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Review

What we know about arbuscular mycorhizal fungi and associated soil bacteria

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Mycorrhizal fungi are common soil microorganisms and are well known for their symbiotic association with the roots of host plants. The soil is a complex environment harbouring a wide diversity of microorganisms. The interaction between soil bacteria and arbuscular mycorrhizal fungi has been shown in several studies to be both beneficial in terms of mycorrhizal establishment and as well as plant growth promotion. This has resulted in groups of bacteria being functionally termed Mycorrhizal Helper Bacteria, Phosphate Solubilising Bacteria and Plant Growth Promoting Rhizobacteria. Several of these groups overlap and in such a complex environment, it is likely that the combinations of microorganisms interacting with arbuscular mycorrhizal fungi enhance the benefits that are attributed to the relationship. Many different microorganisms inhabit the soil. This review will focus on the bacterial interactions and their potential use in agricultural biotechnology.

Key words: Mycorrhizal fungi, bacteria, soil, microorganisms, growth.

INTRODUCTION

Arbuscular mycorrhizal (AM) fungi are obligate biotrophs and associate with the roots of approximately 80% of all plant species. The AM fungi were named because of the finely branched hyphal structures 'arbuscules' that occur within root cortical cells. These are responsible for the exchange of carbon which is required by the AM fungi for energy, and nutrients from the soil needed by the plants (Smith and Read, 2008). The AM associations provide many benefits to their host and the soil environment which includes enhanced nutrient uptake, increased tolerance to drought and root pathogens, and improved soil aggregation (Bago and Bécard, 2002; Finlay, 2004; Smith and Read, 2008).

Nutrients present in the soil are required by plants in varying amounts. The uptake of inorganic nutrients from the root zone creates a depletion zone limiting nutrient uptake by non-mycorrhizal plants but gives mycorrhizal plants a greater advantage as the extraradical hyphal network can increase the surface area available for uptake as well as enhance mobilization (Sylvia and Zuberer, 2001; Smith and Read, 2008; Li et al., 1991).

Macronutrients like nitrogen and phosphorous may be in forms or niches inaccessible to plant roots. Phosphorus is immobile occurring mainly in organic or complex inorganic forms. The AM fungi aid in uptake by secreting phosphatase enzymes into the soil environment which hydrolyses and releases phosphorus facilitating its absorption by extraradical hyphae and translocation to the host plant (Schachtman et al., 1998). Amino acids, peptides, ions (NO_3^-, NH_4^+) and recalcitrant organic compounds are all forms of nitrogen found in the soil. The extraradical hyphae of different *Glomus* sp can assimilate and metabolise both organic and inorganic sources of nitrogen by glutamate synthetase activity (Li et al., 1991).

Pathogenic microorganisms are a major threat affecting plant health and ecosystem stability (Azcon-Aguilar and Barea, 1996). AM fungal colonization of plant roots increases the plants' tolerance to pathogens acting as biological control agents. Reviews on the subject have focused on mechanisms of interaction such as enhanced nutrition, competition, morphological changes, induced plant defence mechanisms and reduced infection sites (Hooker et al., 1994; Azcon-Aguilar and Barea, 1996).

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Ozgonen and Erkilic (2007) investigated growth enhancement by AM fungi in pepper (*Capsicum annuum*) challenged by *Phytophthora* blight (*P.capsici*). Mycorrhizal plants showed significantly increased shoot height and biomass when compared to uninoculated controls. *Gigasopora margarita* had the greatest effect on shoot and root dry weight, increasing them by 34 and 59% respectively. Inoculation with AM fungi reduced *P. capsici* disease severity in pepper plants under field conditions by 57%. The concentration of capsidiol in inoculated pepper plants was increased from 12.5 to 40.3µg.g^{-1} fresh weight. These results indicated that mycorrhizal inoculation not only enhanced plant growth but also stimulated the production of capsidiol, a phytoalexin produced as a plant defence mechanism.

