Soil Environ. 35(2): 106-145, 2016
www.se.org.pk
Online ISSN: 2075-1141
Print ISSN: 2074-9546

Potential, limitations and future prospects of *Pseudomonas* spp. for sustainable agriculture and environment: A Review

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Abstract

Plant growth promoting rhizobacteria (PGPR) are well known microbial community by virtue of their fabulous growth promoting abilities in plants. Among various genera of PGPR including Bacillus, Enterobacter, Klebsiella and Azospirillum, Pseudomonas spp. attain special attention due to its distinctive traits like better root colonization, production of osmolytes, polysaccharides and phytohormones, bearing specific enzymes, stress adaptation abilities and positive interactions with other microbial communities. In spite of a number of scientific publications indicating their significant performance in sustainable agriculture there are also certain uncertainties about the consistent performance of this naturally occurring population, the controversial reports about certain traits of Pseudomonas put a sign of interrogation on their application on commercial scale. To the best of our knowledge, no comprehensive review is available that presents positive and negative impacts of Pseudomonas inoculation on plant growth as well as on soil environment in detail. Present review has been undertaken to discuss the competitive advantage of Pseudomonas spp. over other microbial populations and identify the most important aspects which could be helpful for enhancing plant growth and eliminating the environmental hazards. Also, the areas needing further input about the practical application of these species in the field have been discussed.

Keywords: PGPR, phytohormones, biosurfactants, benefits, limitation, environment

Soil microorganisms are very important naturally occurring population that play significant role in soil fertility, plant growth and maintaining healthier environment. This microbial population may comprise number of microorganisms like bacteria, actinomycetes, cyanobacteria and fungi. Some of these are considered efficient owing to their growth enhancing abilities. Among these naturally occurring populations, plant growth promoting rhizobacteria (PGPR) have been studied extensively due to their optimistic effect on plant growth and protecting the environment from various hazards.

PGPR are free living bacteria that promote plant growth by root colonization (Kloepper et al.1989). These are also termed as plant health promoting bacteria or nodule promoting bacteria (Hayat et al., 2010) and can be categorized as intracellular (iPGPR) and extracellular PGPR (ePGPR) on the basis of their residing sites (Gray and Smith, 2005). Plant growth promotion by PGPR takes place by a number of direct and indirect mechanisms which have been discussed by various workers (Vessey, 2003; Zahir et al., 2004; Podile and Kishore, 2006; Nadeem et al., 2010b; Singh et al., 2011). These growth promoting traits/mechanisms may differ among different genera and even within species of the same genera. However, three general ways by which PGPR promote the plant growth and development include; synthesizing a particular compound, facilitating the nutrient uptake and inducing resistance against diseases (Zahir et al., 2004; Cakmakci et al. 2006; Saravankumar et al., 2009). Although the mechanisms of growth promotion by PGPR are not yet fully understood (Dey et al., 2004), they play a potential role for enhancing crop production on sustainable basis (Shoebitz et al., 2009; Singh et al., 2011).

The PGPR strains proving helpful for enhancing plant growth belong to different genera and some of the important genera include *Azospirillum*, *Pseudomonas*, *Enterobacter*, *Bacillus*, *Serratia*, *Burkholderia*, *Variovorax* and *Klebsiella* (Glick, 1995; Podile and Kishore, 2006; Dardanelli et al., 2009; Nadeem et al., 2010). Among these, *Pseudomonas* which show their abundant presence in rhizosphere (Muleta et al., 2009) attract major attention due to their outstanding growth promoting characteristics like better root colonization, production of enzymes and metabolites, nutrient solubilization, indole acetic acid and siderophores production, acting as biocontrol agent and inducing systemic resistance against diseases (Kloepper et al., 1989; Glick and Bashan, 1997; Ramamoorthy et al., 2001; Podile and Kishore, 2006; Saharan and Nehra, 2011).

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Poonguzhali et al. (2006) found *Pseudomonas* and *Bacillus* spp. as dominant species in the cabbage rhizosphere under fertilized conditions. They found that most of these species carried phosphate solubilization ability and ACC-deaminase enzyme. In an earlier study, Brand (2000) found *Pseudomonas* as a dominant strain followed by *Bacillus*. The rhizosphere soil samples from *Chamaecytisus proliferus* showed a diverse community of many gram negative bacteria dominated by *Pseudomonas*, *Burkholderia* and *Sphingomonas* spp. (Donate-Correa et al., 2005). They demonstrated that among these, *Pseudomonas fluorescens* could be a suitable microorganism for field application owing to its well defined growth promoting traits. Several studies performed and reviewed by different scientists indicate marvelous effectiveness of *Pseudomonas* spp. inoculation for promoting plant growth under normal (Zahir et al., 2004; Cummings, 2009; Hayat et al., 2010) as well as stress environment (Stockwell and Loper, 2005; Glick et al., 2007; Nadeem et al., 2010b; Glick, 2010). This tremendous performance of *Pseudomonas* ssp. was due to their particular characteristics and environmental friendly traits which enable them to survive under stress conditions and exhibit their potential regarding agricultural and environmental issue.

In spite of well established and verified work that showed the valuable performance of *Pseudomonas* spp. for enhancing plant growth and development, there are certain notable reports which question the commercial use of these strains. For example, the production of cyanide by *Pseudomonas* has positive as well as negative impact on plant growth (Saharan and Nehra, 2011). On one hand, it acts as biocontrol agent against certain plant pathogens, while on the other hand, it is reported as growth inhibitor trait of bacteria (Schippers et al., 1990; Heydari et al., 2008). Similarly, phytohormone auxin produced by number of *Pseudomonas* spp. plays dual role in plant growth by enhancing root elongation at low concentration (Patten and Glick, 2002; Egamberdieva, 2010) while inhibits elongation at high concentration (Arshad and Frankerberger, 1991; Xie et al., 1996). Presence of ACC-deaminase enzyme reduces the negative impact of stress-induced ethylene on growth by reducing its concentration (Mayak et al., 2004a,b; Glick et al., 2007) however, reduction in ethylene level has been reported to reduce the seedling germination and emergence (Petruzzelli et al., 2000; Chaudhuri and Kar, 2008). The production of biosurfactants by *Pseudomonas* spp. is an effective environmental trait (Satpute et al., 2010; Darvishi et al., 2011).

The *P. aeruginosa* is a well known biosurfactants producing strain. The biosurfactants produced by this strain are effective in environmental science in a number of ways (Pacwa-Płociniczak et al., 2011; Chaprao et al. 2015). It also has biocontrol potential owing to production of antifungal metabolites (Bakthavatchalu et al., 2013). In spite of its environmental and agricultural important, it is also an opportunistic human pathogen that can cause infection in patients with cystic fibrosis, cancer patients undergoing chemotherapy and severely burned individual (Wagner et al., 2008; Goncalves-de-Albuquerque et al., 2015). Such positive and negative role of same strain demands its careful application for a specific purpose.

There is a need of comprehensive discussion and clarification on the role of *Pseudomonas* spp. so that better application of this naturally occurring population can be made for enhancing plant growth as well as for eliminating several environmental related problems. The present review has been taken up with an objective to study the competitive advantage of *Pseudomonas* spp. over other microbial communities and to analyze the best growth promoting and environment friendly traits so that maximum benefits can be obtained from their inoculation under normal and stress environment. Also, the effectiveness of *Pseudomonas* as a co-inoculant with other microbial species has been discussed. Moreover, the limitations related with *Pseudomonas* application and areas of further research have also been indicated.

Pseudomonas traits with reference to plant growth promotion and Environment

As it was discussed earlier, PGPR promote plant growth by a number of direct and indirect mechanisms and most of these mechanisms are common for several PGPR strains belonging to different genera. However, the occurrence and potential may vary among different genera and even within the genera. Certain species contain more than one and particular growth promoting traits that make them more competitive over the others and also enhance the effectiveness of that strain under variable set of conditions. Owing to the presence of some particular growth promoting traits, *Pseudomonas* is considered as well suited PGPR for enhancing growth and one of the most extensively studied rhizobacteria (Saravanakumar and Samiyappan, 2007; Glick et al., 2007; Harish et al., 2009; Saharan and Nehra, 2011).

Microorganisms enhance soil fertility by decomposing organic matter and increasing the nutrient availability. Egamberdiyeva (2007) found that *P. alcaligenes* PsA15 stimulated the growth of maize and enhanced nutrient uptake in nutrient deficient soil. Similarly, *P. fluorescens* also enhanced the yield and nutrient content of banana plants (Kavino et al., 2010). They suggested that environmental problems raised by the excessive use of chemical fertilizers can be minimized by the application of effective PGPR strains. Phosphate solubilization is a very important characteristic of *Pseudomonas* spp. The gene involved in mineral phosphate solubilization was cloned from *P. cepacia* (Babu-Khan et al., 1995). Hussein and Joo (2015) reported that among 122 microbial isolates, *P. fluorescence* showed highest phosphate solubilizing potential. The release of phosphorus from insoluble source by *Pseudomonas* has been attributed to the production of organic acids (Vyas and Gulati, 2009). The study of Oteino et al (2015) showed that organic acid (gluconic acid) production by endophytic *P. fluorescens* enhanced the growth of *Pisum sativum* L. by solubilizing phosphorus from insoluble source i.e. tricalcium phosphate. Like inorganic phosphorus, organic phosphorus can also be enzymatically mineralized by phosphate solubilizing *Pseudomonas* (Jorquera et al., 2008). *Pseudomonas* spp. can improve P availability through the production of phytases and organic anions. Gluconate that is a major component of *Pseudomonas* organic anion production that play important role in the mineralization of insoluble organic phosphorus. The work of Giles et al. (2015) also showed the phosphate solubilizing ability of *Pseudomonas* sp. They found that wild type strain having ability to produce gluconate can solubilize P from calcium-phytate where as mutant could not.

In iron limiting environment, the production of siderophores by *Pseudomonas* spp. enhances the availability of iron for plant uptake on one hand (Rachid and Ahmed, 2005) while decreases the availability of iron for plant pathogens on the other hand, thus depressing the growth of disease causing organisms (Saharan and Nehra, 2011; Saraf et al., 2008). Some plants may also utilize bacterial iron-siderophores complex by transporting it into its cells, where iron becomes available for plant after releasing from iron-siderophores complex (Crowley et al., 1988).

The biocontrol efficacy of *Pseudomonas* spp. is well documented (Nandakumar et al., 2001; Mathiyazhagan et al., 2004; Paul and Nair, 2008, Kavino et al. 2008). This biocontrol efficacy is due to production of a number of anti fungal metabolites. Saritha et al. (2015) found that *P. putida* able to produce siderophores, ammonia, hydrogen cyanide (HCN), protease, chitinase, urease and ACC-deaminase inhibit the growth of mycelial growth of *F. oxysporum*, *C. fimbriata* and *S. rolfsii*. The biocontrol potential of bacterial strains further increases when two or more strains of *Pseudomonas* are used together compared to single one (Saravanakumar et al., 2009). Similarly, the application of two *Pseudomonas* strains (Pf1 and FP7) caused an increase in chitinase activity that induced systemic resistance in rice (Radjacommare et al., 2004). This might be due to the reason that certain *Pseudomonas* spp. utilize chitin by degrading it owing to their chitinase activity and cause fungal cell lysis (Radjacommare et al., 2004). Vivekananthan et al. (2004) reported that application of *P. fluorescence* amended with chitin caused induction of flowering in mango. The strain protected the mango from anthracnose pathogen *Colletotrichum gloeosporioides* Penz. by virtue of defense-mediating lytic enzymes chitinase and β-1,3-glucanase. As chitin is an important component of gut lining of insects, therefore by virtue of their chitinase activity, *Pseudomonas* may also play important role in insect pest management (Harish et al., 2009). Similarly, *Pseudomonas* sp. also showed tolerance to antibiotics and a number of heavy metals including arsenic, chromium, cadmium and copper (Canovas et al., 2003; Parameswari et al., 2009; Singh et al., 2010; Jafarzade et al., 2012; Lucious et al., 2013; Neethu et al., 2015). *Pseudomonas* spp. like *P. fluorescens* and *P. putida* produce hydroxamate type siderophores in high concentration in modified succinic acid medium (Sayyed et al., 2005). It has been observed in very earlier studies that hydroxomate siderophores enhanced cowpea growth in nickel contaminated soil by binding nickel and iron and therefore increasing the availability of iron to plant and also protecting them from nickel toxicity (Timmusk et al., 1999). Glick (2010) considered *Pseudomonas* as the most predominant and effective group of soil microorganisms that biodegrades complex organic compound.

