Plant Archives Vol. 21, Supplement 1, 2021 pp. 628-634 e-ISSN:2581-6063 (online), ISSN:0972-5210

Plant Archives

Journal homepage: http://www.plantarchives.org
doi link : https://doi.org/10.51470/PLANTARCHIVES.2021.v21.S1.096

FUNCTIONING OF PLANT GROWTH PROMOTING RHIZOBACTERIA (PGPR) AND THEIR MODE OF ACTIONS: AN OVERVIEW FROM CHEMISTRY POINT OF VIEW

Premasis Sukul*, Jony Kumar, Aarti Rani, Abdirizak Mohamed Abdillahi, Ramayanapu Balu Rakesh and Modalavalasa Harish Kumar

Department of Soil Science and Agriculture Chemistry, School of Agriculture,
Lovely Professional University, Phagwara 144411, Punjab, India.
*Corresponding author: Email i.d.: premasis.20644@lpu.co.in

ABSTRACT

In one stage of mankind's struggle to keep pace with ever increasing demand of food due to accelerating world population, chemical fertilizers contributed enormously to produce sufficient food products. However, a stagnation in the crop productivity along with decreasing soil fertility status and environmental pollution due to continuous, excessive, and imbalanced use of chemical fertilizers. In this scenario, plant growth promoting rhizobacteria (PGPR) become a natural choice as an alternative to the fertilizer to alleviate excessive consumption of fertilizers because PGPR not only promote nutrient availability to plants as biofertilizers but also performin several ways to stimulate plant growth and hence their productivity. In this review, an attempt has been made to highlight the main activities of PGPR in soil and plants, and to analyse their mode of actions from chemistry point of view.

Keywords: PGPR, phytohormone, phosphate solubilization, phytoremediation, nitrogen fixation, siderophore, ACC deaminase

Introduction

Plant growth promoting rhizobacteria (PGPR) refer to bacteria, inhabiting rhizosphere and plant roots, and promoting plant growth by various mechanisms. There are two groups of PGPR, based on their working niche; intracellular and extra cellular (Gusain and Bhandari, 2019). Intracellular PGPR are endophytic in nature, that enter inside the host root cell and may develop nodular structures such as Bradyrhizobium, Mesorhizobium, Allorhizobium, Azorhizobium and Rhizobium; while extracellular PGPR stay in the rhizosphere around the plant roots, which include Pseudomonas, Azotobacter, Bacillus, Azospirillum, etc. Many PGPR stay and live within the plant parts as endophytic bacteria (Compant *et al.*, 2010; Kolbas *et al.*, 2015). Although it has been observed that the colonizing process dominates in the root zone, but origination of endophytic bacteria from other plant partsis also very common (Compant *et al.,* 2005; Compant *et al.,* 2010; Kolbas*et al.,* 2015). However, endophytic bacteria work more closely with their host to stimulate plant growth than rhizosphere and phyllosphere microorganisms (Kolbas *et al.,* 2015).

While studying the mode of action of PGPR to stimulate plant growth, it has been observed that they involve in such activities directly by promoting plant nutrient availability (biofertilizers) (Hayat *et al.,* 2010), synthesizing and releasing some compounds (phytostimulators) such as phytohormones, siderophores, and other metabolites that directly promote plant nutrition (Olander and Vitousek, 2004; Kumar *et al.,* 2013; Glick, 2014; Ahemad and Kibret, 2014), or indirectly when they themselves function as biocontrol agents, release antibiotics HCN, phenazines and antifungal metabolites (Oves *et al.,* 2013; Singh *et al.,* 2013) to protect plants from diseases, act as synergist to some beneficial symbiotic association and degrade organic pollutants (rhizoremediators). Extracellular polymeric substances, released by PGPR, promote water holding capacity of soil, alters soil matrix structure, reduce water evaporation from soil and help to induce metabolic adjustments to drought stress (Zheng *et al.,* 2018). Moreover, PGPR can fix atmospheric nitrogen, while they are in symbiotic association with the host plant to which they supply nitrogen and they derive carbon and energy from the host plant. They can also transform bio-unavailable essential plant element to their bioavailable form, more particularly phosphorus by solubilization. Besides, PGPR produce enzymes that regulate plant growth (Ma *et al.,* 2009). Now, in modern agriculture, PGPR are used efficiently as eco-friendly biofertilizers to alleviate the adverse impact of chemical fertilizers (Altaf *et al.,* 2019) and also help to reduce the use of fertilizers (Katiyar *et al.,* 2016), as they are also reported to exert beneficial synergistic effects on improving soil fertility and plant growth stimulation (Tabassum *et al.,* 2017; Sood *et al.,* 2018; Tang *et al.,* 2020). Reports on extensive reviewing on the general aspect of growth promoting substances released by PGPR are available (Gamalero and Glick, 2011; Ahemad and Kibret, 2014; Gusain and Bhandari, 2019). Therefore, this review article is not focusing such issues, but an attempt has been made to highlight the chemical backgrounds of the functioning of PGPR.