RHIZOSPHERE MICROORGANISMS

The soil is a complex environment comprising a diverse range of microorganisms. Mycorrhizal fungi are critical soil microorganisms providing a direct link between plant roots and soil. AM fungal hyphae may directly interact with other soil microorganisms, providing a means of transport in the soil, substrates required for growth as well as a suitable niche environment. These interactions can affect root development and plant growth performance (Johansson et al., 2004). Mycorrhizal formation can either directly or indirectly affect microbial communities through induced changes of root exudates composition, transport of carbon compounds or fungal exudation of stimulatory or inhibitory compounds (Gryndler, 2000). Mycorrhizal fungi interact with beneficial soil organisms such as Mycorrhizal Helper Bacteria (MHB), Phosphate Solubilising Bacteria (PSB) and Plant Growth Promoting Rhizobacteria (PGPR) (Gryndler, 2000). These groupings are functional with several overlapping bacterial genera.

MYCORRHIZAL HELPER BACTERIA

MHB specifically promote the formation of the mycorrhizal symbiosis by stimulating the extension of the mycelia, increasing root-fungus contact and colonization and reducing adverse environmental conditions. MHB may enhance spore germination and the growth of mycelia by producing growth factors, detoxifying antagonistic substances or by inhibiting competitors (Garbaye, 1994). Gram-negative Proteobacteria (*Agrobacterium, Azospirillum, and Pseudomonas*), Gram-positive Firmicutes (*Bacillus, Brevibacillus* and *Paenibacillus)* and Gram-positive Actinomycetes (*Rhodococcus, Streptomyces, and Arthrobacter*) have all been showed to have mycorrhizal helper properties (Frey-Klett et al., 2007).

Rhizobium produces 1-aminocyclopropane-1-carboxylate (ACC) deaminase which modulates ethylene levels in the plant, increasing the tolerance of the plant to environmental stress and stimulating nodulation (Ma et al., 2002). This compound also produced by *Pseudomonas putida* UW4 promoted mycorrhization by *Gigaspora rosea* when inoculated onto cucumber plants (Gamalero et al., 2008).

PLANT GROWTH PROMOTING RHIZOBACTERIA

Rhizospheric bacteria are known to stimulate plant growth, through direct or indirect interactions with the plant roots. These bacteria have been termed Plant Growth Promoting Rhizobacteria (PGPR) (Bloemberg and Lugtenberg, 2001). Interactions between the AM fungi, bacteria and plants occur in the zone of soil surrounding the roots and hyphal network known as the “mycorrhizosphere”. PGPR mainly belong to the genera *Paenibacillus, Burkholderia, Pseudomonas* and *Bacillus* sp (Vessey, 2003; Martinez-Viveros et al., 2010).

Direct positive mechanisms include the production of phytohormones and plant growth auxins such as indole acetic acid (IAA), nitrogen fixation and the solubilisation of phosphorous. Indirect mechanisms include ability to decrease or prevent any deleterious effects of pathogenic microorganisms through the bacterial production of antimicrobial compounds or siderophores (Singh and Kapoor, 1998).

PGPR have a strong stimulatory effect on the growth of AM fungi. Increased mycelial growth from *Glomus mosseae* spores caused by an unidentified PGPR suggests that co-inoculation can be employed to optimize the formation and functioning of the AM fungal symbiosis (Gryndler, 2000).

Phosphate solubilising bacteria

Phosphorous is an essential macronutrient required for growth and development by plants. Many soil bacteria mobilize phosphate ions from organic and inorganic phosphorous sources such as tricalcium phosphate, hydroxyapatite and rock phosphate (Gryndler, 2000; Vessey, 2003; Richardson et al., 2009; Martinez-Viveros et al., 2010). Phosphate solubilised by these bacteria, are taken up more efficiently by the plant through a mycorrhizal-mediated channel between the plant roots and surrounding soil (Rodriguez and Fraga, 1999). Strains of *Pseudomonas, Bacillus* and *Rhizobium* are among the most powerful phosphate solubilisers (Rodriguez and Fraga, 1999; Martinez-Viveros et al., 2010; Suresh et al., 2010). Singh and Kapoor (1998) showed that co-inoculation with *Bacillus circulans*, a phosphate solubiliser, and AM fungi significantly increased plant yield and phosphorous uptake in wheat.

Phosphate solubilisation is as a result of the action of

bacterial producing organic acids, particularly gluconic acid and 2-ketogluconic acid (Khan et al., 2009). Production of chelating substances or inorganic acids such as sulphidric, nitric and carbonic acid may also contribute to the process (Rodriguez and Fraga, 1999; Vessey, 2003; Richardson et al., 2009; Martinez-Viveros et al., 2010).