It is evident from above discussion, owing to the presence of some particular traits, *Pseudomonas* spp. are excellent candidates for application as effective inoculants to enhance growth and development of plant and cleaning of environment.

Stress tolerance abilities of *Pseudomonas* spp.

For better effectiveness of microbial inoculation in stress environment, it is necessary that inoculating bacteria have the ability to survive in adverse conditions. The ability of a strain to flourish in stress environment makes it more competitive for enhancing plant growth. *Pseudomonas* spp. are metabolically very versatile and can maintain their growth in a better way under stress conditions like dry and saline environment (Garbeva et al., 2004; Rajbanshi, 2008). These stress tolerant microbes adopt different mechanisms to maintain their growth under such harsh environment. For example, to maintain growth in saline environment, the bacteria establish and develop their internal pressure above the surrounding environment and they generally achieve this by accumulation of osmolytes in their body (Rhodes and Hanson, 1993; Litchfield, 1998). The survival of *P. aeruginosa* in sea by accumulation of glycine and betain is an example of this mechanism (Bakhrouf et al., 1991).

Betaine is also involved in the biosynthesis of cyclopropane fatty acids to increase the membrane stability of *P. halosaccharolytica* under extreme salty conditions (Monteoliva-Sanchez et al., 1993). Similarly, accumulation of glutamate and glucosylglycerol by *Pseudomonas* sp. under saline conditions was also reported by Pocard et al. (1994). They also postulated that ionic concentration of the media had effect on internal concentration of compatible solutes. Prior to this, the accumulation of glucosylglycerol under saline conditions was only reported in marine cyanobacteria (Reed et al., 1986).

Elevated levels of temperature are generally harmful for the growth and development of living population. In order to isolate and select plastic loving bacteria, Gupta et al. (2010) found that 35 out of 86 bacterial isolates showed temperature tolerance up to 60ºC for 30 minutes and 27 out of 86 isolates showed salt tolerance. They reported that most of these bacteria belonged to genera *Pseudomonas*, *Xanthomonas*, *Flavobacterium*, *Agrobacterium* and *Bacillus*. The ability of *Pseudomonas* spp. to tolerate high level of temperature i.e. up to 40ºC was also reported by Srivastava et al. (2008). This extreme level of temperature tolerance was generally due to biofilm formation by the bacteria. However, they also mentioned that this adaptation was a regulatory process in which different kinds of genes could be involved. Biofilm formation provides a protective mode of growth and enhances the bacterial survival under adverse conditions (Webb et al., 2003). It has been observed that in many *Pseudomonas* spp. their ability to survive in desiccation and other stresses is influenced by the stationary phase sigma factor σ S (Sarniguet et al., 1995; Stockwell and Loper, 2005). This was also due to their ability to produce compounds like exopolysaccharides which protect them from desiccation (Sandhya et al., 2009). Such *Pseudomonas* spp. having ability to tolerate water deficit environment could be used effectively for enhancing crop production in arid and semiarid regions of the world. Polyhydroxyalkanoic acids (PHA) mobilization is also known to enhance stress tolerance in *P. oleovorans* (Ruiz et al., 2001). It is also evident from work of Pham et al. (2004) that PHA accumulation in *P. aeruginosa* plays an important role in stress tolerance by developing biofilm formation. Klebensberger et al. (2006) reported that cell aggregation is an energy-dependent response of *P. aeruginosa* to detergent stress which served as a survival strategy during growth in the presence of a detergent.

The heavy metals are toxic for plant growth as well as microorganisms. However, presence of high levels of heavy metals also promotes resistance in bacteria against metals (Atlas and Bartha, 1997). *Pseudomonas* spp. are found relatively more efficient in bioaccumulation of heavy metals (Hussein et al., 1999) and certain *Pseudomonas* spp. are able to tolerate a high concentration of heavy metals (Hassan et al., 2008; Singh et al., 2010; Abdelatey et al., 2011). *P. aeruginosa* isolated from deep sea sample tolerated cadmium (Cd) concentration up to 5mM. This was attributed to Cd precipitation by the bacteria that reduced its toxic concentration. Andreazza et al. (2010) also reported the tolerance of *Pseudomonas* spp. against Cd. Similarly, *P. putida* can tolerate copper (Cu) up to 3 mmol L^{-1} (Hussein et al. 2005). Microorganism also used other mechanisms to maintain a suitable metals level like chelation and extrusion of metals (Robinson et al., 2001). Canovas et al. (2003) revealed that genome of *P. putida* encodes an unexpected capacity to tolerate heavy metals and metalloids. Zhang et al. (2012) reported that siderophores production and enhancing the activity of antioxidant enzyme might be the main mechanisms of heavy-metal tolerance by *P. aeruginosa*. The microbial resistance to heavy metals also related to variety of detoxifying mechanism such as complexation by exopolysaccharides, binding with bacterial cell envelopes, metal reduction and metal efflux (Singh et al., 2010). Resistance to heavy metals by *Pseudomonas stutzeri* was related to its accumulation in cell wall (Deb et al. (2013). In a recent study, Xu et al. (2015 b, c) found that *P. fluorescens* ZY2 showed resistance against zinc and cefradine. They reported that endogenous nitric oxide and superoxide dismutase act as a mediator against the combined exposure of zinc and cefradine. *Pseudomonas* mediated the endogenous nitric oxide by the activity of nitric oxide synthase to eliminate reactive oxygen species. Liu et al. (2015) reported that *czc*RS genes studied in *P. putida* acts as a resistance mechanism against Zn^{2+}, Co^{2+}, and Cd^{2+}. *Pseudomonas* can also tolerate antibiotics and Zhou et al. (2015) reported that *Pseudomonas* resistance to antibiotics can be affected by the type and concentration of co-exposed heavy metals.

The above discussed review shows that *Pseudomonas* spp. have the ability to tolerate adverse conditions. This tolerant ability is due to presence of certain traits in these strains. According to view of Deepthi et al. (2014) the strains present in contaminated environment containing more traits when compared with normal soil. These traits enable them to grow normally in contaminated environment. Such strains can be used effectively in agriculture and environmental sciences.

Mechanisms of action

The mechanisms of growth promotion are almost common in all rhizobacterial species. Certain strains have competitive advantage over others due to presence of more than one growth promoting traits. Similarly, certain rhizobacteria have the ability to protect the plant from adverse conditions by virtue of their particular mechanisms. A general picture of overall mechanisms used by plant growth promoting rhizobacteria for enhancing growth has been shown in Fig 1.

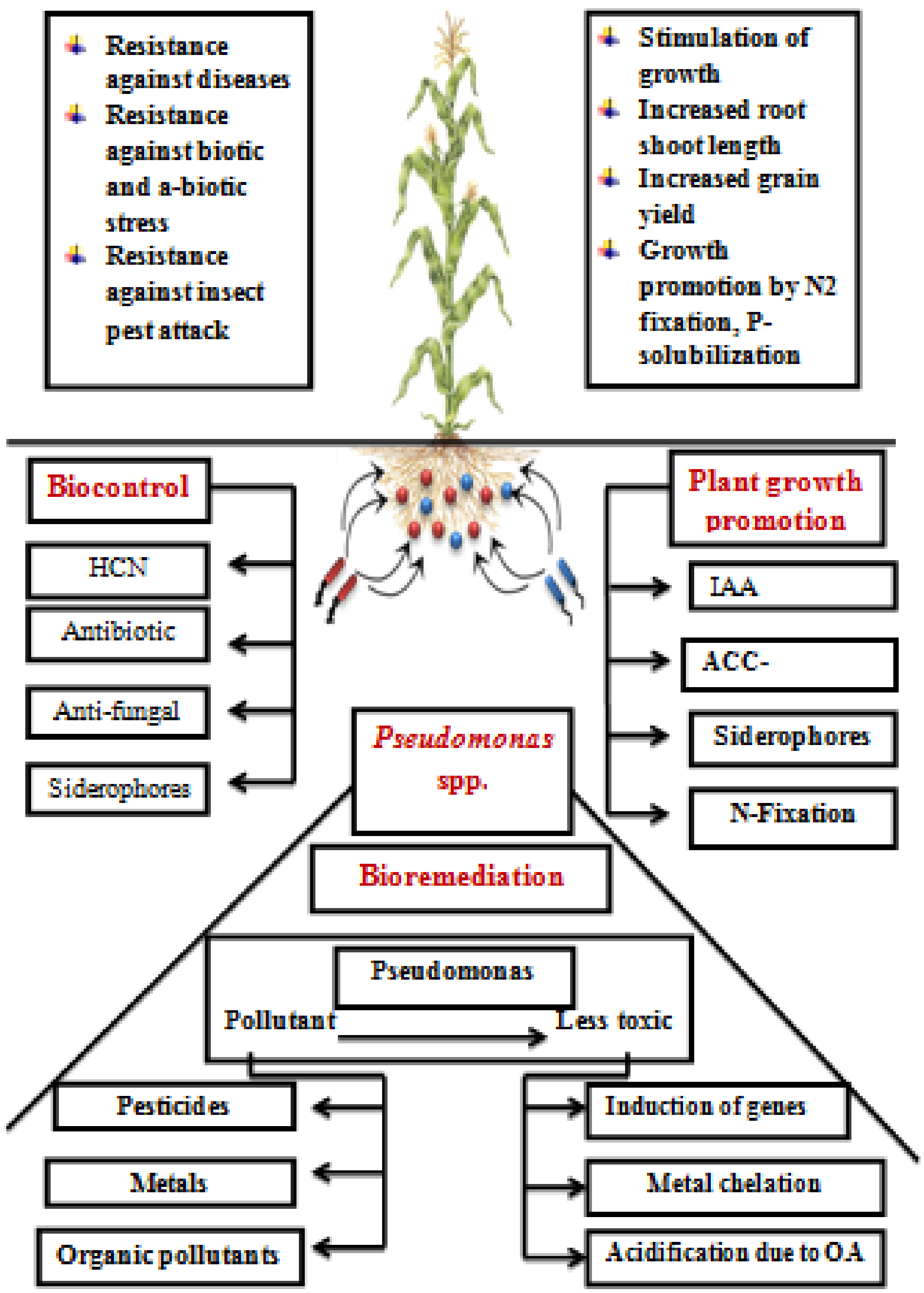

Figure 1: Mechanisms used by *Pseudomonas* spp. for promoting plant growth and remediation of environment

Pseudomonas spp. are well known for their well established growth promoting mechanisms. Certain mechanisms are activated in the stress conditions and therefore enable the plant to maintain their growth in stress environment. Some of the important growth promoting mechanisms include production of growth regulators (phytohormones), mineral solubilization, siderophores production, phosphate solubilization as well as protecting the plant from number of biotic and abiotic stresses by enzymes like ACC-deaminase, chitinase, production of osmolytes and exopolysaccharides (Zahir et al., 2004; Glick et al., 2007; Saleem et al., 2007; Nadeem et al., 2010b; Hayat et al., 2010; Przemieniecki et al., 2015). The presence of all above mentioned growth promoting traits might be rare in strains belonging to single genera. It has been observed that most of the *Pseudomonas* spp. were found positive for these major growth promoting traits (Ahmad et al., 2006; Indiragandhi et al., 2008). Kandasamy et al. (2009) studied the molecular basis of plant growth promotion by *Pseudomonas fluorescens* through protein profiling. They found that twenty three different proteins were expressed in rice leaf sheaths and functional analysis showed that these differential proteins directly or indirectly involved in plant growth promotion.

