisms with good biocontrol potential but capable of growing at human body temperature should be eliminated (Fravel, 2007).

However, rhizobacteria can reduce the activity of pathogenic microorganisms not only through microbial antagonism, but also by activating the plant to better defend itself. This phenomenon, termed “induced systemic resistance” (ISR) was first described by (Van Peer et al., 1991) in carnation that was systemically protected against Fusarium oxysporum f.sp. dianthi upon treatment with strain WCS417, and by (Wei et al., 1991) in cucumber, where six out of 94 rhizobacterial strains protected the leaves against anthracnose caused by Colletotrichum orbiculare. Protection as a result of microbial antagonism was excluded because the inducing rhizobacteria and the challenging pathogens were inoculated at, and remained confined to, spatially separated parts on the same plants. Hence, the protective effect was plant-mediated. ISR confers on the plant an enhanced defensive capacity (Van Loon and Bakker, 2005).

Upon infection with a challenging pathogen this enhanced defensive capacity is manifested as a reduction in the rate of disease development, resulting in fewer diseased plants or in lesser disease severity. The induced resistance is also evident locally and sometimes does not extend systemically (Van Loon, 2000). When only local, it is difficult to prove, because the inducing bacterium and the challenging pathogen are not separated from each
other and direct antagonism is difficult to rule out. Only when specific eliciting components of the inducer are active in stimulating resistance in the plant but inactive in antagonizing the pathogen in vitro on different types of media, can locally induced resistance be inferred. Induction of resistance by live organisms always requires proof that the organisms cannot contact each other, a condition that can be met when an inducing rhizobacterium remains confined to the roots and the challenging pathogen colonizes only the leaves. Under such situations the inducing bacterium must trigger the roots to locally produce a signal that moves to the leaves to activate the enhanced defensive capacity systemically. The nature of this mobile signal has so far remained elusive.

Since its discovery, rhizobacteria-mediated ISR has been documented in at least 15 plant species (Van Loon and Bakker, 2006). Its induction has been shown to share several characteristics, but its expression can involve different physiological mechanisms. ISR can be induced by various non-pathogenic microorganisms and by some types of stress that activate the same response in the plant. In contrast to R-gene-mediated resistance, it is not specific but active against all types of pathogens, as well as against several nematodes and insects. Once induced, plants may remain protected for a considerable part of their lifetime, indicating that when the state of ISR has been triggered in the plant, it is rather stable (Van Loon et al., 1998).

Upon challenge inoculation, ISR is expressed as a result of the altered physiological state of the plant. Expression may take different forms, depending on the activity of the inducing rhizobacterium and the nature of the interaction between the pathogen and the plant (Chester, 1933). In fact, ‘induced resistance’ is an operational term to denote a condition in which a plant becomes less diseased compared to a control plant that was not induced. There are many ways in which developmental and environmental factors can influence plant-pathogen interactions. Damping-off due to infection by Pythium, Fusarium or Rhizoctonia is often confined to the seedling stage. Any condition that results in more rapid plant growth will shorten the vulnerable stage and be apparent as enhanced resistance. Rhizobacteria acting through growth promotion could protect plants through this mechanism. A similar type of ISR could occur in potato where accelerated development leads to enhanced adult plant resistance against late blight caused by Phytophthora infestans (Visker et al., 2003).

Some reports on ISR have indicated reduced symptom expression in the absence of a reduction in pathogen proliferation. This tolerance of the plant to the pathogen must have a physiological basis. Examples are the reduced damage of Pythium ultimum-infected cucumbers and lesser extent of soft rot of potato infected by Erwinia carotovora pv. carotovora upon prior treatment of the plants with ACC deaminase-containing rhizobacterial strains. By lowering the level of stress ethylene in the plant due to pathogenic attack, ACC deaminase acted synergistically with other mechanisms of biocontrol in reducing symptom development without having an effect on the population density of the pathogen (Wang et al., 2000).

Reduced disease can also be the outcome of alterations in the microbial populations in the rhizosphere as a result of altered host physiology. Numbers of resistance-inducing bacteria may be changed, or their expression of resistance-inducing traits may be altered (Mark et al., 2005). Plants commonly react to root colonization by rhizobacteria by increasing the release of exudates, and quantity and composition of root exudates vary with plant developmental stage (Phillips et al., 2004). Thus, plant growth promotion could alter root exudation. Moreover, rhizobacteria that act as minor pathogens or are perceived by the plant as a potential threat, are likely to change the rate and composition of exudates, and to increase the release of lysates. The population densities and the diversity of the root microflora may affect the number and activity of resistance-inducing rhizobacteria. Quorum sensing (QS) within and between bacterial populations is a major regulatory mechanism in bacteria to adjust their metabolism to crowded conditions or other changes in the biotic and abiotic environment (Whitehead et al., 2001). Interference with bacterial QS by host plants has been documented. Plants can produce and secrete various compounds that mimic QS signals of bacteria and, thereby, alter bacterial activities in the rhizosphere (Bauer and Mathesius, 2004). The ecological diversity and its consequences for metabolic activity of rhizosphere bacteria are only poorly known at present and deserve further investigation. Rhizobacteria can also alter plant secondary metabolism, resulting in changed plant-insect relationships. Root colonization of cucumber by four different PGPR reduced the level of cucurbitacin, which acts as a feeding stimulant to cucumber beetles (Zehnder et al., 1997).