Nitrogen fixation

Biological nitrogen fixers (BNF) transform atmospheric nitrogen to ammonia, a plant-utilizable form, using a complex nitrogenase enzyme system. Nitrogenase system is

composed of components such as (i) nitrogenase reductase which is the iron protein and (ii) nitrogenase with a metal cofactor which further may be of Mo-nitrogenase (most common), V-nitrogenase and Fe-nitrogenase. Nitrogenase reductase provides high reducing power, electrons which are utilized by nitrogenase with cofactor for reducing N_2 to NH_3. It is believed that BNF shares nearly two-thirds of the nitrogen fixed globally, whereas the other one-third portion of the nitrogen is synthesized industrially (Rubio and Ludden, 2008). BNF may be of different categories: (a) symbiotic BNF which fix atmospheric N by the mutualistic association (symbiotic) with leguminous (such as Rhizobia BNF)and non-leguminous (such as Frankia BNF) plants (Ahemad and Khan, 2012) and free living non-symbiotic BNF which may be of endophytes also (Bhattacharyya and Jha, 2012). However, BNF is an energy consuming process, that requires 16 mol of ATP for reduction of each mole of nitrogen.

Bacteria (PSB) promoting phosphorus availability

Phosphorus (P) is an essential element for plant development and growth. It contributes about 0.2 % of dry weight of plant. From soil solution, plants obtain P in the form of phosphate anions that exhibit extreme reactivity and formimmobilized precipitation (pH dependent) with Ca^{+2}, Mg^{+2} under extreme alkaline condition, and with Fe^{+3} and Al^{+3} under extreme acidic condition leading to low P availability to plants. However, such immobilization of P in soil depends on soil pH. Under this pretext, PGPR plays a significant role in solubilizing P from its insoluble inorganic phosphate compounds such as rock phosphate, carboxyapatite, hydroxyapatite etc. PGPR have been reported to release organic acids (gluconic, 2-ketogluconic, oxalic, acetic, succinic, and other acids) (Zaidi *et al.,* 2009) and enzyme phosphatases, catalysing the hydrolysis of phosphoric esters (Glick, 2012), that solubilize insoluble phosphates and transform them to plant available P form. Apart from converting unavailable P to plant available P, phosphate solubilizing bacteria (PSB) promote growth and proliferation of BNF and their efficiency, and also increase trace elements availability by producing plant growth promoting substances such as organic chelates etc. (Zaidi *et al.,* 2009). *Beijerinckia, Enterobacter, Pseudomonas, Bacillus, Rhizobium, Erwinia* etc. are among the most powerful phosphate solubilizers (Bhattacharyya and Jha, 2012). It has also been observed that both phosphate solubilization and phosphate mineralization may coexist in the same bacterial strain (Tao *et al.,* 2008). Besides, phosphate solubilizing PGPR as soil inoculatesare reported to accelerate the natural resistance of the host plant against phytopathogens because they can release several compounds that supress the growth of the fungal and bacterial pathogens (Pahari *et al.,* 2020) and consequently enhance the plant growth and development.