The production of growth hormones also called as phytohormones is a well established growth promoting trait of *Pseudomonas* spp. (Ahmad et al., 2005; Hariprasad and Niranjana,2009; Somers et al., 2004; Pallai et al., 2012). The production of growth regulators like cytokinins and auxin is helpful for plant not only under normal conditions but also plays protective role under stress conditions (Caron et al., 1995; Egamberdieva,2009; 2010; Yao et al., 2010; Malik and Sindhu, 2011). Similarly, production of siderophores increases the availability of iron for plant besides protects it from pathogens by making it unavailable for them (Saharan and Nehra, 2011).

The presence of certain enzymes like ACC-deaminase and chitinase makes*Pseudomonas* spp. very useful bioinoclant for plant growth promotion under stress conditions. Under abiotic stress conditions like salinity, drought, heavy metals and temperature, the ethylene concentration in plants increases due to the elevated level of ACC (Glick et al., 2007). The bacteria containing ACC-deaminase dilute the negative impact of stress by degrading ACC into ammonia and α-ketobutyrate (Glick et al., 1998) and therefore reduce the elevated level of ethylene that is injurious for plant growth and development, particularly of root system (Jackson, 1991). The production of exopolysaccharides is helpful for enhancing growth in salinity and drought conditions (Asharf et al., 2004; Sandhya et al., 2009, 2010). In salinity stress, these exopolysaccharides protect the plant from Na^+ ion toxicity by binding it (Kohler et al., 2006) and in drought stress not only enables the bacteria to maintain their growth under water deficit conditions but also protects the plant from desiccation (Sandhya et al., 2009).

The production of antioxidant enzymes like catalases, peroxidases, glutathion and ascarbate is a well established mechanism to protect the plant from stress induced reactive oxygen species like superoxide, hydrogen peroxide and hydroxyl ion (Mittler, 2002; Yan et al., 2010). The *Pseudomonas* spp. have been reported to be useful for enhancing the activity of antioxidant enzymes and enable the plant to maintain their growth under stressed conditions (Fu et al., 2010; Sandhya et al., 2010).

Another important mechanism used by *Pseudomonas* spp. is providing protection against pathogens. This is generally called as biocontrol and is achieved by competition, antibiosis and induced systemic resistance. In competition, bacteria reduce the availability of particular nutrient required by the pathogen for their growth. Reducing the availability of iron is one of the typical examples of biocontrol (Subba Rao, 1993). The mechanism of antibiosis based on the production of a compound/molecule that kill or reduce the growth of pathogen. Production of antifungal metabolites like, HCN, phenazines and pyrrolnitrin by *Pseudomonas* spp. is a prominent feature of these strains that play important role for enhancing the biocontrol activity of bacteria (Beneduzi et al., 2012; Bhattacharyya and Jha, 2012; Sivasakthi et al., 2014).

In induced systemic resistance, bacterial strains increase plant resistance against diseases by bringing a change in host-plant vulnerability (Van Loon, 2007). Similarly, the presence of chitinase enzyme degrades the cell wall of fungal pathogen (Shanmugam and Kanoujia, 2011) and decreases plant susceptibility towards diseases. Flavonoids are antifungal compound that indirectly act as antifungal agents and protect the plant from pathogen attack (Parikh and Jha, 2012). Flavonoids content by improving fruit quality also offer potential benefits for human health in amelioration of chronic diseases. Inoculation of plant with *Pseudomonas* sp. also triggers the production of flavonoids. Work of Garcia-Seco et al. (2015) conducted under filed condition showed that inoculation of blackberry with *Pseudomonas fluorescens* caused increased expression of flavonoid biosynthetic genes and ultimately increase in flavonoids concentration of fruits. They demonstrated that *Pseudomonas* improves the quality of fruit by modifying flavonoids mechanism. Recently, Essarts et al. (2016) found that *Pseudomonas putida* and *Pseudomonas fluorescens* decrease the severity of soft rot and blackleg diseases caused by *Dickeya dianthicola* on potato plants and tubers.

Potential for sustainable agriculture

The *Pseudomonas* spp. have competitive advantage over many other microbial communitiesdue to their variable and well documented growth promoting traits. These growth promoting strains have shown significant result regarding plant growth under normal as well as stress environment. Some selected examples have been mentioned in Table 1 & 2 and comparative performance of *Pseudomonas* spp. have been reviewed and discussed in the following sections.

Table 1: Effect of *Pseudomonas* spp. on growth and yield of crops under normal conditions

Pseudomonas spp.	Experimental condition(s)	Proposed mechanism(s)	Plant response	References
Wheat				
Pseudomonas fluorescens (Q8r1-96 and Q2-87)	Growth room	Root colonization	Increased shoot length, root length and root diameter. Improved wheat yield	Gamalero et al. (2003)
P. fluorescens PsIA12	Pot experiments	Production of plant growth regulators	Increased root and shoot growth, enhanced uptake of N, P, and K	Egamberdiyeva and Hoflich (2003)
P. fluorescens, *P. fluorescens* biotype F	Pot and field trials	ACC-deaminase activity, auxin production, phosphate solubilization	Enhanced root elongation and root weight. Increased number of tillers, 1000-grain weight and grain yield	Shaharoona et al. (2007, 2008)
P. chlororaphis sub sp. *aurantiaca* SR1	Field trial	Production of siderophores and phytohormones, phosphate solubilization	Significant increase in plant height, root length and number of grains per spike	Carlier et al. (2008)
P. putida spp. (Wp1 Cfp10, Wp150)	Field trial	Auxin and siderophores production, phosphate solubilization	Improved plant height and root length. Improved crop yield	Abbas-Zadeh et al. (2010)
P. fluorescens BAM-4	-	Phosphate solubilization, production phytohormones and siderophores	Improved overall growth of wheat plants and enhanced yield	Minaxi et al. (2013)
Maize				
P. putida	Green house experiment	Production of metabolites and IAA	Increased root/shoot weight, inhibit the growth of various fungal pathogens	Mehnaz and Lazarovits (2006)
P. fluorescens	Pot experiment	ACC-deaminase activity	Increased plant height, root weight and total biomass	Shaharoona et al. (2006)
P. corrugata	Pot and field experiment	Root colonization and stimulation of indigenous microflora	Enhanced grain yield of maize, high root-shoot ratio	Kumar et al. (2007)
P. fluorescens	Field experiment	Production phytohormones and phosphate solubilization	Higher biomass production, grain yield and better root colonization.	Naiman et al. (2009)
P. aurantiaca SR1	Field experiment	Root colonization, nutrient mobilization and production of indole acetic acid	Enhanced root growth and yield of wheat and maize compared to uninoculated control	Rosas et al. (2009)
P. putida	Greenhouse and field trials	IAA production and antifungal metabolites	Increases in total dry weights of root and shoot, inhibit fungal growth	Mehnaz et al. (2010)
P. cepacia	Field experiment	Phosphate solubilization and IAA production	Significantly higher P availability, improved P uptake and increased plant biomass	Katulanda and Rajapaksha (2012)

Rice				
Pseudomonas sp. K1	Pot experiment	Phytohormones production	Increase in shoot biomass and grain yield	Mirza et al. (2006)
P. fluorescens	Laboratory, glass house and field conditions	Accumulation of metabolites (chapronin 60)	Improvement in plant growth parameters, seedling vigor and stress tolerance metabolites	Kandasamy et al. (2009)
P. jessenii LHRE62 and *P. synxantha* HHRE81	Glass house condition	Interactive effect of PGPR with cow dung by acting as biopesticide agent	Enhanced root-shoot length and yield, and tolerance against foliar pathogens	Srivastava et al. (2010)
Vegetables				
Pseudomonas spp.	Field trial	Production of IAA, and stress related metabolites	Cuttings produced higher root-shoot biomass and yield	Khan and Doty. (2009)
P. entomophila strain PS-PJH	Field trial	ACC deaminase, production of secondary metabolites and enzymes	Reduced disease severity on pepper plants and enhanced root length	Kamala-Kannan et al. (2010)
P. fluorescens	Glasshouse and field trials	Production of secondary metabolites	Reduced damage due to *Fusarium wilt* in tomato seedlings and 8-fold increase in dry root-shoot weight and fruit yield was observed	Sarma et al. (2011)
*P. chlororaphis*MA 342, *fluorescens* CHA0	Glasshouse and field trials	Production of phtohormones and secondary metabolites	Improved seed emergence, seedling fresh weight and yield of carrot and onion	Bennett et al. (2009)
Legumes				
Pseudomonas spp. (44MS8, 10M3)	Pot experiment	Root colonization and production of secondary metabolites	Increased fresh biomass, pod number, pod wall thickness with no deleterious effect on plant health	Babalola et al. (2007)
Pseudomonas spp. GRP3	Pot experiment	Siderophores production	Reduction of chlorotic symptoms and enhanced chlorophyll level (chlorophyll a, b)	Sharma et al. (2003)
P. alcaliphila AvR-2	Pot experiment	Phosphate solubilization, siderophores and IAA production	Enhanced shoot length, fresh biomass, number of pods and grain yield	Ali et al. (2010)
Pseudomonas sp. AvH-4	Pot trial	Auxin production, ACC deaminase activity	Enhanced root-shoot length, seedling fresh weight and yield	Noreen et al. (2012)
Pseudomonas strains CPS63 and MPS78	Jar experiment	IAA production, root colonization	More nodule formation, gains in plant dry weight and yield	Malik and Sindhu (2008)

Growth enhancement under normal conditions

Plant growth promotion under normal conditions is a common characteristic of most microbial species including bacteria. This growth promotion takes place due to growth promoting traits of PGPR which have been reviewed by various workers (Zahir et al., 2004; Egamberdieva, 2008; Saharan and Nehra, 2011). Some of the selected examples have been mentioned in the Table 1.

