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Role of Plant Growth Promoting Rhizobacteria in Healthy and Sustainable Agriculture

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CONVENTIONAL agriculture plays a vital role in meeting the increasing demands for food which result from the continuous rising of the human population. Nowadays farmers use more and more amounts of chemical fertilizers and pesticides which have a bad influence on soil quality, the ecosystem, and the health of humans. Hence, it is important to explore other approaches to decrease the application of chemical fertilizers and enhance crop productivity. Inoculation of the crop with plant growth promoting rhizobacteria (PGPR) to augment sustainable agriculture production is another strategy that is eco-friendly and could be carried out in the long run. PGPR is a group of bacteria able to colonize the root of plants and increase their growth and yield. They help in increasing water absorption, suppress pathogens, and also enhance the uptake of nutrients from soil. Biochemical applications by which rhizobacteria can stimulate the growth of plants were discussed in this article; (i) bio-stimulants: represented by particular phytohormones synthesized by PGPR for e.g. auxins or indole acetic acid (IAA), cytokinins, gibberellic acid (GA) and ethylene, (ii) biofertilization: through helping the uptake of many nutrients from the environment e.g. biological nitrogen fixation, phosphate solubilization and production of siderophore, (iii) bioprotectants or biocontrol: by preventing plant diseases through antibiotic, lytic enzymes and/or hydrogen cyanide (HCN) production.

Keywords: Hydrogen cyanide (HCN), IAA, PGPR, Phytohormones, Rhizobacteria.

Introduction

Most of the land across the world is used for agriculture. According to the United Nations (UN), the world population will increase from 7.3 billion people to 9.7 billion by 2050 over the world and this creates numerous problems such as food insufficiency and starvation (Goswami & Suresh, 2020). Hence, it is necessary to double the production of crops to moderate the hazard of starvation and food scarcity. To increase the efficiency of agricultural production, farmers use a large amount of chemical fertilizers and insecticides to achieve higher yields. Excessive and indiscriminate use of chemical fertilizers and pesticides generate several bad impacts on soil productiveness and human health as well as causing environmental pollution, decreasing organic matter in soil, loss of beneficial soil microflora, development of resistant pathogens, contamination of ground water and crops by heavy metals and changing the physical properties of the soil (Damalas & Eleftherohorinos, 2011, Alengebawy et al., 2021). So it is necessary to discover an eco-friendly technique which preserves soil fertility and increase crop yield. One of this technique which is economic and participate in sustainable agriculture development is utilization of soil microflora e.g. bacteria, fungi, yeast and algae. The interaction between plant and microbe in the rhizosphere could result in plant growth promoting activity. Plant growth promoting microorganisms are considered as new and crucial tools in agriculture

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development (Deshwal & Kumar, 2013). Plant growth promoting rhizobacteria (PGPR) are free-living soil-borne bacteria that improve growth of plant either directly, by providing plants with nutrients that they lack in the soil as an alternative to the use of chemical fertilizers or indirectly by shielding the plant from soil borne infections (Glick, 2012). Moreover they are convoluted in several biotic activities of the soil system and synthetic pesticide to make it active for nutrient movement and viable for production of crop (Chandler et al., 2008). In addition, they can stimulate growth of plant through organizing nutrients in the soil, synthesis of various plant growth hormones, protection of plants against phytopathogens, improving soil structure, mitigate the effect of abiotic stress e.g. salinity, drought, acidity and humidity, bioremediation of different classes of toxic heavy metals and degradation of synthetic chemical composites (Yousef, 2018; Warrad et al., 2020). This review illustrates the PGPR in rhizosphere, covers plant microbe interaction and explains the various mechanisms which microbes use to stimulate plant growth and productivity.