Similar effects on insects that can transmit viruses, might reduce virus diseases through induced resistance against the insect vector rather than against the virus itself. Finally, non-pathogenic rhizobacteria may activate inducible defence mechanisms in the plant in a similar way to pathogenic microorganisms. Such mechanisms can include reinforcement of plant cell walls, production of anti-microbial phytoalexins, synthesis of pathogenesis-related proteins (PRs) (Hammond-Kosack and Jones, 1996), as well as an enhanced capacity to express these defence responses upon challenge inoculation with a pathogen, a mechanism known as ‘priming’ (Conrath et al., 2006).
Activation of defence reactions suggests that even a beneficial rhizobacterium may be perceived by the plant as a potential threat, and that such perception involves production of resistance-eliciting compounds that act mechanistically similar to elicitors produced by plant pathogenic fungi and bacteria. Both nitrogen-fixing Rhizobia in legume root nodules and vesicular-arbuscular (VA) mycorrhizal fungi in roots have been shown to activate plant host defences when the symbiotic interaction becomes unproductive (Hause and Fester, 2005). Plants possess sensitive mechanisms to perceive both fungi and bacteria through conserved components that are specific to their kingdoms and act as general elicitors. These are commonly referred to as ‘pathogen-associated molecular patterns’ (PAMPs) (Nu¨rberger and Lipke, 2005).

During compatible plant-pathogen interactions and effective symbioses, the microorganisms actively suppress defensive activities in the host (Da Cunha et al., 2006). The relationship between root-colonizing, resistance-inducing PGPR and their hosts seems substantially less intimate than with either Rhizobia or mycorrhizal fungi, but the idea that PGPR may at the same time trigger and suppress defence reactions in the host, deserves consideration.

3.2. Mechanisms involved in the AM-mediated biocontrol

Reduction in the deleterious effects of soilborne pathogens after root colonization with AM fungi was described a long time ago (Gerdemann, 1974) and has been observed on various fungi, stramenopiles, nematodes and bacteria (Whipps, 2004). Glomus mosseae in symbiosis with clover plants cv. Sonja was even able to totally prevent infection by Pythium ultimum (Carlson et al., 2008). The characteristics of this biological control regarding to its amplitude related to the pathogen/AM fungus/plant taxa association, conditions of culture, level of root colonization, time of AM/pathogen inoculation and harvest, etc. and the mechanisms hypothesized to be involved were described in various reviews (Akhtar and Siddiqui, 2009). The disease symptoms induced were even shown to be systemically reduced in non-mycorrhizal roots of plants grown in split-root systems inoculated with AM fungi (Khaosaad et al., 2007).

Various hypotheses have been put forward in an attempt to explain the AM-mediated biocontrol of soilborne phytopathogens. The fact that pathogen induced symptoms are systemically regulated by AM colonization suggests the establishment of induced systemic resistance (Pozo and Azcón-Aguilar, 2007). New isoforms of superoxide dismutases and peroxidases (Garmendia et al., 2006), PR-1 proteins (pathogenesis-related proteins type 1; Cordier et al., 1998) and higher concentrations of phenolic acids (Zhu and Zao, 2004) (ISR-related compounds) were detected in plants colonized with AM species with biocontrol activities. Accumulation of jasmonic acid involved in the rhizobacteria-mediated ISR (Pozo et al., 2004) in mycorrhizal roots (Isayenkov et al., 2005) could be related to the systemic pathogen biocontrol. Additionally, (Cordier et al., 1998) identified local cell-wall modifications such as callose accumulation around arbuscule-containing cortical cells of tomato roots.