For promoting plant growth, the introduced bacteria should have the ability to colonize the root and also survive and proliferate in the rhizosphere (Lugtenberg and Kamilova, 2009). *Pseudomonas* spp. are particularly considered as an effective rhizosphere colonizer owing to their ability to utilize diverse carbon sources present in

Table 2: Potential of *Pseudomonas* spp. for biotic/abiotic stress tolerance of crops

Test crop	Pseudomonas spp.	Proposed mechanism(s)	Specific comments	References
		Waterstress (deficient / waterlogging)		
Maize	*P. aeruginosa* (Pa2)	EPS-production, antioxidant enzymes activities	Improved relative water content, protein, sugar content, and total plant biomass	Naseem and Bano (2014)
Maize	*P. fluorescens* (153 and 169) and *P. putida* (4 and 108)	Production of plant growth regulators and metabolites	Protect plants from drought stress by partial amelioration of drought induced growth inhibition	Ansary et al. (2012)
Aleppo pine	*P. fluorescens* CECT 5281	Osmotic adjustment and root colonization	Improved growth, nutrition and tolerance to water stress	Dominguez-Nunez et al. (2013)
Pea	(*P. putida and P. fluorescens*	ACC deaminase production	Enhanced shoot growth, flowering pod formation and grain yield	Arshad et al. (2008)
Mung bean	*P. simiae* strain AU	ACC deaminase production	Enhanced plant growth and induced systemic drought tolerance by reducing stomata size and net photosynthesis	Kumari et al. (2016)
		Salinity stress		
Maize	*Pseudomonas* sp. 54RB	Osmolyte production and nutrient solubilization	Increased accumulation of proline content, leading to a higher water potential gradient. Improved water uptake and growth	Bano and Fatima (2009)
	Pseudomonas spp.	Production of osmolyte and improved nutrient uptake	Enhanced growth and yield under salinity stress	Bano and Fatima (2009)
Mungbean	*P. syringae*, Mk1, *P. fluorescens*, Mk20 and *P. fluorescens* Biotype G, Mk25	ACC deaminase activity	Increased root-shoot biomass, nodulation, yield and water use efficiency	Ahmad et al. (2011)
Silybum marianum	*P. extremorienttail* TSAU20	ACC deaminase activity, nutrient mobilization and phytohormones production	Improved root length, shoot length and total fresh weight	Egambrdieva et al. (2013)
Alfalfa	*P. fluorescence*	Production of osmolyte and improved nutrient uptake	Under stressed and unstressed conditions, inoculation enhanced growth of plants	Younesi et al. (2013)
Common bean	*P. extremorientalis* TSAU20 and *P. chlororaphis* TSAU13	Rhizosphere colonization	Increased root and shoot length	Egamberdieva (2011)
Rice	*P. pseudoalcaligenes* MSP 538	Synthesis of osmolytes and root colonization	Increased growth and yield	Diby et al. (2005)
Tomato	*P. fluorescens* YsS6 and *P. migulae* 8R6	ACC-deaminase activity	Wild type strains with ACC-deaminase protect the plant from salinity compared to their mutant i.e deficient of ACC-deaminase	Ali et al. (2014)

Soybean	*P. simiae* strain AU	Synthesis of IAA and ACC-deaminase. Production of putative volatile and vegetative storage proteins	Induce systemic tolerance against salinity and enhanced soybean growth compared to control.	Vaishnav et al. (2015)
		Temperature stress (heat and cold stress)		
Potato	*Pseudomonas* sp. PsJN	Production of abscisic acid	Inoculation significantly increased stem length, root-shoot biomass, tuber number and weight compared to mutant	Bensalim et al. (1998)
Wheat	*P. corrugata* (NRRL B-30409)	Phosphate solubilization, production of organic acids	At low temperature, inoculation enhanced all plant growth parameters and soil enzymatic activities	Trivedi and Sa (2008)
Tomato	*P. vancouverensis* OB155-gfp and *P. frederiksbergensis* OS261-gfp	Activation of antioxidant system	Induce chilling resistance by reducing membrane damage and reactive oxygen species	Subramanian et al. (2015)
		Pathogen stress		
Banana	*Pseudomonas aeruginosa*	Production of atibiotics, siderophores and IAA	Higher frequency of germination. Enhanced plant height and reduced the vascular discolouration	Ayyadurai et al. (2006)
Grapevine	*P. fluorescens* (WSM3455 and WSM3456)	Hydrogen cyanide production	Inhibited growth of both wild radish and ryegrass	Flores-Vargas and Hara (2006)
Tomato	*P. putida*	Production of secondary metabolites	Improved growth, yield, root-shoot length and enhanced resistance against diseases caused by *Pythium ultimum*	Gravel et al. (2006)
Pea	*P. fluorescens*	Production of volatiles compounds, competition for Fe and root colonization	Higher reduction in galling and nematode multiplication and enhanced disease resistance	Siddiqui and Zehra (2012)
Wheat	*P. fluorescens*	Production of antifungal metabolites	Suppressed soil borne fungal pathogens, enhanced growth and yield	Okubara and Bonsall (2008)
Wheat	*P. fluorescens* HC1-07	Production of cyclic lipopeptide (CLP)	Effective biocontrol agent against take-all disease and improved root growth	Yang et al. (2014)
Chir-pine	*P. aeruginosa* (PN1-PN10)	Production of siderophores, IAA and root colonization	Increased plant growth and biomass, strong antagonistic property against *M. phaseolina*, suppression of disease	Singh et al. (2010)
Medicago truncatula	*P. fluorescens*	Production of diffusible and volatile sulfur-containing compound	Enhanced resistance against grey mold disease caused by *Botrytis cinerea*	Hernandez-Leon et al. (2015)
Common bean	*Pseudomonas spp.*	Production of lytic enzyme, cyanide, IAA and siderophores	Protect the plant from bacterial blight, caused by *Xanthomonas axonopodis* pv. *phaseoli*	Giorgio and Cantore (2016)

		Inorganic pollutant (Heavy metal)		
Canola	*P. putida biovar* B	IAA production and ACC deaminase activity	Increased plant biomass and nickel uptake by shoots and roots	Rodriguez et al. (2008)
Canola (*Brassica napus*)	*P. tolaasii* ACC23	IAA, siderophores and ACC deaminase activity	Enhanced plant growth under normal and Cd stress	Amico et al. (2008)
Black gram	*P. aeruginosa* MKRh3	ACC deaminase activity, siderophores production, phosphate solubilization and auxin synthesis	Reduced cadmium uptake and enhanced plant growth	Ganesan (2008)
Brassica juncea	*P. fluorescens* Pf 27	Acidifying rhizosphere and production of IAA and siderophores	Increased uptake of water soluble and exchangeable metal content. Enhanced plant biomass and chlorophyll content,	Fuloria et al. (2009)
Tomato	*Pseudomonas* sp. RJ10	ACC deaminase activity, siderophores production, and auxin synthesis	Increased root elongation	He et al. (2009)
Orychophra gmusviolac eus	*P. aeruginosa*	ACC deaminase activity, siderophores production, and auxin synthesis	Zn tolerant bacteria enhanced Zn availability and Zn uptake by plants and increased root elongation	He et al. (2010)
Lens esculenta	*Pseudomonas* sp. Sp7d	Indole acetic acid and siderophores production	Inoculation enhanced radical growth in the presence of heavy metals	Franco-Hernández et al. (2010)
Elsholtzia splendens	*Pseudomonas putida* CZ1	Indole acetic acid and siderophores production	Stimulate the growth of plant and improve phytoextraction	Xu et al. (2015a)
Miscanthus sinensis	*Pseudomonas koreensis* AGB-1	Indole acetic acid and ACC-deaminase	Decrease heavy metal toxicity and promoted plant growth. Also enhanced Soil dehydrogenase and acid phosphatase activities	Babu et al. (2015)
		Pesticide/herbicide/fungicide		
Green gram	*P. aeruginosa*	Production PGRs, secondary metabolites biosynthesis	Regulated many physiological activities of plants, such as, cell enlargement, cell division, root initiation and growth rate	Ahemad and Khan (2011)
Green gram	*P. aeruginosa*	Exopolysaccharides production, production of metabolites	Increased plant biomass and nutrient content, formation of polymeric network around fungicide, prevented the uptake of fungicide	Ahemad and Khan (2012)
- Green gram	*P. aeruginosa* PS1	Hydrogen cyanide and ammonia synthesized, EPS production	Increased total chlorophyll content, leghemoglobin, root-shoot NP, seed yield and protein content	Ahemad and khan (2010)

Root exudates (Kremer, 2006). This ability of *Pseudomonas* enables them to enhance plant growth in control as well as under field conditions. It is evident from the work of Smyth et al. (2011) who showed that the results obtained *in vitro* could not be fully reproduced under green house conditions. Among eighteen (18) bacterial strains belonging to different genera including, *Pseudomonas*, *Bacillus*, *Acinetobacter*, *Exiguobacterium*, *Lysinibacillus*, *Micrococcus* and *Stenotrophomonas* only one of the *Pseudomonas* sp. gave similar results in field as were produced *in vitro*. They postulated that although they could not check the survival of all these strains through out the experiment, however, they observed the survival of *Pseudomonas* throughout the season in their previous unpublished work. Rosas et al. (2009) applied *P. aurantiaca* SR1as an inoculant to study its effect on wheat and maize under field conditions. *P. aurantiaca* SR1 colonized the root system of both crops and also enhanced the yield. It was also observed that *Pseudomonas* inoculation increased the yield of both crops with fertilizer dose lower than commercially applied. Similarly, Shahroona et al. (2006) found better performance of *P. fluorescens* in the presence and absence of nitrogen fertilizer.

Pseudomonas and *Brevibacillus* sp. caused significant increase in forage growth of corn in pot as well as in filed study compared to commercial strain i.e *Azospirillum* (Piromyou et al. 2011).They demonstrated that better performance of *Pseudomonas* sp. might be due to phosphate solubilization characteristic of the said strain. Banchio et al. (2008) reported that among the bacterial strains isolated from the rhizosphere of *Origanum majorana* L. only *P. fluorescens* and *Bradyrhizobium* sp. produced significant increases in shoot length, shoot weight, root dry weight and oil content of the plant compared to untreated control and other isolates including*B. subtilis*, *Sinorhizobium meliloti* and *Bradyrhizobium* sp.

Pseudomonas spp. (*P. fluorescens* and *P. putida*) significantly increased the grain yield of wheat up to 26% (Abbaspoor et al., 2009). In earlier studies, these species were also reported to increase the root and shoot elongation in canola (Glick et al., 1997) and root dry weight and harvest index of wheat (Walley and Germida, 1997). *P. fluorescens* increased growth, leaf nutrient contents and yield of banana cv. Virupakshi (Musa spp. AAB) plants (Kavino et al., 2010). Similarly, seed germination and growth parameters of maize seedlings in greenhouse and also grain yield of field grown maize improved through *Pseudomonas* inoculation (Gholami et al., 2009) that indicated their potential for agricultural exploitation and could be used as natural fertilizer (Cakmakc et al., 2006; Gholami et al., 2009). Study of Naveed et al. (2008) showed that *P. fluorescens* and *P. putida* containing ACC-deaminase improved the wheat growth even with low doses of nitrogen. Similarly, working on banana crops, Kavino et al. (2010) found significant impact of *P. fluorescens* on leaf nutrient content and yield of banana. They suggested that due to excessive use of fertilizers and high production cost, such PGPR strains could be an effective source for sustainable agriculture.

The production of organic acids that seems to be frequent agent for phosphate solubilization is another characteristic of *Pseudomonas* spp. (Rodriguez and Fraga, 1999). *Pseudomonas* also expresses a significant level of acid phosphatase (Gugi et al., 1991). Similarly, IAA production that is a common characteristic of *Pseudomonas* spp. (Ahmad et al., 2005; Karnwal, 2009; Khare and Arora, 2010; Jangu and Sindhu, 2011) is helpful for enhancing the lateral and adventitious roots that increase the nutrient uptake and also due to the production of root exudates bacterial population proliferates on the root surfaces (Steenhoudt and Vanderleyden, 2000). This better root colonization enhances the plant root growth and more root density per unit volume obtained. This ultimately enables the plant to absorb water and nutrient from greater soil volume.

In certain crops, cuttings are used to propagate their growth. Chemicals are used to stimulate growth in such cases but these chemicals have environmental concerns. Plant growth promoting rhizobacteria have the ability to stimulate the growth of such cuttings. The application of PGPR including *Pseudomonas* spp., *Bacillus*, *Burkholderia* sp. and *Agrobacterium* sp. on mint cuttings have shown growth promoting abilities (Kaymak et al., 2009). Prior to this, Mayak et al. (1999) showed that *P. putida* which was proven as a suitable inoculant for seeds to enhance root development was also suitable for development of cuttings.