Production of phytohormone

PGPB can produce IAA, cytokinin, and gibberellin and significantly influence the hormonal balance of the plant. Auxins, produced by the PGPB, directly influence the plant's endogenous pool of auxin in such a manner that the bacterial source of IAA may exert either positive or negative effect on the root growth depending upon the total amount of IAA available to the plant and also upon the sensitivity of the plant to the hormone. If the endogenous auxin pool maintains a low level, bacterial auxin may then induce a boost in the growth. However, at optimal level of endogenous auxin pool, the extra addition of auxin from PGPR source may inhibit or suppress the growth (Gamalero and Glick, 2011). Bacterial IAA promotes lateral and adventitious root development that increases the nutrient uptake efficiency. It also stimulates the root exudation. Interestingly, it is a fact that more root exudation causes more proliferation of bacteria and it goes on in a cyclic process. However, this is also true that the production of IAA alone does not account for growth promotion capacity because it indirectly inhibits root elongation (Riov and Yang, 1989). This is attributed to IAA's capacity to stimulate ACC synthase that normally catalyses ACC synthesis in the plant roots, leading to higher level of ACC which, in turn, gives rise to more ethylene production, resulting in inhibition of root elongation. Cytokinins are N6-substituted aminopurines. They influence plant cell division, quiescence of dormant buds, seed germination, accumulation of chlorophyll, leaf expansion, and delay of senescence. Most importantly, the gene coded for a protein, expansin, is regulated by cytokinins (Downes *et al.,* 2001). Expansin is responsible for loosening of plant cell walls, leading to a turgor-driven plant cell expansion. Thus, the size and the shape of the cells are affected. PGPB are reported to produce cytokinins and to alter their levels in plants (Gamalero *et al.,* 2009). Gibberellins, diterpenoid acids consisting of isoprene units, are produced by plants and microorganisms. They influence cell division, seed germination, stem elongation, flowering, fruit setting, and delay of senescence and many other physiological processes. Gibberellins are reported to interact with other phytohormones and affect the hormonal balance and in turn, affect plant growth. Several PGPR are reported to produce and regulate these phytohormones such as IAA, cytokinin, gibberellins etc. in significant amount and thereby influence the plant growth and development.

Siderophore production

Improvement in plant growth through rhizobacterial inoculations, which can produce various siderophore and thus increase the availability of iron to plants, has been extensively studied (Rajkumar *et al.,* 2010; Kobayashi and Nishizawa, 2012; Kumar *et al.,* 2013). Iron is anessential nutrient for plants and microorganisms, that participate in various biochemical processes such as chlorophyll biosynthesis, electron transport chain, oxygen transport, respiration, thylakoid biogenesis and many others (Kobayashi and Nishizawa, 2012). Several enzymes, that are essential for cellular processes, contain ferric residues as cofactors. In soil, rhizobacteria release a wide variety of high-affinity iron-chelating low molecular weight organic compounds that have distinct affinity towardiron. Siderophores, are secondary metabolites that scavenge iron from environmental stocks and supply it to cells via specific receptors.These siderophores as secondary metabolites, secreted from the PGPR, may affect other community members through cooperative and competitive interactions (Kramer *et al.,*2020). The siderophores form soluble ferric complexes and help to increase iron availability to the plants and microorganisms through specific transporter channels under iron starvation (Crowley and Kraemer, 2007; Rajkumar *et al.,* 2010). In *Vigna radiata* plants, chlorophyll content and iron nutrition were promoted by inoculating *Pseudomonas* strain GRP3, siderophore-producing bacteria

(Sharma *et al.,* 2003; Dimkpa *et al.,* 2009). Siderophores, much more than just iron carriers, may act as important mediators of interactions between members of microbial assemblies and the eukaryotic hosts they inhabit (Kramer *et al.,* 2020). Apart from its mobilization of iron and other elements, siderophores are involved in virulence processes and in oxidative stress tolerance (Albelda-Berenguer *et al.,* 2019). Cadmium-siderophore complexation, originated from the cyanobacterium *Anabaena oryzae in the paddy field*, may be used for the sequestration and detoxification of cadmium ions from the environment (Singh *et al.,* 2016; Chakraborty *et al.,*2019). There are mainly three classes of siderophores that includes catecholate, hydroxamate and carboxylate. However, there are a number of other siderophores also isolated and identified from different microbes (Singh *et al.,* 2008). Although initially they were identified for iron chelation, it has been evidenced that they can bind other metal ions too (Singh *et al.,* 2010).