Rhizosphere

The rhizosphere concept was firstly introduced by Hiltner (1904), a German researcher, as the slim layer of soil surrounding the root in which microbial population colonize plant root directly or indirectly and affected by the compounds exuded by the root as well as the microorganisms that feed on these compounds (Sharma & Verma, 2018). The term rhizosphere is derived from the Greek word ‘rhiza’, meaning root, and ‘sphere’, meaning surrounding or area of influence but recently the term rhizosphere has been developed to include the volume of soil influenced by the root and the root tissues inhabited by microorganisms (Huang et al., 2014). The rhizosphere is more affluent with bacteria than the near-bulk of soil. One gram of rhizosphere soil contains larger number of microorganisms nearly from 10 to 1000 times compare to that found in bulk soil (Yadav et al., 2015; Adeleke et al., 2019). The chemical attractants released by roots are defined as root exudates; the structure of these exudates depends upon the biological status, the microorganisms and plant species (Grover et al., 2021). Root exudates act as signaling molecules that increase communication between useful microbial population and plant and as a result enhance growth, yield and resistance of the plant (Singh et al., 2016). This agree with Park et al. (2017) who illustrated that plant-microbe interaction is a broad communication process between plant root and related microorganisms through chemical compounds secreted by plant root and microorganisms that may work as toxic, nutrient or signaling molecules. The process of releasing volatile, soluble and particulate exudate materials is called rhizodeposition. The exudates of the root are translocated across the cell membrane and expelled to the rhizosphere. There are many factors that affect concentration and composition of the exudates such as plant species, developmental stage, and nutrition of plant, soil nature and environmental factors such as temperature, soil water potential and light intensity (Noumavo et al., 2016). Root exudates in the rhizosphere, with their nutritional value, can attract beneficial and pathogenic microorganisms including bacteria, fungi, and viruses. The interaction between soil plant, and soil microflora, that takes place in rhizosphere, is responsible for various important processes such as sequestration of carbon, mitigation of environmental factors, and nutrient cycling. Plant-microbe interaction is affected by the composition of root exudates and the type of microorganisms nurturing on these exudates (Gupta et al., 2017). The rhizosphere is very rich with various types of chemical components as well as primary and secondary metabolites (Table 1), such as mucilage, ions, free oxygen, water, sugars, organic amino acids and hormones some of which are required for plant growth (Swamy et al., 2016). Rhizo-microbiome composition varies according to composition of the root exudate which changes by developmental stage of plant and plant genotype (Vachero et al., 2013). It was reported that cucumber root exudes of citric acid attracts *Bacillus amyloliquefaciens* SQR9 leading to formation of biofilm and enhance its root colonization. In addition, fumaric acid exudate from banana root attracts *Bacillus subtilis* N11 and motivates biofilm formation (Mhlongo et al., 2018). The rhizosphere is divided into three zones depending on their relative intimacy and their influence on the plant root (Choudhary et al., 2016). First zone, the outermost zone, is the exo-rhizosphere or ecto-rhizosphere, the outermost zone, surrounding the root which remains close to root after hearty shaking and contain root hairs, plant and bacterial mucilage (Chandra & Singh, 2016). The second zone is the rhizoplane it is considered as a part of the system and is also known as the root surface which corresponds to the medial area that include the root epidermis in addition to mucilaginous polysaccharide layer and is colonized by certain types of endophytic microorganism which has the ability to colonize internal root tissues and root itself (Nihorimbere et al., 2011). Endophytes are usually identified as bacteria or fungi existing inside plant tissue without negatively affecting its growth and can be isolated from plant after surface sterilization (Gaiero et al., 2013). Finally the third zone is the endo-rhizosphere, interior of root tissue, containing cortex and endodermis and is colonized by endophytic bacteria and does not form synergetic structures with plant (Reinhold-Hurek et al., 2015). Furthermore, there is another zone known as myco-rhizosphere in which mycorrhiza fungi colonize the plant roots (Noumavo et al., 2016). Most of plants are able to form rhizosheath as an adeptive trait against abiotic stress (Ndour et al., 2020). Rhizosheath is the thick, highly sticky layer adheres to the roots after excavation that includes root hairs, soil particles, mucus and microbes (Prashar et al., 2014; Zhang et al., 2020).

TABLE 1. Various compounds found in root exudates of different plant species. Adapted from (Dakora & Phillips, 2002)

Amino acids	α-Alanine, β-alanine, asparagines, aspartate, cystein, cystine, glutamate, glycine, isoleucine, leucine, lysine, methionine, serine, threonine, proline, valine, tryptophan, ornithine, histidine, arginine, homoserine, phenylalanine, γ-aminobutyric acid, α-aminoadipic acid
Organic acids	Citric acid, oxalic acid, malic acid, fumaric acid, succinic acid, acetic acid, butyric acid, valeric acid, glycolic acid, piscidic acid, formic acid, aconitic acid, lactic acid, pyruvic acid, glutaric acid, malonic acid, tetronic acid, aldonic acid, erythronic acid
Sugars	Glucose, fructose, galactose, ribose, xylose, rhamnose, arabinose, desoxyribose, oligosaccharides, raffinose, maltose
Vitamins	Biotin, thiamin, pantothenate, riboflavin, niacin
Purines/nucleosides	Adenine, guanine, cytidine, uridine
Enzymes	Acid/alkaline-phosphatase, invertase, amylase, protease
Miscellaneous compounds	Auxins, scopoletin, fluorescent substances, hydrocyanic acid, glycosides, saponin (glucosides), organic phosphorus compounds, nematode-cyst or egg-hatching factors, nematodes attractants, fungal mycelium growth stimulants and inhibitors, zoospore attractants