Therefore, *Pseudomonas* spp. by virtue of their growth promoting traits are very useful inoculums for enhancing plant growth and development. Inoculating the plant with specific strain not only enhances crop production but also minimizes the cost of production by reducing the rate of inputs.

Protection against stress

Biotic and abiotic stresses limit plant growth and productivity of most of the field crops. A number of strategies including chemical and biological ones have been used to dilute the depressing effect of stresses. The application of beneficial microbes is gaining much importance due to environmental concerns about the use of chemicals.

Pseudomonas has the ability not only to tolerate stress conditions (Sandhya et al., 2009) but also enables the plant to maintain their growth under stress conditions (Saharan and Nehra, 2011). The role of *Pseudomonas* spp. for enhancing plant stress tolerance has been mentioned in Table 2. These growth promoting abilities of *Pseudomonas* are attributed to their particular traits including, ACC-deaminase activity, phytohormones production, phosphate solubilization ability, siderophores production, better root colonization and presence of pathogen degrading enzymes (Bakker et al., 2007; Stockwell and Stack, 2007; Zahir et al., 2009; Nadeem et al., 2010b). For example, the application of four PGPR strains including *Pseudomonas* sp., *Citrobacter* sp., *Enterobacter* sp. and *Klebsiella* sp. for enhancing the growth of ryegrass under salinity stress showed that *Pseudomonas* sp. performed comparatively better under high salinity level than other ones (Ji and Huang, 2008). The difference in growth promotion by these bacteria was attributed to difference in root colonization and ability to hydrolyze ACC.

Pseudomonas strains also differ in their abilities to enhance plant growth owing to their particular traits. For example, the better performance of *P. fluorescens* over *P. putida* for promoting the growth and yield of pea under drought stress compared to *P. putida*was due to its better root colonization (Arshad et al., 2008) whereas *P. putida* GR12-2 protected the canola plant from chilling injury (5ºC) due to production of antifreeze protein that protected the bacteria from damage of extracellular ice formation (Sun et al., 1995). On the other hand, *P. aeruginosa* enhanced sorghum growth at elevated temperature level i.e. up to 50ºC at both sterile and non sterile conditions (Ali et al., 2009) showing the presence of high molecular weight protein in the inoculated plants. However, this difference was not significant at ambient temperature. The enhancement in growth by *Pseudomonas* was also due to increase in the level of cell metabolites. Kurz et al. (2010), by using biochemical approaches, reported that *P. Syringae* produced different osmolytes which differentially contributed to water stress tolerance and interacted at the level of transcription.

The ethylene production under stress environment negatively affects plant growth by root inhibition and causes certain physiological disorders like epinasty, abscission and senescence (Mattoo and Suttle, 1991; Nadeem et al., 2010b). This can be effectively controlled by the application of ACC-deaminase containing bacteria that degrade the immediate precursor of ethylene ACC, and therefore enhance the plant growth under such environment (Glick et al., 2007). The presence of ACC-deaminase enzyme has been reported in a number of *Pseudomonas* spp. (Saleem et al., 2007; Nadeem et al., 2010b).

The nutrient availability can be increased under nutrient limiting environment by solubilizing phosphatase and the production of chelating substances like siderophores. *Pseudomonas* spp. are well known for their ability to produce siderophores (Ali and Vidhale, 2011). In iron limited environment, siderophores increase the availability of iron for plant (Powell et al., 1980; Crowley et al., 1991). Microbial siderophores are also helpful for reducing the impact of pathogens on plant growth by decreasing the iron availability (Arora et al., 2001; Saikia et al., 2005). Due to great affinity of siderophores for iron, *Pseudomonas* producing siderophores have competitive advantage on pathogenic organism for iron uptake.

The production of exopolysaccharides by *Pseudomonas* spp. is another important characteristic that enables the plant to withstand stress environment. Exopolysaccharides producing bacteria increase plant resistance against stress (Bensalim et al., 1998) and increased production of exopolysaccharides has been reported by *Pseudomonas* spp. under desiccation (Roberson and Firestone, 1992). The exopolysaccharides protect the plant in saline environmenton one hand by decreasing the ion toxicity particularly sodium (Ashraf et al., 2004) and on the other hand alsoplays an important role to reduce negative impact of water stress on plant underdesiccation (Sandhya et al., 2009). Exopolysaccharides form an organomineral sheath around the cell that enhances micro aggregation which promotes aggregate stability (Alami et al. 2000). It has been reported that exopolysaccharides producing *P. putida* provide protection to sunflower seedlings against drought stress by biofilm formation (Sandhya et al., 2009). The inoculated seedlings showed improved soil aggregation and root adhering soil and higher relative water content in the leaves.

Enzymes play very important role in plant growth and development. A number of plant enzymes become active in response to any stimulus. For example, under stress environment, reactive oxygen species are produced that are detrimental for normal plant functions (Mittler, 2002; Hajiboland and Joudmand, 2009). In response to these species, antioxidant enzyme systems operate and dilute the impact of these substances. Some of the important enzymes include ascorbate, peroxidases, catalases and reductases (Mittler, 2002; Abdel, 2011). It has been observed that *Pseudomonas* spp. also contribute significantly to enhance the activity of these antioxidant enzymes to dilute the impact of these deleterious species. The effectiveness of *Pseudomonas* spp. for promoting plant growth owing to enhancing the activities of these enzymes has also been reported (Fu et al., 2010; Jaleel et al., 2010). *P. mendocina* was used as a protectant against oxidative stress caused by drought due to its ability to enhance the activity of antioxidant enzyme (Kohler et al., 2008). It has also been observed that plants inoculated with *Pseudomonas* showed significantly better growth compared to un-inoculated ones but the concentration of these enzymes was comparatively less in inoculated plants compared to control (Sandhya et al., 2010). They demonstrated that it was due to decrease in impact of stress by inoculation and therefore reactive oxygen species were produced at low concentration. Thus these studies showed that *Pseudomonas* inoculation protected the stressed plants in two ways, either by enhancing the activity of antioxidant enzymes and/ or by diluting the impact of stress so that reactive oxygen species are produced at low concentration.

Similarly, the accumulation of compatible solutes under stress conditions is also common strategy adopted by the plant to maintain their growth under stress environment (Martino et al., 2003; Chen et al., 2007; Farouk, 2011). The PGPR like *Pseudomonas* sp. also contribute effectively for enhancing the ability of plant to accumulate compatible solutes so that the effect of stress can be reduced (Sandhya et al., 2010). It has been observed that inoculation with *Pseudomonas* sp. increased plant resistance against stress by enhancing its ability to accumulate proline compared to un-inoculated plants (Heidari et al., 2011). It has also been observed that mechanism of stress protection by PGPR may differ. As is evident from the work of Djavaheri et al. (2009), that induced systemic resistance against pathogen in *Arabidopsis* caused by *P. fluorescens* WCS374r was not regulated by iron-regulated metabolites Psb, Psm or SA. However, ISR mediated against TCV depended on production of both SA and Psb. This indicates that different elicitors of WCS374r trigger signal-transduction pathways that are differentially effective against pathogens. Similarly, Liddycoat et al. (2009) studied the effect of bacteria on asparagus (*Asparagus officinalis* L.) by using *Pseudomonas* sp. under drought stress. They found that inoculation helped the plant to tolerate the stress conditions and effect of inoculation was differed with respect to cultivar. Inoculation enhanced the growth of 'Guelph Millennium' cultivar under optimum conditions whereas Jersey Giant' seedlings under drought stress.

The growth promoting abilities of *Pseudomonas* under stress was also examined by application with other strains and also using different carrier materials. *P. moraviensis* was applied alone and in combination with *Bacillus cereus* to improve wheat growth under salt stress (Hassan and Bano, 2015). Ground maize straw and sugarcane husk were used as carriers. Co-inoculation of PGPR with both the carrier materials significantly decreased electrical conductivity and Na^+ content of soil compared to un-inoculated control.

The role of PGPR for protecting the plant from pathogens is well established (Van Loon, 2007). *P.* and *Bacillus* spp. are well documented for their ability to protect the plant from pathogens. The cyanide production is a common characteristic of most of the *Pseudomonas* spp. (Ahmad et al., 2008). The cyanide producing bacteria caused negative impact on pathogens growth and it has been observed in several studies that cyanide producing bacteria significantly protected the plant from diseases (Saharan and Nehra, 2011). Another important aspect of *Pseudomonas* inoculation which attains major attention is the ability to induce systemic resistance in plant. This systemic resistance can be incorporated by different mechanisms like modifying cell wall structure, enhancing the activity of pathogenesis related proteins, better root colonization and synthesis of stress proteins (Van Peer and Schippers, 1992; Wei et al., 1996; Siddiqui et al., 2005). Paul and Nair (2008) found that *P. fluorescens* MSP-393, used as biocontrol agent against pathogen effectively colonized the plant roots in the presence of high concentration of salts. Similarly, prior to this, it had been observed that better root colonization of *P. fluorescens* A506 inhibited the growth of plant pathogen and caused reduction of disease (Lindow et al., 1996). Recently, Hernandez-Salmeron et al. (2016) reported the presence of genes in *P. fluorescens* UM270 involved in biological control. Prior to this, Hernandez-Leon et al. (2015) reported that this strain protected the plant from onset of disease by the production diffusible and volatile compounds.

Certain PGPR strains have ability to tolerate and maintain their growth under contaminated soils stress conditions. *Pseudomonas* and *Bacillus* spp. are reported to tolerate heavy metals (Joseph et al., 2007). Cadmium resistant *P. tolaasi* and *P. fluorescens* enhanced the growth of *Brassica napus* under cadmium stress (Dell'Amico et al. 2008). It was demonstrated that this growth enhancement was due to accumulated effect of growth promoting traits including production of indole acetic acid, siderophores and ACC deaminase. Similarly, *Pseudomonas* sp. enhanced root growth and tolerance of *Lens esculenta* against lead and arsenic stress as reported by Franco-Hernandez et al. (2010). They found that even in the presence of high concentration of arsenic that was toxic for *L. esculenta* the inoculation enhanced the root length and this response could be related to their ability to produce siderophores. However, they observed significant difference among bacterial strains for enhancing the growth of *L. esculenta*.

In order to study the *Pseudomonas* ability to protect the plant from contaminants, different plant colonization methods (seed soaking, root soaking and leaf painting) was adopted to get significant results (Sun et al., 2015). An endophytic *Pseudomonas* sp. Ph6-gfp was used to protect the plant from phenanthrene toxicity. Compared with the Ph6-gfp-free treatment, the accumulation of PHE in Ph6-gfp-colonized plants was lower. Root soaking was most efficient colonization method for improving of phenanthrene removal in whole plant bodies by increasing the cell numbers of Ph6-gfp in plant roots. The application of *Pseudomonas* spp. with Ag-nano particles mitigated the negative impact of waste water on maize growth by enhancing the root area and root length (Khan and Bano, 2016).

Recent work of Zerrouk et al. (2016) showed that inoculation of maize with *Pseudomonas fluorescens* protect the plant from dual stress of salt and aluminum. Similarly, Tiwari et al. (2016) reported the *Pseudomonas putida* ability to protect the chickpea (*Cicer arietinum* L.) from drought stress. They showed that inoculated strain altered certain physical, physiological and biochemical parameters by causing positive impact on water status, membrane integrity, accumulation of osmoprotectants, antioxidative enzyme activities. The inoculation also modulated differential expression of at least 11 stress-responsive genes. They demonstrated that *Pseudomonas* inoculation not only improve the growth of desi chickpea but also enhanced the growth of drought sensitive kabuli cultivar that indicating its greater potential for enhancing agricultural yield economically important legume.