Organic phosphate sources are mineralised by the action of several phosphatase enzymes. Phosphatase activity involves the hydrolysis of phosphor-ester or phosphor-anhydride bonds, thereby catalysing the bound phosphorous into inorganic phosphorous (Rodriguez and Fraga, 1999; Richardson et al., 2009; Martinez-Viveros et al., 2010). Phytate (Myo-inositol hexakis-phosphate) constitutes 80% complexed inorganic phosphorous in the soil making it one of the most abundant sources of phosphorous for plants (Lim et al., 2007). Several PGPR (*Bacillus, Burkholderia, Pseudomonas, Serratia* and *Staphylococcus*) produce the enzyme phytase, which degrades phytate to lower phosphate esters (Hariprasad and Niranjana, 2009).

Hariprasad and Niranjana (2009) showed that an *Enterobacter* sp. which was able to solubilise calcium phosphate through the production of gluconic acid significantly increased growth of tomato (*Lycopersicon esculentum*). Fernandez et al. (2007) investigated the influence of phosphate solubilising ability of bacterial isolates on soybean (*Glycine max*) growth under greenhouse conditions. Inoculation with *Burkolderia* significantly increased plant height by 40%.

Another study by Akhtar and Siddiqui (2009) examined the effects of phosphate solubilising bacteria on the growth of chickpea (*Cicer arietinum*) under field conditions. Results indicated that *Paenibacillus polymyxa*, *Pseudomonas putida*, *Pseudomonas alcaligenes* and *Pseudomonas aeruginosa* significantly increased shoot dry weight, seed weight and yield with *P. polymyxa* having the greatest effect. Canbolat et al. (2006) examined the effects of PGPR on barley (*Hordeum vulgare*) seedling growth. Four *Bacillus* isolates all solubilised phosphate. Available phosphate in the soil was significantly increased by seed inoculation with two of these isolates. The isolates also increased root and shoot weights.

Nitrogen fixation

Nitrogen is an essential plant nutrient. Symbiotic and non-symbiotic nitrogen fixation is a function of some PGPR. Non-symbiotic nitrogen fixation is carried out by free-living diazotrophs and can stimulate non-legume plant growth. These bacteria belong to the genera *Azoarcus, Azospirillum, Burkholderia, Gluconacetobacter* and *Pseudomonas* (Antoun and Prevost, 2005; Richardson et al., 2009; Martinez-Viveros et al., 2010). Symbiotic nitrogen fixers including *Rhizobium,* develop symbiotic relationships with legume plants and convert atmospheric N_2 to an inorganic form within nodules, providing 90% of the nitrogen requirements of the plant. Endophytic diazotrophs appear to have an advantage over root-surface organisms since they are capable of colonising the interior of roots and establish themselves within niches that are more conducive to effective N_2 fixation, transferring the fixed nitrogen to the host plants. In addition to their potential for supplying nitrogen through N_2 fixation to the host plants they may also promote plant growth through various other mechanisms such as phytohormone production (Richardson et al., 2009).

Phytohormone production

PGPR can have an influence on plant growth through the production of phytohormones such as auxins, cytokinins and gibberellins. Auxins contribute to the endogenous pool of phytohormones produced by the plant (Martinez-Viveros et al., 2010). The production of indole acetic acid (IAA) has been shown to be widespread among PGPR (Xie et al., 1996; Patten and Glick, 2002) and is predominantly synthesized by an alternate tryptophan-dependant pathway which is carried out through indole-pyruvic acid. The role of IAA produced by the PGPR in plant growth is still undetermined. IAA in plants is the main auxin which controls many important physiological processes including cell enlargement and division, tissue differentiation and responses to light and gravity (Patten and Glick, 2002; Spaepen et al., 2007; Shahab et al., 2009; Martinez-Viveros et al., 2010). Therefore, PGPR which produce IAA have the potential to interact with any of the fore-mentioned processes. IAA produced by PGPR can promote root growth (Spaepen et al., 2007), subsequently increasing mycorrhizal contact (Garbaye, 1994). PGPR which produce IAA belong to the following genera: *Aeromonas, Bacillus, Burkholderia, Enterobacter, Pseudomonas* and *Rhizobium* (Martinez-Viveros et al., 2010).