The plant growth promoting rhizobacteria (PGPR)

Rhizobacteria in the rhizosphere occupy approximately 95% of microbial community due to their ability to utilize various nitrogen and carbon sources and rapid growth rate (Govindasamy et al., 2010; Glick, 2012). Plant physiology is affected by rhizobacteria through different ways. Thus, plant growth is either neutrally, beneficially or harmfully affected by the existence of rhizobacteria in the rhizosphere (Haghighi et al., 2011; Shilev et al., 2019). The existence of neutral rhizobacteria in the rhizosphere has possibly no influence on plant health. In contrast, phytopathogenic rhizobacteria (*Enterobacter*, *Desulfovibrio*, *Agrobacterium, Chromobacter and Erwinia*, etc.) has negative effect on the growth and physiology of plant as it produces phytotoxic substances such as ethylene and hydrogen cyanide (Martínez et al., 2010). While the beneficial rhizobacteria (*Pseudomonas, Bacillus, Azospirillum*, etc.) have positive effect on plant growth and crop yield via different mechanisms of action, these beneficial rhizobacteria are defined as PGPR (Noumavo et al., 2016). PGPR is a word invented by Kloepper around 1970s; it is the soil bacteria found in the rhizosphere inhabiting the roots of plants, and promoting plant growth directly or indirectly. It is also known as nodule promoting rhizobacteria (NPR) and plant health promoting rhizobacteria (PHPR) (Hayat et al., 2010; Joseph et al., 2012). According to their position in rhizosphere, PGPR can be categorized as either extracellular PGPR (ePGPR) present in the rhizosphere, between the space of root cortex in addition to rhizoplane so they gain high advantage from root exudates for e.g. *Flavobacterium, Agrobacterium, Azotobacter, Burkholderia, Azospirillum, Caulobacter, Bacillus, Arthrobacter, Chromobacterium, Serratia, Erwinia, Micrococcous,* and *Pseudomonas* (Verma et al., 2010), or intracellular PGPR (iPGPR) present inside the root cells, such as endophytic bacteria which form nodules for *Azorhizobium, Mesorhizobium, Bradyrhizobium, Allorhizobium,* and *Rhizobium* belongs to family Rhizobiaceae (Figueiredo et al., 2011). This later group contains a large number of Gram-negative rods and lower numbers of Gram-positive cocci**,** rods or pleomorphic (Bhattacharyya & Jha, 2012). Apart from bacteria, certain yeasts such as *Saccharomyces cerevisiae* are able to produce several metabolites which promote plant growth and increase crop productivity (Massoud et al., 2014). According to Kumar et al. (2020), PGPR have the ability to colonize the root surface, survive, germinate, compete with other microbiota and express their plant growth promotion activities. The over use of chemical fertilizers will be reduced through bio-inoculation of plant growth promoting rhizobacteria (PGPR) which help in the uptake and availability of nutrients, support sustainable agriculture and reduce environmental contamination (Etesami & Adl, 2020) (Fig. 1). PGPR are categorized according to their functional activities into: (i) biofertilizers, which facilitate the uptake of certain nutrients from the environment (ii) phytostimulators, which synthesize particular compounds or phytohormones to the plant. (iii) bioprotectants or biocontrol which protect the plants from diseases via producing antifungal metabolites and/or antibiotics (Antoun & Prévost, 2005; Lugtenberg & Kamilova, 2009).