Use of Pseudomonas spp. in environmental science

It is necessary not only to improve crop yields and also to find out new energy resources to fulfill the food and energy requirements of overgrowing population. No doubt, the use of agrochemicals and synthetic plant growth regulators enhance the plant growth and crop production. However, environmental concerns related to these substances motivate the scientists to find out environment friendly approaches for sustainable agriculture. Among microbial populations, *Pseudomonas* attains special attention due to its environment friendly traits. The use of *Pseudomonas* spp. containing ACC-deaminase enzyme (biological inhibitor of ethylene) instead of chemical inhibitor aminoethoxyvinyleglycine (AVG) to reduce the stress-induced ethylene is an environment friendly approach. Similarly, the use of phosphate solubilizing bacteria plays important role in the availability of phosphorus, therefore reducing the use of chemical fertilizers and decreases the cost of production.

In modern era of industrialization, the environmental problems are increasing day by day to an alarming situation. The waste products of industry and also the municipal waste materials are the major environmental hazards. These types of waste materials contain high concentration of heavy metals (Glick, 2003) that are injurious for living population. Similarly, petroleum hydrocarbons are the main source of energy and their transportation and consumption increases the soil and water contamination due to leakage (Rahman et al., 2002). The environmental hazards can be reduced, if not eliminated completely, by the use of effective microbial strains (Table 3). The bacterial population in the rhizosphere is typically 10- to 1000-fold greater than bulk soil. Such large population enables them to enhance plant stress tolerance and accelerated remediation of polluted soils. Phytoremediation is a promising and relatively cost effective strategy for removal of contaminants from the soil. The remediation efficiency of bacterial strains differs with respect to genera and metal toxicity. Deepthi et al. (2014) observed a variable metal tolerant ability of *Pseudomonas* and *Rhizobium* sp. The application of metal tolerant bacteria may be vital for detoxifying the contaminated soils (Glick et al., 2003). The success of phytoremediation depends upon significant interactions among soil, bacteria, heavy metal and plant (Hi et al., 2013). Being a better root colonizer, *Pseudomonas* spp. are most dominant group of microorganisms that degrade complex organic and inorganic compounds/environmental pollutants including carcinogenic and mutagenic ones (Zhao and Wong, 2009; Haritash and Kaushik, 2009; Glick, 2010). The degradation of certain organic and inorganic compounds is an important aspect of these strains (Adebusoye et al., 2007; Das and Chandran, 2011). Recently, Vojtkova et al. (2015) reported that *P. monteili* showed significant potential to degrade a number of organic pollutants including anthracene, fluorene, naphthalene and phenanthrene.

The low solubility of hydrocarbons is a limiting factor for the degradation of these compounds by microbes. However, the production of biosurfactants by the bacteria increases their bioavailability and enhances their uptake (Barathi and Vasudevan, 2001). Biosurfactants are amphiphilic compounds and due to their structural and functional diversity, they are ableto partition at the oil/water interfaces and reduce the interfacial tension (Darvishi et al., 2011). Microbial biosurfactants are gaining much importance because these are environment friendly due to biodegradablity, low irritancy and non toxic nature (Banat et al, 2000; Cameotra, and Makkar, 2004; Sivapathasekaran et al., 2010; Kiran et al., 2010; Satpute et al., 2010). Due to environmental concerns about chemical surfactants the biosurfactants are environmental compatible and can also work in extreme environmental conditions (Dastgheib et al., 2008). As it is evident from the work of Flasz et al. (1998) who compared the microbial biosurfactants with a synthetic surfactant to evaluate their toxicity and mutagenic properties. Chemical derived surfactant was found highly toxic and mutagenic whereas biosurfactant produced by *P. aeruginosa* was non toxic and non mutagenic.

Pseudomonas spp. are also present hydrocarbon rich environment and produce many kinds of biosurfactants which have great potential for biotechnological and biomedical applications (Raaijmakers et al., 2006; Sinnaeve (2007). They reported the protection against damping off disease in chili and tomato by rhamnolipids producing *Pseudomonas*.The rhamnolipids biosurfactants are first identified from *Pseudomonas* sp. (Jarvis and Johnson, 1949). *Pseudomonas aeruginosa* is well known due to its ability to produce biosurfactants and their biosurfactants production and biodegradation activity have been reported by many workers (Cameotra and Singh, 2008; Obahiagbon et al., 2009). Biosurfactants produced by *Pseudomonas* and *Acinetobacter* spp. enhance the bioavailability and degradation of pesticides and petroleum and polycyclic aromatic hydrocarbons (Singh et al., 2009; Sharma et al., 2009; Zhao and Wong, 2009). Based on their chemical nature, different types of biosurfactants like lipopolysaccharides, glycolipids, lipopeptides and oligosaccharides have been reported to be produced by different bacteria (Banat et al., 2000, 2010; Franzetti et al., 2010). Rhamnolipids biosurfactants are also helpful for reducing the impact of diseases as reported by Sharma et al. and Akhabue, 2009). Rhamnolipidic type biosurfactants enhance the biodegradation of crude oil (Rocha and Infante, 1997) and this type of tensio-active glycolipids are produced by *P. aeruginosa* which have the ability to degrade wide variety of oil components (Muthusamy et al., 2008). Although the rhamnolipids main biosurfactants produced by *P. aeruginosa* by various workers (Rahmanet al., 2002, 2010; Cameotra and Singh, 2009), the production of lipopeptide biosurfactant from *P. aeruginosa* has also been reported (Thavasi et al., 2011a). Recently, Rikalovic et al. (2015) critically reviewed the production of rhamnolipid

Table 3: Role of *Pseudomonas* spp. in environmental science

Specie name	Mechanism used	Response	Reference
P. putida W619-TCE	Lowered evapotranspiration of trichloroethylene (TCE).	Promoted plant growth, reduced TCE phytotoxicity and increased shoot biomass	Weyens et al. (2010)
P. aeruginosa	Biosurfactants production	Biosurfactants produced bacteria showed a good stability above pH of 5 and at higher salinity	Xia et al. (2011)
P. fluorescens strain P13	Production of catechol 2, 3-dioxygenase	Enhanced corn growth and reduce phenol concentration in contaminated environment	Yang et al. (2011)
P. extremaustralis	Polyhydroxyalkanoates (PHAs) production, biosurfactant production	Inoculation enhanced hydrocarbon remediation under extreme environment	Tribelli et al. (2012)
P. putida KT2440	Enzymes production and expression of genes involved in the oxidative stress and higher colonization	Complete mineralization of [^{14}C] naphthalene, the rate of mineralization was at least 2-fold higher in the rhizosphere than in bulk soil	Fernandez et al. (2012)
P. aeruginosa	Biosurfactants production	Bacterization was effective in crude oil degradation under contaminated environment	Zhang et al. (2012)
P. aeruginosa AB11, *P. fluorescens* AB56, *P. alcaligenes* AB44, *P. putida* AB58 and AB67	Production of surfactants	Enhanced biodegradation of petroleum tar, also produce intermediates	Tanti and Buragohain (2013)
P. putida AK5	Degradation via salicylate-gentisate pathway	Enhanced the degradation of naphthalene	Izmalkova et al. (2013)
Pseudomonas sp. strain B2	Degradation was accompanied by release of chloride ion	Degraded CF to clodinafop acid and 4-(4-Chloro-2-fluoro-phenoxy)- phenol within 9 h	Singh (2013)
Pseudomonas sp. strain GE-1	Co-precipitation and adsorption	Enhanced the removal of arsenic through arsenic immobilization by induction of ferrihydrite	Xiu et al. (2015)

biosurfactant from *P. aeruginosa* and their application in environmental science. They demonstrated that in spite of certain drawbacks, *P. aeruginosa* are the most promising candidates for rhamnolipid biosurfactant production. According to their view, there is great scope for the application of rhamnolipid biosurfactant in the field of bioremediation, biodegradation of hydrocarbons and removal of heavy metals. The effectiveness of rhamnolipid biosurfactant has already been documented due to their remarkable tensio-active and emulsifying properties (Soberon-Chavez et al. 2005; Liu et al. 2014). Similarly, glycolipid type biosurfactants produced by *P. aeruginosa* showed great potential to degrade petroleum hydrocarbons including eicosane, pristane and fluoranthene (Sharma et al., 2015). The production of biosurfactants is variable among bacterial spp. andalso depends upon the medium. It is evident from the work of Priya and Usharani (2009) that among four oils i.e. vegetable oil, kerosene, petrol and diesel, the production of biosurfactants was more in case of diesel. *P. aeruginosa* had higher biosurfactants activity than *B. subtilis*.

Maier (2003) reported that the degradation effectiveness was affected by the strain potential and this potential of bacterial strain to degrade hydrocarbon was linked with their ability to produce biosurfactants. It has been reported that proper mineral nutrition is necessary for microbial biosurfactants production and limited use of bacterial biosurfactants is due to expensive substrates and limited product concentrations (Syldatk and Hausmann, 2010). It was observed that providing mineral nutrition to the bacteria enhances the process of biosurfactants production (Mukherjee et al., 2008; Manif et al., 2012) that accelerates the process of degradation. However, it was also reported by Maki et al. (2003) that application of mineral nutrition only stimulated the initial process of biosurfactants production and final degradation efficiencies were independent of fertilizers (Maki et al. 2003). The work of Thavasi et al. (2011b) also supported this argument. They investigated the effects of biosurfactants in the presence and absence of fertilizer on biodegradation of crude oil by using three biosurfactants producing bacterial strains; *B. megaterium*, *Corynebacterium kutscheri* and *P. aeruginosa*. They found that the *P. aeruginosa* caused maximum degradation compared to other strains. Although fertilizer application enhanced the degradation process, biosurfactants alone were also capable of promoting biodegradation to a large extent. It indicates that efficacy is related to nature of biosurfactant produced by the bacteria. Such biosurfactants would be useful for minimizing the risk of fertilizer which are generally washed away with surface agitation and are mixed in the aquatic environment.

Due to cost effectiveness and environment friendly approach, phytoremediation is one of the emerging technologies over conventional methods (Chehregani et al., 2009; Kotrba et al., 2009). For effective phytoremediation, the bioavailability of metals, better root development and tolerance of plant against metal is pre-requisite (Pilon-Smits, 2005). Although chemical substances like ethylene diamine tetracetic acid (EDTA) and hydroxyethyl-ethylenediamine-triacetic acid (HEDTA)are very effective chemical enhancers used to increase the availability of heavy metals(Huang and Cunningham, 1996;Vassil et al., 1998; Chen and Cutright, 2001; Chen et al., 2003;Turan and Esringu, 2007), the growth of metal accumulating plants is also affected if the concentration of available metals increases and thereby reducing their biomass and efficiency of phytoremediation (Li et al., 2007). Sinha and Gupta (2005) also reported the growth inhibition by elevated levels of heavy metals. Application of chemical chelating agents is not only harmful for environment but it can also have phototoxic effect that inhibit the plant growth and therefore lowers the efficiency of phytoextraction (McGrath and Zhao, 2003; Ma et al., 2009). Certain bacterial strains increase the bioavailability of metals and therefore enhance their removal (Ibrahim et al., 2009). Therefore, the use of bacteria for enhancing biomass and metal uptake of metal accumulating plants could be very effective (Sheng and Xia, 2006; Rajkumar et al., 2009).