Rapid establishment of roots can be achieved either by the elongation of primary roots or by the proliferation of lateral and adventitious roots. This is advantageous for young seedlings as it increases their stability in the soil and survival through rapid access to water and nutrients (Patten and Glick, 2002). Dobbelaere et al. (1999) showed that increased rooting was directly related to IAA synthesis by *Azospirillum*. Increased plant mineral uptake and root exudation in turn stimulated bacterial colonisation further enhancing the inoculation effect. Patten and Glick (2002) showed that low concentrations of bacterial produced IAA stimulated primary root elongation. High IAA concentrations stimulated the formation of lateral and adventitious roots. IAA produced by PGPR can therefore have many beneficial influences on plant growth by altering root development. Shahab et al. (2009) investigated two IAA producing strains of *Bacillus*

thuringensis and *Pseudomonas aeruginosa* inoculated onto mung beans (*Vignia radiate)* in greenhouse experiments. The *P. aeruginosa* isolate showed the most significant root and shoot effects, suggesting a direct effect on metabolic processes. Development of lateral roots and increased root hair proliferation increased the surface area available for nutrient uptake and increased shoot and root growth (Shahab et al., 2009).

Cytokinins are phytohormones which promote cell division and enlargement, tissue expansion and root hair development. Cytokinin production has been shown in various PGPR including *Azospirillum, Pseudomonas fluorescens* and *Paenibacillus polymyxa* (Madhaiyan et al., 2010). Gibberellins enhance the development of plant tissues, particularly stem tissue and promote root elongation and lateral root extension. Production of gibberellins has been reported in *Azospirillum, Bacillus punnilus, Bacillus licheniformis* and *Rhizobium* (Vessey, 2003; Martinez-Viveros et al., 2010).

Ethylene effects plant growth by inhibiting root elongation. Plants produce 1-aminocyclopropane-1-carboxylate (ACC) which is the precursor for ethylene. Some ACC is released into the soil and reabsorbed by the roots, which leads to diminished root growth. Some PGPR have the ability to synthesize ACC deaminase, an enzyme which cleaves ACC which thereby decreases ethylene production, promoting root lengthening. ACC deaminase activity has been reported in the genera *Achromobacter, Azospirillum, Bacillus* and *Pseudomonas* (Vessey, 2003; Martinez-Viveros et al., 2010.

Madhaiyan et al. (2010) studied the effect of co-inoculations of *Methylobacterium oryzae* with *Azospirillum brasilense* and *Burkholderia pyrrocinia* on the growth of tomato (*Lycopersicon esculentum*), red pepper (*Capsicum annum*) and rice (*Oryza sativa*). Results showed that *M. oryzae* through the production of phytohormones such as IAA and cytokinins improved plant growth. Other mechanisms such ACC deaminase and the production of siderophores have also been documented. *Azospirillum* is a known nitrogen fixer and a producer of IAA whereas *Burkholderia* has been shown to solubilise phosphate and have ACC deaminase activity. Under greenhouse conditions, there was a significant increase in all plant growth parameters by the bacterial isolates compared to the non-inoculated control plants. In tomato, individual inoculation of *M.oryzae* or its co-inoculation with *A. brasilense* / *B. pyrrocinia* produced significant increases in root length compared to control or individual inoculations. In red peppers, inoculation with *M.oryzae* produced the greatest root and shoot lengths while a greater root and shoot growth was found with the dual inoculation of *M.oryzae* with *B. pyrrocinia*. In rice, no significant increases in root length were recorded. Cytokinins produced by *M.oryzae* may enhance stomatal opening and promote cell division in the presence of auxins resulting in an enhanced uptake of water and other nutrients from the soil. Thus cytokinin and IAA production by *M.oryzae* may have a positive effect on plant growth (Madhaiyan et al., 2010).

Mena-Violante and Olalde-Portugal (2007) showed in a greenhouse trial that inoculation of tomato with *Bacillus subtilis* significantly increased root dry weight and root length by 18 to 26% and 13 to 15%, respectively in two experiments. Yield per plant was increased by 21 to 25% and fruit weight and length was significantly greater. These significant effects were attributed to the production of hormones, which are believed to change assimilate partitioning patterns in plants, altering growth in roots, fructification process and development of fruit.