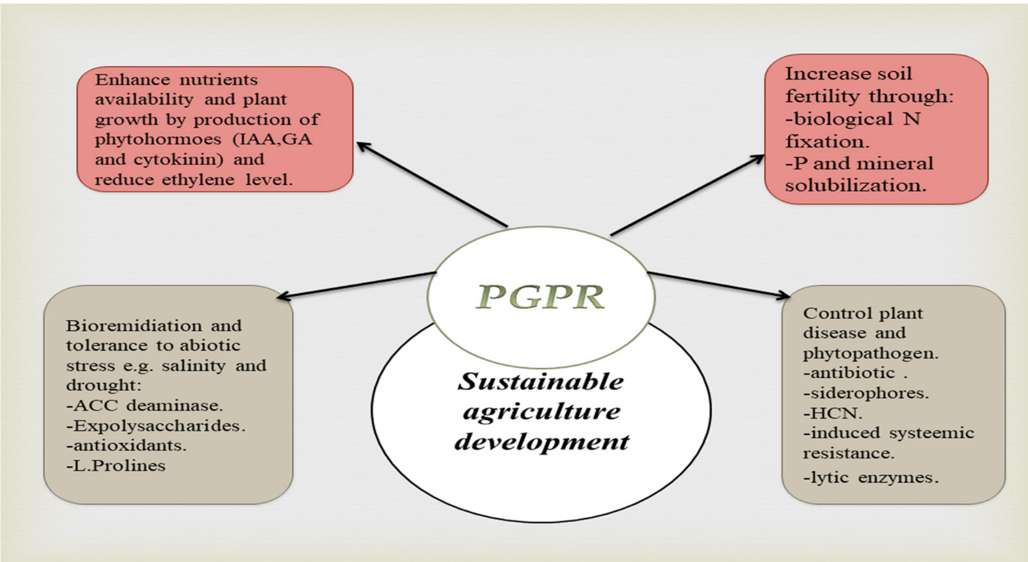

Fig. 1. Different mechanisms and application of PGPR

Applications of PGPR

Biofertilizers

Biofertilizers are one of the most favorable applications which can advance fertility of soil and enhance crop production. They also help in reducing contamination through reducing the excessive consuming of chemical fertilizers (Stefan et al., 2008). The term biofertilizers differ from organic or biological fertilizers, where organic fertilizers are organic compounds which increase plant growth directly. The biofertilizers should contain living organism(s) which colonize plant roots and facilitate the uptake of nutrients by increasing root surface area (Vessey, 2003). This opinion was accepted by Bhardwaj et al. (2014) indicating that biofertilizers generally rely on natural microflora in the soil which consists of all kind of bacteria as well fungi and are known as PGPR. The application of biofertilizers to plant contributes in nutrient cycling and increase crop yield. Many reports showed that biofertilization provide the crop with nearly 65% of its nitrogen source (Nihorimbere et al., 2011; Nehra & Choudhary 2015). Bio-fixation and bio-solubilization process occurring by PGPR possibly take vital part in soil fertilization.

Biological nitrogen fixation (BNF): Nitrogen is one of the main nutrients necessary for the growth of all living organisms as plants and bacteria, so deficiency of nitrogen in soil has led to consuming huge quantities of nitrogenous fertilizers which increase production costs for the farmers. Furthermore excess N_2 loss to the environment causes serious problems such as groundwater nitrate contamination, greenhouse gas emissions and soil acidification (Zhang et al., 2015). Nitrogen is an important component of nucleotides, lipids membrane and amino acids that forms enzymes and structural proteins (Marschner, 2011). Although, N_2 occupies about 78% of the atmosphere, it is unobtainable to plants because its inert nature leading to plant species being unable to convert atmospheric dinitrogen to ammonia and utilize it for their growth directly. N-fixation takes place through three different ways, (i) geochemically by lightning, (ii) biologically by the action of nitrogenase enzyme which present in certain microorganisms, (iii) industrially through Haber–Bosch process (Hoffman et al., 2014). Every year, nearly 152 megatons of nitrogen are fixed and converted into ammonia through Haber–Bosch process to enhance agricultural production and crop yield (Flores-Tinoco et al., 2020). Furthermore, ineffective use of nitrogen causes contamination of soil by nitrate leading to harmful effects on human health as well as agricultural sustainability (Santi et al., 2013). Nitrogen fixing bacteria connected to rhizosphere are progressively used with non-legume crop species such as wheat, maize, sugar beet; sugarcane and rice (Kaymak 2010). The biological fixation of atmospheric nitrogen is an essential microbial action to maintain life on earth through photosynthesis achieved by using photosynthetic organisms (Prasad et al., 2019). Biological nitrogen fixation (BNF) is the process of enzymatic reduction of inert atmospheric N_2 into reactive NH_3 (ammonia) using a complex enzyme system known as nitrogenase.

$$N_2 + 8H^+ + 8e^- + 16Mg\text{-}ATP \xrightarrow{\text{nitrogenase}} 2NH_3 + H_2 + 16Mg\text{-}ADP + 16\,P$$