The application of *Pseudomonas* spp. protect the plant from negative impact of heavy metals (Arshad et al., 2008; Dell' Amico et al., 2008) and also play an important role for degradation and phytoextraction of these metals (Jing et al., 2007; Yancheshmeh et al., 2011; Baharlouei et al., 2011). Not only the rhizospheric bacteria but also endophytic *Pseudomonas* spp. have been reported to enhance the growth of *Brassica napus* and accumulation of copper (Zhang et al., 2011). In addition to providing protection against pathogens as mentioned in the previous sections, the siderophores producing strains also enhanced metal accumulation in plant (Idris et al., 2004) and could be useful for phytoremediation. Similarly, exopolysaccharides producing *P. stutzeri* showed significant potential in the treatment of heavy metals-contaminated water (Maalej et al. 2015). They reported that exopolysaccharides produced by the strain showed metal adsorption capacity in the order of Pb >> Co > Fe > Cu >> Cd. Recently, Khan and Bano (2016) reported that the application of *Pseudomonas sp.* with Ag-nano particles enhanced the bioremediation potential of the strain for Pb, Cd, and Ni. According to their view municipal waste water can be used effectively by treating it with bacteria and Ag-nano particles for enhancing bioremediation of heavy metals.

Pseudomonas spp. may also be useful for reducing the use of herbicides to inhibit weeds growth. The excessive use of chemical herbicides causes negative impact on human and environment and also results in the development of herbicide resistant to weeds (Heap, 1997). Although there are certain reports showing the effectiveness of *Pseudomonas* strains for inhibiting the growth of weeds (Tranel et al., 1993; Gealy et al., 1996; Kremer, 2006; Saharan and Nehra, 2011), might be due to the production of phototoxins (Nehl et al., 1997).There are also some perceptions that these weed growth inhibiting strains could also be harmful for valuable plants. The work of Mejri et al. (2010) negated this opinion by observing the specificity of *Pseudomonas* against particular weed. They evaluated the growth inhibiting ability of *P. trivialis* against great brome (*Bromus diandrus* Roth.) weed grown alone and together with durum wheat (*Triticum durum* Desf.). They found that *P. trivialis* did not affect the growth of durum wheat. However, it suppressed the growth of great brome by affecting its root architecture. They demonstrated that the production of indole acetic acid by *P. trivialis* could be the cause of weed growth suppression and durum wheat growth promotion which also indicated the specificity of this hormone. In earlier study, Sarwar and Kremer (1995) also observed the growth inhibition of field bindweed (*Convolvulus arvensis* L.) by indole acetic acid producing *Enterobacter taylorae*.

Role in biotechnology

In recent decades, significant advances have been made in agriculture sector by developing more productive as well as stress resistance crop varieties. One of these developments has been the generation of transgenic plants which have the ability to cope with stress environment. The plant growth promotion observed in response to inoculation with suitable bacterial strains provoked scientists to develop transgenic plants with the expression of gene of interest. Being a well established growth promoting traits *Pseudomonas* spp. also considered as a suitable candidate for biotechnological research. To eliminate the negative impact of stressed induced ethylene Klee et al. (1991) developed tomato transgenic plants by insertion of genes responsible for ACC-deaminase activity, isolated from *Pseudomonas* sp. 6G5. They observed reduced ethylene concentration in transgenic plants. Transgenic tomato lines with reduced ethylene concentration were also prepared by obtaining gene from *P. chlororaphis* (Reed et al., 1995). Similarly, expression of a *P. aeruginosa* citrate synthase gene in tobacco (*Nicotiana tabacum*) improved Al tolerance of the tobacco plant (de la Fuente et al. 1997). These studies show that in addition to inoculation with *Pseudomonas* spp. the transfer of specific gene to construct transgenic plant could be useful for protecting the plants from stress environment.

Nitrous oxide is a green house gas and there is a need of effective strategy for mitigation of this gas. The enzyme nitrous oxide reductase that catalyzes the final step of denitrification is naturally present in bacteria. Wan et al. (2012) demonstrated that bacterial nitrous oxide reductase from *P. stutzeri* expressed in plants can convert nitrous oxide into inert nitrogen. They demonstrated that incorporation of such bacterial gene in to crops may be useful for reducing the atmospheric concentration of nitrous oxide.

The above discussion indicates that *Pseudomonas* spp. are equally effective for enhancing the growth of plant under normal and stress conditions as well as protecting the environment from harmful impact of hazardous substances. It is evident from above discussion that certain bacterial traitsare also very useful fromenvironment point of view and can be used effectively in environmental science. Such strains can be used as inoculums and/or gene of interest can be transferred to construct transgenic plants.

Co inoculation of *Pseudomonas* with other microbes

The effectiveness of microbial inoculation for enhancing plant growth and combating environmental problems is well documented. However, it has also been seen in certain cases thatsingle inoculationwas not effective or was less effective for that particularpurpose (Lucy et al., 2004; Akhtar and Siddiqui, 2009). This might be due to the environmentalfactorsthat limit the survival of that strain in soil and/or inability of strain to compete with indigenous population. Similarly, the results obtained in laboratory are not so effective in green house or field conditions (Smyth et al., 2011). This limitation inspired the scientist to use consortium of strains so that maximum benefit can be obtained from this naturally occurringpopulation.

For better results, the combined application of PGPR could be effective under different conditions. For example, the use of *Pseudomonas* spp. with *Rhizobium* to enhance the growth of legumes under normal as well as stress conditions was very useful (Sindhu et al., 2002; Egamberdieva et al., 2010; Stajkovic et al., 2011). Some selected examples of the impact of co-inoculation has been presented in Table 4.

The tripartite association composed of legume plant, rhizobia and *Pseudomonas* spp. has been reported to

Table 4: Interactive effect of *Pseudomonas* spp. with beneficial microorganism for improving growth and yield of crops

Interactive microbe	*Pseudomonas* spp.	Test crop / Experimental conditions	Effect on crop	References
		Plant Growth Promoting Bacteria (PGPB)		
B. caryophylli	*P. fluorescens*	Wheat / pot and field trial	Increased root-shoot elongation, biomass, and yield	Shaharoona et al. (2007)
Bacillus OSU-142 and *Bacillus* M-3	*Pseudomonas* sp. BA-8	Strawberry / field trial	Increased fruit weight, yield and total reducing sugar contents	Pırlak L and Kose M (2009)
A. brasilense	*P. fluorescens*	Wheat / field trial	Increased aerial biomass, root biomass, plant height and grain yield	Naiman et al. (2009)
R. leguminosarum-PR1	*Pseudomonas* sp. strains (NARs1, PGERs17)	Lentil / greenhouse conditions	Increased nodulation, leghaemoglobin content, physiologically available iron, total iron, chlorophyll content, and NP uptake	Mishra et al. (2011)
Bacillus sp. M7c	*Pseudomonas* sp. FM7d	Alfalfa / field	Increased root-shoot dry weight, length, and surface area of roots	Guinazu et al. (2010)
A. brasilense	*P. fluorescens*	Marigold / pot	Shoot fresh weight was significantly higher, total phenolic content was 2-fold higher compared to control	Cappellari et al. (2013)
R. galegae bv. *orientalis* HAMBI540	*P. trivialis* 3Re27	Fodder galega / greenhouse	Increased shoot-root dry matter, nodule number, biomass, and nitrogen content	Egamberdieva et al. (2010)
S. meliloti RMP1	*P. aeruginosa* GRC2	*Brassica juncea* Field Trials	Bacterization increased biomass and yield	Maheshwari et al. (2010)
R. leguminosarum	*P. jessenii*, *P. fragi* and *Serratia fonticola*	Lentil / Pot and field	Increased number of pods per plant, number of nodules, dry nodule weight, grain yield, and straw yield	Zahir et al. (2011)
Mesorhizobium sp.	*Pseudomonas* sp.	Chickpea/Field trial	Co-inoculation of IAA producing *Pseudomonas* significantly increase plant dry weight and nodulation. However, higher concentration of IAA reduced growth	Malik and Sindhu (2011)
Bacillus OSU-142 and *Bacillus* M-3	*Pseudomonas* BA-8	Strawberry/Field experiments	Inoculation alone or in combination significantly increased fruit yield, plant growth and leaf P and Zn contents	Esitken et al. (2010
Acinetobacter sp. RG30	*P.* putida GN04	Green house trial	Enhanced maize growth and chlorophyll content and protect the plant from copper toxicity	Rojas-Tapias et al. (2014)
Rhizobium pisi	*Pseudomonas monteilii*	*Phaseolus vulgaris* L	Increased the nodulation, growth parameters and yield. The impact on genotype BAT-477 was more than DOR-364.	Sanchez et al. (2014)
Rhizobium spp.	*Pseudomonas sp.*	*Vicia faba*.L. /Vineyard trial	Enhanced plant growth under copper contaminated soil	Fantassi et al. (2015)
		Arbuscular Mycorrhiza Fungi (AMF)		
P. indica	*P. striata*	Chickpea/ pot experiment	Synergistic effect on population buildup, plant dry biomass	Meena et al. (2010)
G. mosseae and G. intraradices	*P. fluorescens* SBW25	Winter wheat / greenhouse trial	Increased plant growth and dry biomass, and reduced pathogens attack	Jaderlund et al. (2008)

T. aharzianum T22 and *T. viride* S17a)	*P. fluorescens* CHA0	Onion and carrot / glasshouse and field trials	Improved seedling emergence and yield of crops	Bennett et al. (2009)
P. agglomerans 050309 and *Mycobacterium* sp.	*P. fluorescens* PsIA12	Wheat / pot trial	Increased root and shoot growth, higher N, P, and K contents of plant	Egamberdiyeva and Hoflich (2003)
AMF and *Azotobacter chroococcum* (Ac) .	*P. fluorescens* (Pf)	Sesamum/ pot experiment	Enhanced root-shoot length, number of capsules, biomass and phosphorus uptake	Sabannavar and Lakshman (2011)
A. vaga BAM-77	*Pseudomonas fluorescens* BAM-4,	Mung bean / pot trials	Increased root-shoot length, dry biomass, leaf area and photosynthetic yield	Jha et al. (2012)
G. fasciculatum and G. aggregatum	*Pseudomonas* spp.	Sorghum / pot experiment	Increased plant biomass, leaf area, total chlorophyll and mycorrhizal infection	Kumar et al. (2012)
Arbuscular mycorrhizal fungi	*P. jessenii*, R62, *P. synxantha*, R81	Rice, wheat and black gram / field	Inoculation improved grain yield, mineral nutrient concentration of tested crops. Effect was more on wheat. Also improved soil enzymatic activites	Mader et al. (2011)
G. mosseae	*P. putida* (HM590706)	Guava / glasshouse	Higher leaf, stem, shoot, and root dry masses, total biomass, and total leaf area	Panneerselvam et al. (2012)
G. fasciculatum	*P. monteilii*	*Coleus forskohlii* / field	Improved AM root colonization, higher tuber yields and improved tuber contents of inoculated plants	Singh et al. (2013)
Arbuscular mycorrhizal fungi	*Pseudomonas spp.*	Strawberry/field	Co-inoculation increased flowering, number of fruit, fruit size and quality under conditions of reduced fertilization	Bona et al. (2015)

increase root and shoot weight, plant vigor, nitrogen (N) fixation and grain yield in various legumes (Bolton et al., 1990; Dashti et al., 1998; Sindhu et al., 1999). Even enhancement of growth in non legumes was also observed by co-inoculation. The co-inoculation effect of *Pseudomonas* and *Rhizobium* on maize under salinity stress conditions decreased the electrolyte leakage, increased proline accumulation and maintained the water content of leaves with selective uptake of K ion (Bano and Fatima, 2009). They observed that under unstressed conditions *Rhizobium* was more effective than *Pseudomonas* but under stress, *Pseudomonas* stimulated the plant growth. According to their view the growth promoting effect of *Pseudomonas* was due to more phosphorus accumulation and greater membrane stability that reduced the electrolyte leakage.