Effects of floral and foliar inoculation of *Pseudomonas* and *Bacillus* rhizobacteria on the growth of sweet cherry (*Prunus avium* L.) was investigated by Esitken et al. (2006). *Pseudomonas* produces transzeatin and *Bacillus* has the ability to fix nitrogen and produce IAA. The bacterial treatments alone and in combination significantly affected to varying degrees yield per trunk cross-section area, fruit weight and shoot length. This indicates that these PGPR are not restricted to the soil environment, application to above plant parts has great potential for commercial applications.

A similar study by Orhan et al. (2006) examined the effects of two *Bacillus* isolates, both of which had nitrogen fixing properties and one with phosphate solubilising capabilities on the growth of raspberry. A significant 75% increase in yield was achieved with co-inoculation of the two isolates. The authors also reported increased N and P content of rapsberry leaves, and a decrease in pH of the soil, due to the production of organic acids. Similar significant yield increases have also been reported in apple (*Malus domestica* L.) cv Granny Smith when co-inoculated with *Bacillus* and *Microbacterium* (Karlidag et al., 2007).

Banchio et al. (2008) demonstrated improved plant growth and essential oils composition in *Origanum majorana* L. by the PGPR strains *Pseudomonas fluorescens, Bacillus subtilis, Sinorhizobium meliloti,* and *Bradyrhizobium* sp. Inoculation with *P. fluorescens* or *Bradyrhizobium* sp. induced significant increases in number of leaves, shoot length, and number of nodes. Leaf number was 80% higher in *P. fluorescens* inoculated plants resulting in a 3.2-fold increase in shoot fresh weight. Plants inoculated with *P. fluorescens* or *Bradyrhizobium* showed significant increase in total essential oil yield, 24 - and 10-fold, respectively.

Pathogen inhibition

PGPR have been shown to mediate in the biological control of plant pathogens. The mechanisms involved can be direct via the production of antibiotics, siderophores, hydrogen cyanide, hydrolytic enzymes (chitinases, proteases and cellulases) or indirectly by competition with the pathogen for ecological niches such as infection and

nutrient sites (Linderman, 2000; Bloemberg and Lugtenberg, 2001; Sharma and Johri, 2002).

PGPR have been shown to produce various antibiotics effective against phytopathogens under laboratory conditions. These antibiotics include butyrolactones, zwittermycin A, kanosamine and 2.4-diacteylphloroglucinol (2, 4-DAPG). 2, 4-DAPG is one of the most efficient antibiotics and is produced by *Pseudomonas* strains. It has a wide spectrum including being an antifungal, antibacterial and antihelmintic (Whipps, 2001; Martinez-Viveros et al., 2010). Some PGPR such as *Alcaligenes, Aeromonas, Bacillus, Pseudomonas* and *Rhizobium* are capable of producing hydrogen cyanide (HCN), a volatile secondary metabolite which suppresses the development of other microbes (Whipps, 2001; Martinez-Viveros et al., 2010).

Iron is an essential element required for growth in all organisms and bioavailable iron in the soil is deficient. Under iron-limiting environments, PGPR produce siderophores, low molecular weight compounds which competitively sequesters ferric iron. The bacterium, takes up the iron-siderophore complex through specific receptors specific on the outer cell membrane. Once inside the bacterium, the iron is released and available to support microbial growth (Siddiqui, 2005). The siderophores deprive pathogenic fungi of the available iron in the soil as the PGPR siderophores have a greater affinity for the iron. Some PGPR can sequester iron from heterologous siderophores produced by other soil microorganisms. Siderophore producing bacteria have been found to belong to *Bradyrhizobium, Pseudomonas, Rhizobium, Serratia,* and *Streptomyces* (Martinez-Viveros et al., 2010).

The root surface and its surrounding rhizosphere are significant sources of carbon. Therefore, along the surfaces of the roots there are a variety of nutrient rich niches which attracts a wide range of microorganisms, including phytopathogens. Competition for these nutrient niches is one of the major mechanisms by which PGPR protect the plant from pathogens. PGPR have the ability to reach the surfaces of the roots through active motility by their flagella and are guided by chemotrophic responses. They are also carried by mycorrhizal hyphal network (Compant et al., 2005).