Action of bacteria and AM fungi on plants subjected to heavy metal stress

Phytoextraction of metal(loid)s from contaminated soils and use of engineered plants to improve their effectiveness through more shoot biomass and shoot-metal concentration with the help of PGPB is a major concern now-a days. Several literatures are available on using bacteria or AM fungi as a tool for increasing phytoremediation efficiency in a heavy metal polluted soil (Ma *et al.,* 2009; Vangronsveld *et al.,* 2009; Mench *et al.,* 2010; Ma *et al.,* 2011; Luo *et al.,* 2012). It is believed that inoculation with consortia may result in synergism to deliver better pronounced beneficial effects on plant biomass production as compared to inoculation with single strains. Although limited, but literatures on such studies during reclamation of heavy metal polluted sites are also available. It has been evidenced that doubly inoculated *Trifolium repens L.* (white clover) by an indigenous Cd-adapted AM strain of *Glomus mosseae* and a Cd-adapted bacterium (*Brevibacillus sp.*) exhibited improved root biomass and nutrient acquisition, particularly nitrogen and phosphorus, with reduced uptake of Cd in Cd polluted soil (Vivas *et al.,* 2003). Similar performance was achieved in Zn and Ni polluted soil, when white clover was doubly inoculated with AM and *Brevibacillus* strains with their Zn (Vivas *et al.,* 2006a) and Ni (Vivas *et al.,* 2006b) adaptations. It is believed that both microorganisms improve the soil nutrient status, synthesize ACC deaminase to dissipate stress, and synthesize phytohormones. Although many scientists argue on the capability of bacteria to stimulate mycorrhizal fungi (Gamalero *et al.,* 2008) under stressful condition such as high salinity, presence of heavy metal etc., there are thoughts (Gamalero *et al.,* 2009) that bacteria may help stimulating fungal development, so that mycorrhizae lower down the metal availability due to their high sorption capacity.

Endophytic bacteria usually contribute to exhale beneficial effects towards host plant growth and development through utilization of ACC, production of IAA and siderophores, and phosphate solubilization. Plants must release ACC in sufficient amounts to maintain a static level of ACC in the extra cellular medium, so that ACC may not be converted into ethylene due to its utilization by PGPB (Glick, 2014), that normally limit ethylene production in stressed plant with the help of ACC deaminase and in this regard IAA plays a vital role, convert ACC into ammonium and α-ketobutyrate. It has been evidenced that root endophytes enhance root functions which causes an increase in the uptake of trace elements by releasing protons and exuding siderophores, organic acids, phenolic compounds and polyamines (Rajkumar *et al.,* 2009). It has also been observed that metal binding peptides are exuded by PGPB to promote plants metal uptake efficiency as a mechanism for plant growth enhancement. Phytochelatins, metallothioneins and metallohistins that act as the efficient metal binder were reported to be produced under metal stresses by several PGPB (Sessitsch *et al.,* 2013).

Reduction of ethylene level by PGPB using ACC deaminase

Ethylene regulates plant growth, promoting seed germination and seedling growth, helping to develop adventitious roots and root hair formation at low concentration. However, at higher concentration it may exert toxicity to plants, inhibiting root growth. Therefore, it is essential to maintain ethylene levels in plants at minimum levels. This may be achieved if level of 1-aminocyclopropane-1-carboxylic acid (ACC), that acts as the precursor molecule of ethylene, is reduced. It has been evidenced that several soil bacterial and fungal strains show deaminase activity that degrade ACC to ammonia and α-ketobutyrate, reducing ethylene generated stress(Glick *et al.,* 1998; Glick *et al.,* 2007). It has been observed that L-methionine acts as a precursor for synthesis of S-adenosyl-l-methionine (SAM) that gives rise to ACC by ACC oxidase. ACC is then transformed to ethylene, carbon dioxide and cyanide by ACC oxidase (Figure 1). The total process in higher plants is regulated by switching on – off mode for the expression of ACC synthase and ACC oxidase genes. However, it is also now established that ACC,once it is released from plant roots, is hydrolyzed to ammonia and 2-oxobutanoate by rhizobacteria by ACC deaminase. It is a known fact that when plants are subjected to various biotic and abiotic stresses such as salinity, drought, high or low temperature, pest incidence etc., ethylene biosynthesis in plants is enhanced (Glick *et al.,* 2007). Even sometimes, the accelerated ethylene level is treated as an effective stress indicator (Belimov *et al.,* 2009). Hence, under salinity stress when plants are inoculated with PGPR that exhibit ACC-deaminase activity such as Pseudomonas sp., ethylene concentration in plants are significantly reduced and consequently the negative effect of salinity stress on plant root growth is remarkably decreased (Nadeem *et al.,* 2010). However, it was also observed that PGPR strains exhibited their capability to yield exopolysaccharides that bound Na^+ cations, facilitating reduced Na^+ uptake by plants (Ashraf *et al.,* 2004). Thus, reduced availability of Na^+ to plants brings down the adverse effect of salinity stress on the plant growth and its development. It has been evidenced that transgenic plants showed enhanced growth under salinity stress than the non-transgenic plants (Sergeeva *et al.,* 2006). Hence, genetically engineered plants with enhanced expression of bacterial ACC-deaminase could be an alternative approach to overcome salinity and other stresses.