Nitrogenase is an essential metalloenzyme catalyzing important reactions including reduction of nitrogen to ammonia, a main step in global nitrogen cycle; as well as reduction of carbon monoxide (CO) and carbon dioxide (CO_2) (Hu & Ribbe, 2016). Thus, nitroginase has the potential for biotechnological applications such as: the Haber-Bosh process for fertilizier production and the Fischer-Tropsch process for feul production (Rohde et al., 2020; Oehlmann & Rebelein, 2022). The structure of nitrogenase was elucidated by several investigators (Dean et al., 1993; Ribbe et al., 1997; Hu et al., 2005). Nitrogenase is a multi-component metalloenzymes consisting of (i) dinitrogenase reductase, iron protein, which is a dimer of two identical subunits that contains the sites for Mg ATP binding and hydrolysis, and provides electrons with high reducing power, (ii) dinitrogenase which has a metal cofactor and uses these electrons to reduce N_2 to NH_3 (Smith & Eady, 1993; Eady, 1995). There are different types of dinitrogenase based on the site of the active co-factor binding enzyme: (a) iron (Fe) Nitrogenase is less unique as it is a part of other electron carrier as cytochromes and ferredoxin. (b) Vanadium (V) nitrogenase. (c) Molybdenum (Mo) nitrogenase is the most common type in the nitrogen fixing bacteria (Hu & Ribbe, 2015; Mahmud et al., 2020). Biological nitrogen fixation usually takes place at moderate temperatures through nitrogen fixing rhizobacteria, which are generally dispersed in the environment (Raymond et al., 2004). Nitrogen fixing organisms can be divided into, symbiotic N_2 fixing bacteria (SNF) that convert atmospheric N_2 to ammonia and other compounds to be transported directly to the growing plants in the form of amino acid like asparagine and glutamine as well as forming symbiotic correlation with root of leguminous plant such as *Rhizobia* and non-leguminous trees as *Frankia* (Ahemad & Khan, 2012; Shin et al., 2016). This type of symbiotic relationship constitutes a complex host - symbionts interaction. Finally, nodulation occure and bacteria colonize as intercellular symbionts (Fig. 2), and a symbiotic nitrogen fixing such as *Azocarus*, *Azotobacter*, *Gluconoacetobacter, Azospirillum*, diazotrophicus, and cyanobacteria for e.g. *Nostoc* and *Anabaena* are free-living bacteria in close association with the root (associative) and are also able to convert atmospheric N_2 to ammonia (Bhattacharyya & Jha, 2012; Dal Cortivo et al., 2020).

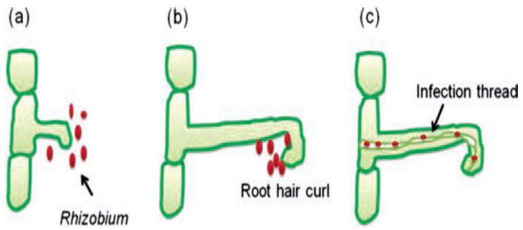

Fig. 2. Nodule formation method; (a) adhesion of bacteria with host lectin and attachment of rhizobial with root cell. (b) nod factors are exudate by rhizobia and curling of root hairs (c) diffusion of bacteria into root hairs forming a contaminated filament then reach to the cortical region in the cell and form bacteroid state, in this manner nodules are formed (Adapted from Ahemad & Kibret, 2014)

Biological nitrogen fixation are generally known as diazotrophs including free living bacteria, some sulfate reducing bacteria and symbiotic diazotrophes such as Rhizobium (Sun et al., 2021). Symbiotic bacteria are able to fix more nitrogen than non- symbiotic bacteria (Glick, 2012). The *nif* genes responsible for biological nitrogen fixation.There are three structural genes; *nif* D, *nif* K, *nif* H that encode for the Mo-nitrogenase polypeptide, Mo-protein subunits, and Fe protein, respectively, which form the structural components of nitrogenase complexes (dintroginase reductase and dinitroginase) (Reed et al., 2011; Shin et al., 2016). N-fixing bacteria contain different gene sets responsible for promoting symbiotic association. These are *nod*, *nif* and *fix* genes, which are collectively known as *sym* genes.The bacterial *nod* gene set is accountable for the formation of nodule during the interaction with host nodulin genes, while *fix* gene plays a vital role in regulation and metabolism of oxygen concentration for *nif* genes expression (Sheoran et al., 2021). Oxygen has negative effect on the process of nitrogen fixation, due to the sensitivity of *nif* genes to oxygen. So bacterial hemoglobin may be introduced to bind free oxygen and prevent its inhibitory effect on nitrogen fixation (Kundan et al., 2015) (Fig. 3). The inoculation of biological N_2-fixing PGPR in crops and in crop fields enhances the action of growth promotion, controls plant diseases also raises the number of nodules in root system and keeps the level of nitrogen in agronomic soil (Damam et al., 2016). Reduced ratio or nitrification inhibition offers long time for plant to assimilate nitrogen. Hence, secondary metabolites such as phenolic acids and flavonoids are produced by plant to inhibit nitrification. For example, *B. humidicola* produce nitrification inhibitor as root exudates that inhibit nitrifying bacteria, with no antagonistic effect on other soil microflora (Gopalakrishnan et al., 2015).