ENDOSYMBIOTIC BACTERIA OF AM FUNGI

Endocellular bacteria are reported to be found only in a few fungi including AM fungi. The cytoplasm of AM fungi contains many bacteria-like organisms. Microscopy revealed these bacterial cells as Gram-negative and rod shaped, occurring singly or in groups, often inside fungal vacuoles in both spores and hyphae and have been described as being related to *Burkholderia* and were placed in a new unculturable taxon named '*Candidatus Glomeribacter Gigasporarum*'(Bianciotto and Bonfante, 2002; Bonfante and Anca, 2009).

The functional significance of these endosymbionts is unclear but they are thought to affect AM fungal performance through the release of substances which affect fungal gene expression, introduction of chemical compounds into the spores stimulating germination, increasing fungal attachment by producing lectins and degradation of fungal cell walls (Artursson et al., 2006; Bonfante and Anca, 2009; Miransari, 2011).

Endosymbiotic bacterial genes have been partially identified, some of which are involved in nutrient uptake, such as a putative phosphate transporter operon, *pst,* a gene involved in colonisation events by bacterial cells, *vac* and nitrogenase coding genes, *nif* (Bianciotto and Bonfante, 2002).

INTERACTIONS BETWEEN AM FUNGI AND RHIZOSPHERE MICRO-ORGANISMS

The use of AM fungi to enhance plant growth and yield of various crops is gaining importance. The interactions between AM fungi and other rhizosphere micro-organisms therefore have the potential to synergistically enhance crop production. Several studies have been carried out to analyse the interactions between AM fungi and rhizosphere micro-organisms.

Interactions between AM fungi and MHB

Studies investigating the interactions between AM fungi and MHB on plant growth have shown that MHB increase AM fungal colonisation in the plant roots. Mamatha et al. (2002) investigated the interactions between AM fungi and *Bacillus coagulans* in field established mulberry and papaya plants. Mulberry plants inoculated with *Glomus fasciculatum* showed a significant increase in plant height and number of leaves and in papaya plants inoculated with *Glomus mosseae* and *Glomus caledonium* a significant increase in plant height and and stem girth compared with the control given 100% recommended P. There was no significant difference in plant growth parameters between treatments with the AM fungi alone or the AM fungi with *Bacillus coagulans*. Mycorrhizal colonisation however, was highest in plants inoculated with the AM fungi and *B.coagulans*, a possible mechanism here may be that MHB produce hydrolytic enzymes which cause the cortical cells to dilate, providing a larger intercellular surface area with which the AM fungi can penetrate and colonise more easily, increasing the percentage root colonisation, thereby providing more nutrients to the plant (Mamatha et al., 2002).

Interactions between AM fungi and PGPR

The improvement of plant growth and nutrition through

the synergistic interaction between AM fungi and PGPR has been described in several studies. In P-deficient soils, phosphate-solubilising micro-organisms release phosphate ions which are transferred by the AM fungi to the plant (Artursson et al., 2006).

Khan and Zaidi (2007) examined the co-inoculation of a nitrogen-fixing (*Azotobacter chroococcum*), a phosphate-solubilisng bacterium (*Bacillus sp.*), and *Glomus fasciculatum* on the growth of wheat (*Triticum aestivum L.*). The dual inoculations of *A.chroococcum* and *Bacillus*; *A. chroococcum* and *G. fasciculatum*; and *Bacillus* and *G. fasciculatum* increased dry matter significantly. The co-inoculation of *Bacillus* and *G. fasciculatum* enhanced dry matter accumulation in roots, shoots and whole plants by 1.7, 1.5 and 1.6-fold, respectively and was superior to other single or dual inoculation treatments. The triple inoculation of *A.chroococcum, Bacillus* and *G. fasciculatum* increased total dry matter and doubled the grain yield of wheat. Increased number of AM spores and percentage root colonisation was also recorded. The results were attributed to solubilisation of inorganic phosphate by *Bacillus*. *A.chroococcum* is a phyto-stimulator as well as nitrogen-fixer, providing plant growth promoting substances such as hormones (Khan and Zaidi, 2007).