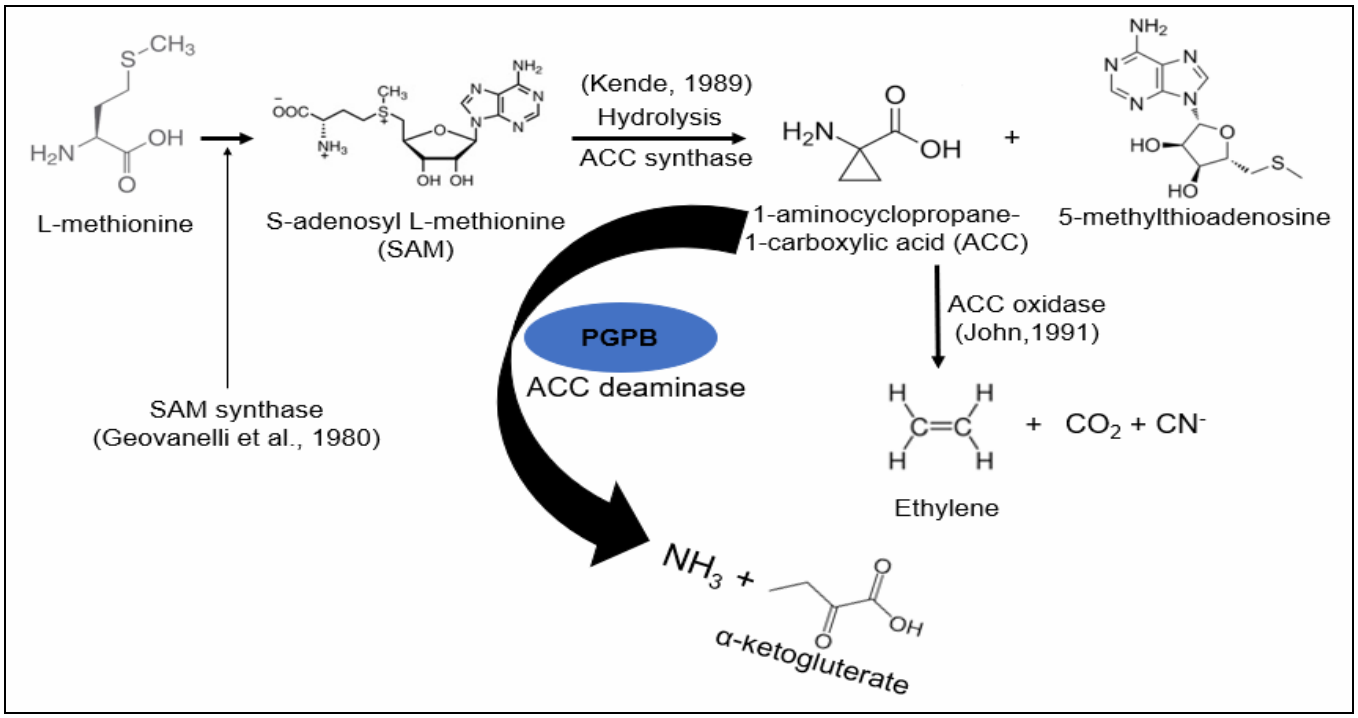

Fig. 1 : Simultaneous process of biosynthesis of ethylene in plant and reduction of ethylene level by PGPB in rhizosphere