Phosphate solubilization: Plants need adequate amount of phosphorus (P) to achieve their optimum growth. Moreover, it has a significant role nearly in all metabolic processes such as signal transduction, energy transfer, and photosynthesis (Zhu & Whelan, 2018). Phosphorus is important for formation of the seed which has the largest amount of phosphorus in the plant (Noumavo et al., 2016). Contrary, phosphorus deficiency may cause reduction in size and growth of plant (Sharma et al., 2013). Phosphorus has the lowest concentration among vital nutrients ranging from 0.001mg/L in poorly soil to 1mg/L in highly enriched soil (Satyaprakash et al., 2017). About 95–99% of phosphorus is found as immobilized (adsorbed on the soil minerals or precipitation through reaction with free cations like Al_3^+, Fe_3^+ and Ca_2^+ in the soil solution), precipitated or insoluble forms consequently, plants are unable to absorb phosphorus (Anand et al., 2016). Plants absorb phosphate only in the form of monobasic ($H_2PO_4^-$) or dibasic (HPO_4^{-2}) ions. Insoluble phosphorus exists as an inorganic mineral e.g. apatite, hydroxyapatite, and oxyapatite or in organic forms containing inositol phosphate also known in soil as phytate, phosphomonoesters, phosphodiesters or phosphotriesters (Glick, 2012; Pérez-Montaño et al., 2014). In general, phytate is biologically unavailable to plant root due to the very small quantity of phytase enzyme that degrade it (Olanrewaju et al., 2017). Therefore, phosphate fertilizer is used in limited amount to face the deficiency of phosphorus in the soil (Kaminsky et al., 2018). Extensive utilization of fertilizers may have negative influence on the microbial function and plant production in soil. In addition, the price of phosphate fertilizers is quickly amplified and their qualities are reduced (Daneshgar et al., 2018).

Smaller quantities of applied phosphatic fertilizers are absorbed by plants while the rest is quickly changed into insoluble complexes and triggered in the soil (Singh et al., 2020a). Most of excess phosphorus in the soil is present in insoluble form so plant becomes unable to assimilate it. For this reason extra phosphorus is unfavorable to plant (Itelima et al., 2018). So it is important to explore another approach which is eco-friendly and economic to increase crop yield with low P concentrations. PGPR has a vital role in the conversion of insoluble phosphorus into a soluble form which can easily be absorbed by the plant. Phosphate solubilizing bacteria (PSB) is a kind of bacteria capable to solubilizing phosphorus, where they transform insoluble inorganic phosphate plus insoluble organic phosphorus and make it available to plant (Alori et al., 2017; Hauka et al., 2017). Bacterial species such as *Rhizobium, Enterobacter, Azotobacter*, *Mycobacterium, Flavobacterium, Beijerinckia, Bacillus*, *Burkholderia, Pseudomonas, Serratia,* and *Erwinia* are described as the greatest phosphate solubilizing bacteria (Bhattacharyya & Jha, 2012). The main mechanisms for phosphate solubilization employed by PGPR include secretion of organic acids for example propionic acid, succinic acid, formic acid, lactic acid, fumaric acid, glycolic acid (Vazquez et al., 2000), malic acid, acetic acid, gluconic acid, oxalic acid, 2-ketogluconic, and citric acid (Zaidi et al., 2009), which are formed as a result of utilization of sugar present in root exudates (Fig. 4). These acids act as good chelating agents and remove associated divalent Ca^{2+} cations releasing phosphates from its insoluble phosphatic complex (Patel et al., 2015). The soil pH is reduced by these acids owing to the releasing of proton/bicarbonate in addition to gaseous exchanges "O_2/CO_2" (Sharma et al., 2011). The ratio of organic phosphorus in the soil is approximately from 30 to 50%. Organic materials such as phytate also known myo-inositol hexa-phosphate, are the most important source of organic phosphorus in the soil comprising about 80% of the total organic phosphate (Goswami et al., 2016). Plant roots create very small amount of phytate degrading enzymes, so phytate is usually unavailable to plant. Conversely, various PGPR are able to solubilize phytate also mineralize the insoluble organic phosphate via the secretion of extracellular enzymes for instance phosphatases, else C-P lyases and phytases (Weyens et al., 2010). Organic phosphorus compounds which have high molecular-weight for example phospholipids, phosphomonoesters, nucleic acids and phosphodiesters, are degraded into smaller molecular weight organic phosphate, easy for cellular assimilation. Mineralization of phosphorus means the solubilization of organic phosphorus and it's breaking down into smaller residual parts in the soil (Olanrewaju et al., 2017). It is observed that solubilization of inorganic phosphate and mineralization of organic phosphate may exist together inside the same phosphate soulbilizing bacteria (Katiyar et al., 2016; Kumari et al., 2020). Utilization of PGPR to solubilize phosphate in agronomic applications is stimulated for numerous reasons as they improve fertility of soil and enhance crop yield by boosting the availability of nutrients (Bechtaoui et al., 2020). Moreover, they are eco-friendly; do not affect the soil health, and have antagonistic potential against pathogenic microflora (Mitra et al., 2020).