Furthermore, the synthesis of constitutively and additional isoforms of defense related enzymes such as chininases, chitosanases, ß-1,3-glucanases, peroxidydases and superoxide dismutase has been locally detected in mycorrhizal roots (Pozo et al., 1999). Nonetheless, the level of production of these enzymes or of flavonoids was shown to be unrelated to the capacity of biocontrol of the AM species (Carlson et al., 2008). Moreover, transcript profiling and real-time quantitative PCR used to explore the transcriptional changes triggered by AM colonization revealed a complex pattern of local and systemic changes in gene expression in roots of Medicago trunculata (Liu et al., 2007) but, transcripts for defense-related proteins were only locally expressed. Furthermore, concentrations of defense related compounds such as rosmarinic and caffeic acids, phenolics and essential oils were not increased by colonization with G. mosseae protecting basil plants against Fusarium oxysporum f. sp. Basilica highlighting the role of other mechanisms in the AM-mediated biocontrol than the stimulation of systemic and localized plant defense mechanisms (Toussaint et al., 2008).

The most frequently documented response to AM colonization is an increase in phosphorus nutrition of the host plant which would consequently be more vigorous and more resistant to pathogen invasion. Nonetheless, the AM mediated biocontrol was shown to be unrelated to the soil P availability and/or the P status in plant tissues and then more dependent on other mechanisms (Toussaint et al., 2008). AM fungi would compete for space and nutrients with soilborne pathogens within the mycorrhizosphere and the host roots. (Larsen and Bødker, 2001), using signature fatty acids profiles, demonstrated the decrease in biomass and energy reserves of both G. mosseae and Aphanomyces euteiches co-occupying pea roots.

(Cordier et al., 1996) also showed that Phytophthora nicotianae and G. mosseae never occupied simultaneously the same tomato root tissues. A reduction in the extent of mycorrhizal colonization by different plant pathogens has been reported (Krishna and Bagyaraj, 1983) indicating the possible occurrence of competitive interactions. Because of this competition, the AM fungus is often inoculated before the pathogen in order to favor
biocontrol efficiency. However, F. solani f. sp. Phaseoli (Fsp) genomic DNA quantified using quantitative real time PCR was significantly reduced not only in the mycorrhizosphere and the mycosphere but also in the bulk soil of a compartmentalized soil-root system inoculated with G. intraradices (Filion et al., 2003).

The AM genomic DNA was not significantly modified by the pathogen in the soil. Reduction in Fsp growth as well as root rot symptoms as a result of colonization with G. intraradices would not be the consequence of competition for resources and habitat between the two fungi but mostly caused by the biotic and/or abiotic characteristics of the established mycorrhizosphere. The G. intraradices extraradical network has been shown to directly reduce the growth of the nematodes Radopholus similis and Pratylenchus coffeae and of conidial formation of the fungus F. o. f.sp. chrysanthemi (Foc) in root and other microorganism-free in vitro conditions (Elsen et al., 2003). However, these negative impacts were not significant for all nematode developmental stages and were unrelated to the AM fungus mycelial or spore densities (Elsen et al., 2003). Furthermore, the Foc spore germination and hyphal growth were significantly increased in presence of the AM fungus suggesting that the direct inhibition of pathogen development by AM structures would be weakly involved in biocontrol (St- Arnaud et al., 1995).

Studies on the impact of exudates from extraradical AM network or mycorrhizal roots both grown in vitro on pathogen can lead to results in contradiction. Crude extracts from G. intraradices extraradical network unambiguously reduced Foc conidia germination (Filion et al., 1999). Analogous inhibitive effects were observed with exudates liberated by strawberry roots colonized by G. etunicatum and G. monosporum on the pathogen P. fragariae sporulation (Norman and Hooker, 2000). Meanwhile, depending on the harvest time, exudates from in vitro grown tomato roots colonized with G. intraradices were repulsive or more attractive than exudates from non-AM inoculated roots to P. nicotianae zoospores (Lioussanne et al., 2008). Moreover, microconidia germination of F. o. f. sp. lycoopersici (Fol) was more than doubled in the presence of root exudates from tomato plants grown in soil and colonized with G. mosseae compared with exudates from non-mycorrhizal plants (Scheffknecht et al., 2006).

The only study of the direct impact of exudates from mycorrhizal plants in the AM mediated biocontrol directly measured in soil conditions by quantification of the capacity of root infection by the pathogen was performed by (Lioussanne et al., 2009d). Application of root exudates from tomato plants colonized with G. intraradices or G. mosseae on tomato roots had no impact on P. nicotianae intraradical growth while direct inoculation of these AM fungi significantly reduced this data suggesting that exudates from mycorrhizal plants would not directly or indirectly (through stimulation of other beneficial microorganisms) inhibit the capacity of pathogen intraradical proliferation. Furthermore, no compound antagonistic to pathogen development directly exuded by AM fungi has yet been identified.