Bacteria assisted phytoremediation

Sometimes mercury, cadmium, chromium, lead, copper, zinc, arsenic and many other heavy metals accumulate in soil, due to biogenic, geogenic and excessive anthropogenic activities for intensive agriculture, at a level which is more than their critical levels and express their toxicity to entire living community including humans by entering the food web. Thus, remediation of such toxic heavy metal polluted soil is essential to protect the living community (Gamalero *et al.,* 2009; Ahemad and Kibret, 2014; Gusainand Bhandari, 2019). Among many, phosphate-solubilizing bacteria-assisted phytoremediation is an emerging, widely accepted and more convincing approach as compared to other existing techniques to decontaminate metalliferous soils. Although hyperaccumulator plants are more efficient than other plants to remove metals from metal contaminated soils, as such low bioavailability of metals and metal induced stress affect the efficiency of the hyperaccumulating plants. Under such situation, use of phosphate-solubilizing bacteria (PSB) increases the efficiency of hyperaccumulator plants as the bacteria involve in bringing more amount of phosphorus in the available form that assists to increase plant growth and biomass (Ahemad, 2015). PSB not only increase phosphorus solubility, but also they protect plants from pathogenic activities by synthesizing and releasing HCN, phenazines, antibiotics and antifungal metabolites (Singh *et al.,* 2013) as well as fix nitrogen (He *et al.,* 2013). PSB are reported to release lactic, formic, oxalic, malonic, citric, 2-ketogluconic and many other organic acids that possess chelating properties (Panhwar *et al.,* 2013) with various metals such as Zn,Ni, Cu etc. (Becerra-Castro *et al.,* 2011; He *et al.,* 2013; Arunakumara *et al.,* 2015) and are known to produce biosurfactant (Gamalero and Glick, 2012) that enhances the availability of metals by releasing from their sequestered form in soil.

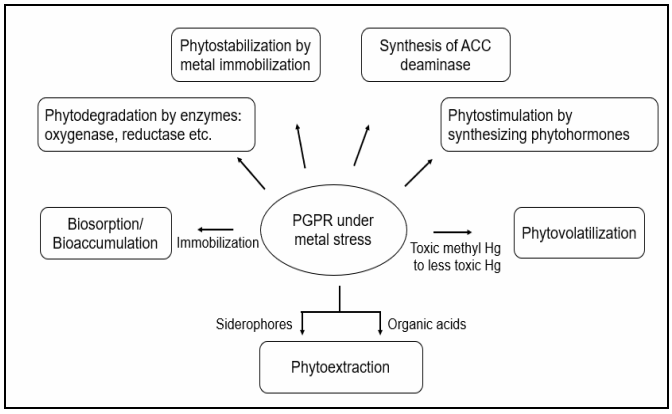

Fig. 2 : Working nature of PGPR under metal stress

Apart from these, PSB are also responsible for production of siderophore (Gamalero and Glick, 2012), IAA (Glick, 2012; Hao *et al.,* 2012), and ACC deaminase (Arshad *et al.,* 2007; He *et al.,* 2010) that cause a stimulation to plant growth. Thus, PGPR help in accelerating the efficiency of phytoremediation of contaminated soil (Figure 2).

Conclusion

In addition to promoting plant growth, which consequently results in increasing crop yield, PGPR assist in the phytoremediation as well as they themselves work well as bio-remediators of polluted soil and water, particularly contaminated with organic pollutants such as petroleum hydrocarbons, pesticides etc. and also inorganic pollutants such as toxic heavy metals. PGPR produce several chemical compounds that directly or indirectly participate in various physiological and biochemical processes in plants, that facilitate congenial conditions for plant growth and development by regulating hormonal balance in plants, controlling harmful plant pathogens, by improving soil structure and aggregate stability and actively participating in the major transformation of unavailable form of nutrients to their plant available form. Hence, they are becoming

promising alternatives to chemical fertilizers and pesticides and are providing an opportunity to strengthen the concept of sustainable ecosystem under the backdrop of overloading the environment with chemical inputs, if PGPR strains are used as biofertilizers.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Conflict of interests

The author declares that there is no conflict of interest regarding the publication of this paper.

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