Biostimulation

Biostimulants are organic chemical complexes which affect growth of plant and are identified as plant growth regulators or phytostimulants which increase the efficacy of nutrient consumption and find new routes of nutrient acquirements by plant (Ravari & Heidarzadeh, 2014; Du Jardin, 2015). Also, biostimulants are identified as "every microorganism or substance added to plant and facilitate nutrient uptake, increase tolerance to abiotic stress or improve crop quality" (Van et al., 2017). They are classified into auxin (indole-3-acetic acid (IAA)), gibberellic acid (GA), cytokines and ethylene (Kenneth et al., 2019). The mechanism of cytokinin and gibberellin synthesis by PGPR is not yet fully understood (Backer et al., 2018). Phytohormones present at low concentrations (<1mM), may promote, inhibit, or modify growth and development of plants (Gouda et al., 2018). These organic compounds are synthesized and transported from higher concentration to lower concentration (Mehmood et al., 2018). Despite that these chemical molecules are synthesized endogenously in the plant, they remain based on external source (exogenous) to achieve their best performance (Kenneth et al., 2019). The exogenous plant hormones are synthesized exogenously through natural and artificial means and are similar to normal plant hormones (Odoh, 2017). The application of exogenous phytohormones may stimulate metabolism and growth under environmental stress. Recent investigations showed that phytohormones produced by rhizospheric microorganism may be essential for metabolic engineering aiming to induce host plant tolerance to abiotic stress (Egamberdieva et al., 2017).

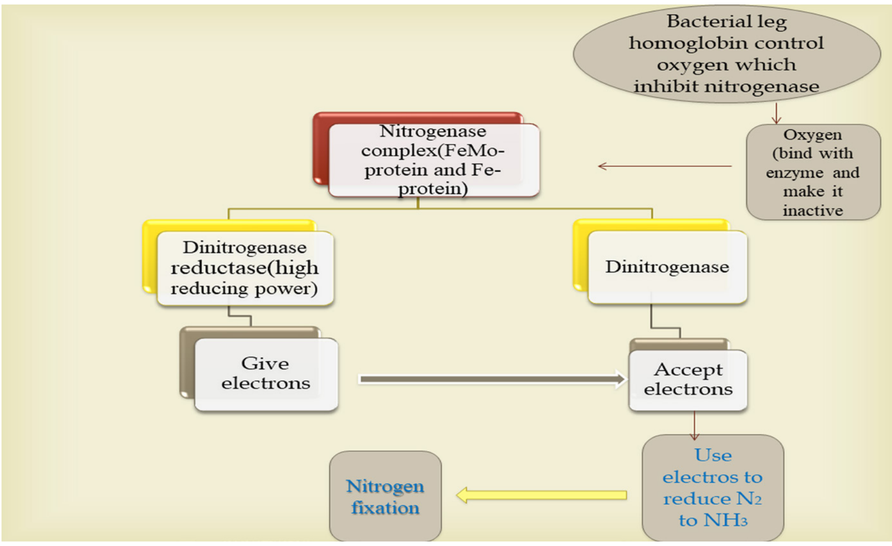

Fig. 3. N_2 fixation mechanism by plant growth promoting rhizobacteria (PGPR) using enzyme known as nitrogenase complex (Mahanty et al., 2017)