### 3.3. The mycorrhizosphere: a zone unfavorable to pathogen development

The mycorrhizosphere has been hypothesized to constitute an environment conducive to microorganisms antagonistic to soilborne pathogen proliferation. Indeed, co-culture of the non-mycorrhizal species Dianthus caryophyllus with the mycorrhizal species Tagetes patula in presence of G. intraradices clearly reduced the disease caused by F. o. dianthi in D. caryophyllus in a manner clearly unrelated to plant nutrition which suggests a reduction in the pathogen development within the mycorrhizosphere (St-Arnaud et al., 1997). Moreover, a reduction in the number of infection loci of tomato roots pre-colonized with G. mosseae and inoculated with P. nicotianae zoospores infers that the pathogen may be affected prior to root penetration in the mycorrhizosphere (Vigo et al., 2000).

The mycorrhizosphere influenced by the rhizobacteria- AM-root tripartite association presents specific characteristics, in which each actor influences the others growth and health. Notably through the liberation of glycoproteins such as glomalin, AM fungi favor the formation of aggregates which provide stable microsites favorable to root and microbe establishment (Rillig and Mummey, 2006). The AM extraradical network also constitutes specific microsites which favor the growth of some bacteria. Among Plant growth promoting rhizobacteria (Bowen and Rovira, 1999), P-solubilizing and N-fixing-bacteria have been shown to synergistically interact with AM fungi, increasing P and N availability to the plant and promoting its growth and probably favoring its capacity to counteract pathogen impact on plant growth (Lioussanne et al., 2009b).

PGPR can also display biocontrol properties and impact pathogen proliferation through direct liberation of toxic compounds, competition for space and nutrients, reduction of Fe and Mn availability, modification of the plant hormone balance and stimulation of plant defense mechanisms (Bowen and Rovira, 1999). A synergistic or additive control of pathogen impact on plant growth by dual inoculation of AM fungi with rhizobacteria showing biocontrol properties would depend on the bacterial/fungal species combination used, the soil nutritional status and probably other environmental conditions (Barea et al., 2005).
Maximum reduction in galling and nematode multiplication causing root-rot in chick pea was observed with combined inoculation of G. intraradices with the biocontrol agents Pseudomonas straita and Rhizobium sp. (Akhtar and Siddiqui, 2008) and dual inoculation of G. mosseae with Pseudomonas fluorescens (Siddiqui and Mahmood, 1998). (Järderlund et al., 2008) showed that interactions between the two PGPR P. fluorescens SBW25 and Paenibacillus brasiliensis PB177 with G. mosseae and G. intraradices investigated on winter wheat infested with Microdochium nivale were fungal and bacterial species specific. Several studies have demonstrated that microbial antagonists to pathogens, either fungi or PGPR, do not exert any negative effect against AM fungi (Barea et al., 2005). Mycorrhization Helper Bacteria (MHB), defined by (Garbaye, 1994) as bacteria which consistently promote mycorrhizal development, would even increase AM impact on pathogens. Rhizobacteria and conditions of stimulation of mycorrhizal symbiosis have been listed by (Frey-Klett and colleagues, 2007).

4. CONCLUSION

Mycorrhiza forming species strongly modify the structure and dimension of rhizospheric microorganisms, either by direct interactions, or indirectly by influencing the release of the root exudates in rhizosphere. The mycorrhizae exercise, generally, a strong selective pressure on rhizospheric habitats, stimulating the development of mutualistic or comensal microbiota. The mycorrhizae influence all the relations established between different categories of organisms in rhizospheric microhabitats under late successional stages, and in young rhizospheric microhabitats the myorrhizations success depends on the microbial community already established. The plant benefits from all of mutualistic relations established between mycorrhizal species and the soil organisms, while the fungal partner often competes with different soil organisms for the plant carbohydrates. The elucidation of the intimate mechanisms that underline the structure of microbial community and the processes that influence the mycorrhizal intensity and rate are premises in the elaboration of the efficient ecological reconstruction strategies or for the sustainable agriculture development. There are needed some extensive researches concerning signal phase prior to tripartite mutualistic relations development and the involved factors, in order to use and optimize them in the purpose of integrated pest management strategies development.

From these results we concluded that interaction between hormones and AM fungi signals and PGPR mediated the expression of the majority of different PR-proteins leading to increasing defense mechanism against diseases infection. Thus, reduction in disease symptoms and enhancing in growth and metabolic activities in crop plants treated with AM fungi and/or hormonal elicitors and PGPR might be related to its roles in the activation of biochemical and structural defense systems that helps word off the spread of pathogen and consequently increase crop production. Finally, the new mechanism of the combination strategy between bioagent and hormonal signals (either synergistically or antagonistically) played important role for altering expression of defense genes leading to different PR-proteins and also working together to increased resistance in crop plants against diseases.

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