Bharadwaj et al. (2008) investigated the effects of the AM fungal spore-associated *Pseudomonas putida* biotype A on potato (*Solanum tuberosum L.)* growth. The bacteria was shown to solubilises phosphate and produce IAA and significantly increased the number of primary roots by 100%, the number of lateral roots by 65% and root length by 76%, shoot length by 73% and the number of leaves by 81%. This isolate also increased the root colonisation by *G. mosseae.* Gamalero et al. (2004) investigated the impact of two pseudomonads (*Pseudomonas fluorescens* 92rk and *Pseudomonas fluorescens* P190r) and *G. mosseae* on tomato (*Lycopersicon esculentum* Mill.) plant growth. *Pseudomonas fluorescens* 92rk increased mycorrhizal colonisation by 41%. *Pseudomonas fluorescens* 92rk and *Pseudomonas fluorescens* P190r significantly increased both the shoot and root fresh weights whereas *G.mosseae* alone increased the shoot fresh weights. Co-inoculation of 92rk and *G. mosseae* induced significant increases in shoot fresh weight. Co-inoculation of all three microorganism increased shoot and root fresh weights relative to all other treatments.

Khan and Zaidi (2006) investigated interactions between *Bacillus subtilis*, *Bradyrhizobium sp.* and *Glomus fasciculatum* on greengram (*Vignia radiata* (L.) Wilczek). Dual inoculation of *G. fasciculatum* and *B. subtilis* significantly increased the root length at the flowering stage. The most significant inoculation combination was that of *Bradyrhizobium, G. fasciculatum* and *B. subtilis* which increased the dry matter production significantly by 200 and 183% at flowering and harvest stages respectively. The more efficient use of P through the interaction with *Bacillus* enhances nitrogen fixation which is highly dependant on P. Plant growth and yield of greengram plants was therefore increased.

Kohler et al. (2007) studied the interactions between a *B. subtilis* and *Glomus intraradices* and their effects on lettuce (*Latuca sativa*). Dual applications had the highest effect (77%) on shoot biomass and this was attributed to an enhanced P and K nutrition. *B. subtilis* has been shown to be a phosphate- and potassium-solubilising rhizobacterium releasing these nutrients from silicates in the soil which are than translocated by extra-radical AM hyphae and transferred to the crop plant (Kohler et al., 2007; Rodriguez and Fraga, 1999).

Mar Vazquez et al. (2000) inoculated maize (*Zea mays* L.) with *Azospirillum brasilense,* known to produce IAA and was found to have a significant increase in shoot and root dry weight in the dual inoculation with *Glomus deserticola.* They confirmed the ability of growth promoting substances to stimulate plant susceptibility to mycorrhizal colonisation, enhance spore germination and mycelial growth, which in turn increased the chance of contact between fungal hyphae and plant roots, indicating a functional compatibility between saprotrophic and symbiotic micro-organisms.

Medina et al. (2003) similarly investigated interactions between *G. mosseae, G. intraradices* and *G. deserticola* and *Bacillus pumillus* and *Bacillus licheniformis* on alfalfa plants (*Medicago sativa)*. *B. pumillus* and *B. licheniformis* produce IAA and gibberellins respectively. Single bacterium treatments did not have an effect on plant growth parameters. *G.intraradices* and *G. deserticola* increased shoot weight. *G. deserticola* and *B. pumillus* was the most efficient treatment resulting in 715% increase in shoot weight and 190% increase in root length.

CONCLUSION

Interactions between AM fungi, PGPR and P solubising bacteria occur naturally since they share common habitats such as the root surface (Barea et al., 2004). It is well known from the many studies cited that these interactions increase plant growth through several mechanisms carried out by both the AM fungi and the bacteria (Antoun and Prevost, 2005; Miransari, 2011). In combination this has a beneficial effect on plant growth and health. The challenge in agrobiotechnology is harnessing these interactions either through promotion of bacterial growth in the soil or through the development and application of inoculants. These inoculants can be applied separately or formulations of effecitive multiagents combined with AM fungi should be further investigated. Harnessing the soil microbial communities is required in order to substantially enhance crop production with reduced chemical inputs and environmental damage.

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