As it was mentioned earlier, a number of *Pseudomonas* spp. containing ACC-deaminase enzyme could be helpful for reducing the ethylene concentration that caused negative impact on root growth and also on nodulation in legumes under stress environment. The co-inoculation can also reduce this impact of stress as is evident from the work of Ahmad et al. (2011) who observed that co-inoculation of *Pseudomonas* and *Rhizobium phaseoli* enhanced the growth and nodulation of mungbean under salinity stress conditions. They observed that co-inoculation of *Pseudomonas* spp. with rhizobium reduced the negative impact of salinity. They demonstrated that this growth enhancement was due to suppression of stress-induced ethylene that was injurious for proper nodulation. Similarly, co-inoculation of *Mesorhizobium* sp. with IAA producing *Pseudomonas* increased the nodule number and nodule biomass of chickpea (*Cicer arietinum*). The plant dry weight was significantly higher in case of co-inoculation compared to control and where the *Mesorhizobium* was applied alone (Malik and Sindhu, 2011). They also observed that inoculation of *Pseudomonas* inhibited the root growth at initial stages. However, after 10 days, root and shoot growth increased. They demonstrated that this initial inhibition might be due to the production of high

IAA that caused negative impact on root growth. It is also evident from earlier work that high IAA producing PGPR inhibited the root growth (Xie et al., 1996) rather than promoting it.

The co-inoculation of *Pseudomonas* also proved helpful for suppressing plant disease. Recent work of Lachisa and Dabassa (2016) showed that application of *Pseudomonas* with *Bacillus* and composted manure efficiently reduced the onset of *Fusarium wilt* disease of tomato. They observed that impact of *Pseudomonas* was better compared to *Bacillus* and more efficient results were obtained when both strains were applied with composted manures. Similarly, Mani et al. (2016) found that co-inoculation of *P. putida* with *Thiobacillus thiooxidans* enhanced the phytoremediation ability of *Gladiolus grandiflorus* L in the presence of vermicompost and elemental sulpher. Such studies show that efficacy of *Pseudomonas* can be enhanced by co-inoculation with suitable strain and by applying suitable amendment.

For getting effective results, it is important to use compatible strains. Such compatibility could be very effective for attaining desire results. The incompatible combination could be result in poor performance. For example, phosphate solubilizing *Pseudomonas* was co-inoculated with *Rhizobium* to evaluate their effect on alfalfa and soybean (Rosas et al., 2006). For inoculating alfalfa, *P. putida* was co-inoculated with *Sinorhizobium meliloti* and for soybean, it was co-inoculated with *Bradyrhizobium japonicum*. It was observed that co-inoculation effect was more significant in case of soybean than alfalfa. It might be due to the incompatibility of *Bradyrhizobium japonicum* with *P. putida*.

The co-inoculation of *Pseudomonas* with arbuscular-mycorrhizal (AM) fungi is also effective for promoting plant growth. The work of Ortiz et al. (2015) showed that co-inocualtion of AM fungus with *P. putida* and/or *B. thuringiensis* induced drought tolerance in *Trifolium repens.* They reported that synergistic or additive mechanisms are involved in this stress tolrance. The co-inoculation maintained water status and plant nutrition. Also improved osmotic adjustment and regulated the antioxidants systems. The combine application of *P. aeruginosa* and *Trichoderma harzianum* in soil amendment with *Vernonia anthelmintica* seed's powder induce systemtic resistance against *Rhizoctonia solani* and *Fusarium oxysporum* in okra (Shafique et al., 2015). They observed that mycorrhizal spores were more arround the plant root treated with *P. aeruginosa* alone or in combination. Also more phosphorus contents were observed in treated plants. Prior to this Bokhari et al. (2014) also reported the improved phosphorus contents and mycorrhizal spores around the root of mung bean inoculated with fluorescent *Pseudomonas*.

Limitations and alternate use

In spite of a number of studies reviewed and discussed in the previous sections, indicating better performance of *Pseudomonas* spp., there are certain reservations and/or limitations regarding the use of *Pseudomonas* spp. on commercial basis. For examples, IAA producing bacterial strains is effective for enhancing the root and shoot growth of plants but at the same time the inhibition of growth due to IAA has also been reported (Xie et al., 1996). However, this root inhibition was generally observed at high concentration of IAA (Arshad and Frankenberger, 1992; Xie et al., 1996). Therefore, the strain specificity should be kept in mind for obtaining better results.

Pseudomonas aeruginosa is an effective strain for degrading hydrocarbon material and is used extensively in environmental science. It is also an opportunistic pathogen that causes certain infections like bloodstream, skin and soft infections, otitis exterma and pneumonias (Driscoll et al., 2007). Such infections may lead to high rate of mortality in immunocompromised hosts and also in patients with cystic fibrosis or severe burns (Markou and Apidianakis, 2013). Therefore, care should be taken in its use.

The release of allelochemicals like cyanide, phenolic acids, phenazine-1-carboxylic acid and phytotoxins suppress germination of seeds and plant growth (Suslow and Schroth, 1982; Bakker and Schippers, 1987; Nehl et al., 1997; Karen et al., 2001). Cyanide production is a dominant characteristic of many of the *Pseudomonas* spp. Although the cyanide producing bacteria are known for their inhibitory effect on pathogens and play important role in inducing disease resistance in plants (Saharan and Nehra, 2011; Parikh and Jha (2012), HCN also causes an inhibitory effect on plant growth. Kremer and Souissi (2001) showed that cyanide production by *Pseudomonas* sp. caused the growth inhibition of lettuce and barnyard grass. They reported that cyanide production by the bacteria was a potential and environmentally compatible mechanism for biological control of weeds (Heydari et al., 2008). It has been observed that application of *P. fluorescens* suppressed the emergence of green foxtail (*Setaria viridis* L.) up to 90% (Daigle et al. 2002). Cyanide producing *P. entomophila* can be used as biocontrol agent for reducing pathogenecity caused by other bacteria (Ryall et al., 2009). Cyanide producing *Pseudomonas* spp. proved useful for reducing the fungal growth *Macrophomina phaseolina* (Tassi.) Goid and can be used as biocontrol agent (Reetha et al. 2014). Such strains can be used effectively as bioherbicides for inhibiting weed growth which are silent robbers of plant nutrients and soil moisture (Kamei et al., 2014).

Future prospects

There are number of reports available, some of these also discussed in this article, that indicating the effectiveness of PGPR for enhancing growth and development of plant. There are still lack of evidences that show the consistent performance of these microbes particularly under field conditions. This mightbe due to low quality of inoculum (Brockwell and Bottomley, 1995) and inability of bacteria to compete with the indigenous population under adverse environmental conditions (Catroux et al., 2001). As reported by Cattelan et al. (1999), for better performance, the PGPR strains must be rhizosphere competent that could be able to survive and colonize. Therefore, the most significant factor that affects the effectiveness of inoculating strain is its ability to compete with the indigenous population for limiting resources as well as the compatibility between the rhizodeposition of compounds by the plant host and the ability of the inoculated bacteria to utilize them (Strigul and Kravchenko, 2006).

In certain cases, the result obtained in the lab cannot be reproduced in the field (Zhender et al., 1999; Smyth et al., 2011). It might be due to the reasons that the inoculating strains could not compete with the indigenous population. According to Mitter et al. (2013) this inconsistency might be due to selection of inappropriate strain, inability of strain to produce particular secondary metabolites and specificity of strain to colonize roots of some specific plant. For effective inoculation it is necessary that inoculating microbe could be able to tolerate environmental stresses so that it may play a role in plant growth promotion. The development of inoculum for soil, subjected to several environmental stresses needs guarantee that strains will remain effective under such adverse conditions. In cases where single inoculation is not so effective multiple inoculation might be useful for enhancing plant growth (Liddycoat and Wolyn, 2009). Rajasekar and Elango (2011) observed that multi-strains inoculum was more effective compared to single strain inoculation.

The method of inoculation is also might be one of the reasons of inconsistent results. Different inoculation techniques include peat based inoculants, liquid inoculation and seed coating are used to introduce the candidate microbes in to the soil. The carrier material used to prepare a good formulation play a key role to protect the microbes from unfavorable conditions during storage, transport and their stay in the soil. John et al. (2011) critically review the problems related the low viability of microorganisms during storage and field application. They reported that lack of knowledge regarding the best carrier in conventional formulations (solid and liquid) is one of the reasons of poor performance of microbial community under natural conditions. According to their view, microencapsulation is an advanced technology that can be used effectively to overcome these drawbacks. Correa et al. (2015) reported that coconut fiber is a carrier of superior performance in maintaining shelf life of *Pseudomonas* strains. They concluded that densities of viable cells in coconut fiber decline significantly during 224 days. Recently, Stephan et al. (2016) while investigating the practicability of freeze-drying to formulate and stabilize *Pseudomonads* reported that *Pseudomonads* can be freeze-dried without loss of viability. They demonstrated that selection of suitable cryo-protective agents not only enhancing its viability, storability but also improve efficacy of *Pseudomonads* to protect the plant from biotic stress.

It has been observed that plant genotypic background and bacterial traits affect the interaction between plant and rhizobacteria containing ACC-deaminase (Belimov et al., 2001). Also the ability of bacteria to utilize ACC accompanied by other properties, like indole acetic acid and ethylene production probably could affect their interaction with plants. Therefore, these aspects should also be kept in mind while studying the effectiveness of such strains. In certain cases, it has been seen that certain growth promoting traits may interact with each other and have influence on plant growth. For example, in one of our study (submitted for publication) bacterial strains having both ACC-deaminase and IAA activity behaved differently. The strain having high ACC-deaminase activity and low IAA and/or high ACC-deaminase and high IAA performed better compared to a strain having high IAA and low ACC-deaminase. Therefore, such aspects need further research so that most effective strains or combinations of strains can be selected.

Other beneficial aspects of bacterial inoculation also need special attention. For example, the addition of ice-nucleating bacteria to agriculture has potential benefits of protecting crops from frosts dropping below freezing, which might contribute to a solution of the world-wide problem of starvation and chronic hunger. The application of these bacteria could be an effective technology for enhancing plant growth at low temperature. Similarly, cyanide producing bacteria can be used effectively for disease suppression. Certain *Pseudomonas* strains produce allelochemicals that can be used as bioherbicides to minimize the use of chemicals and therefore eliminate environmental hazards.

Conclusion

Increasing crop production in limited resources for overgrowing population is a challenge for scientists and presence of unfavorable environment further increases the intensity of this challenge. The use of chemical inputs like fertilizers, insecticides and herbicides although enable us to achieve this goal. However, the environmental concerns related with these, decrease their effectiveness. The use of naturally occurring microbial community can provide opportunities to solve this problem. Among this, strains belong to *Pseudomonas* group attains special attention due to its tremendous performance for enhancing plant growth and development as well as protecting and solving environment related problems.

The plant growth promoting abilities of *Pseudomonas* spp. under normal as well as stress conditions validate their role in sustainable agriculture. The intensity of biotic and abiotic stresses can be reduced by inoculating the seed or seedling with suitable strains of *Pseudomonas*. The degradation of hazardous compounds both organic and inorganic further increases their importance for protecting our environment. The effective performance of *Pseudomonas* in phytoextraction and remediation further validates their positive role in environmental protection. The *Pseudomonas* trait that caused negative impact in one condition could be effective against some particular aspect in other environment. This also indicates the specificity of such traits for some particular purpose. Overall, *Pseudomonas* spp. are an environment friendly microbial population that can be used to tackle grand challenge and management options if used wisely. It is hoped that *Pseudomonas* spp. will be major inoculant in future for sustainable agriculture and environment.

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