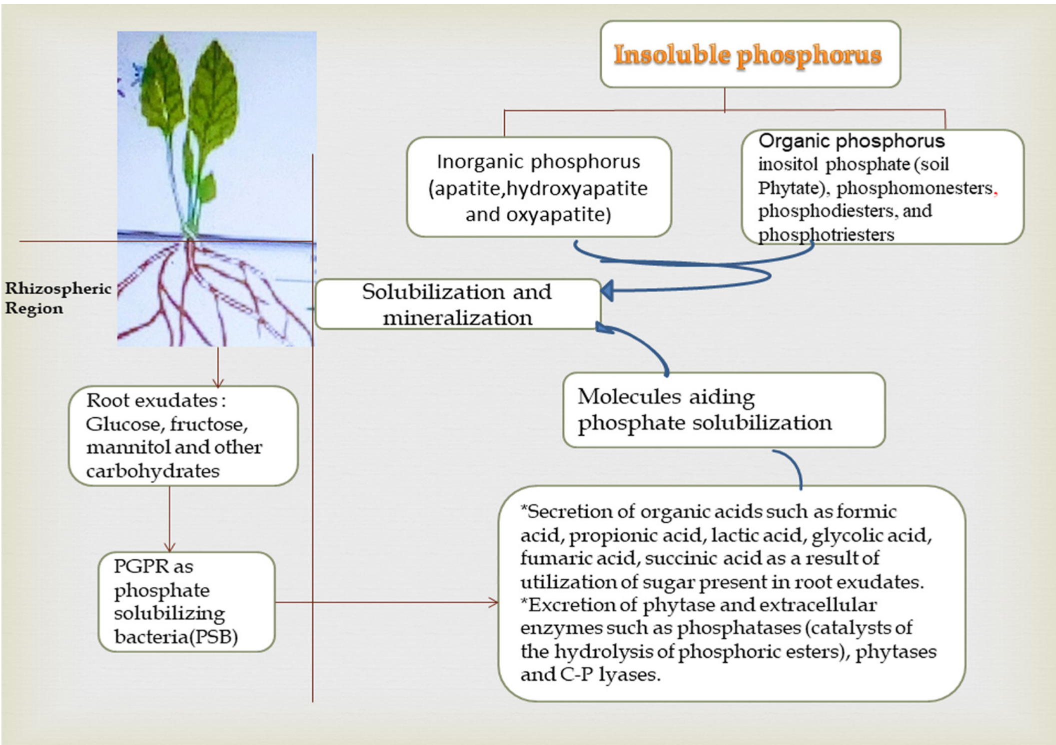

Fig. 4. Mechanism of phosphorus solubilization (Goswami et al., 2016)

Auxins

It is the most essential phytohormone which that is required to stimulate plant growth and development. Also, it is important for development of cell cycle, reducing size and density of stomata and increase root biomass (Minakshi et al., 2020). It also influences the dimension of the shoot and the root meristems. Auxin has a significant role in gravitropism and phototropism of shoots and roots as well as for shadow avoidance (Tsukanova et al., 2017; Khan et al., 2020). Indole-3-acetic acid (IAA) is the most abundant and famous plant hormone of the auxin family, with wide biological effects on plant (Backer et al., 2018). There are other types of auxins such as indole-3-butyric acid (IBA) and phenyl acetic acid (PAA) but their complexity and mode of actions aren't yet fully understood (Kenneth et al., 2019). Application of Indole to plant may have negative effects on auxin signals inside the plant. Furthermore, while indole can be altered into auxin, the level of auxin remains constant in the plant, thus inhibit the ability of plant to response to external auxin. This suggests that indole may act as an auxin antagonist in the plant (Verbon & Liberman, 2016). IAA can be produced and released by microorganisms colonizing rhizosphere of different plants as secondary metabolites because the rhizospheric soil is rich with root exudates required for growth of microorganism compared to non-rhizosphere soils. Plant growth-promoting rhizobacteria (PGPR) including *Pseudomonas, Azospirillum, Bacillus, Azotobacter, Burkholderia,* and *Rhizobium* are able to synthesize IAA or correlated auxins. Eighty percent of the rhizobacteria isolated from the rhizosphere are able to produce IAA. Reports showed that Gram-positive free-living soil bacteria lack IAA production. While another report proved that Gram-positive phytopathogen *Rhodococcus fascians* is able to synthesize IAA (Idris et al., 2007). The ability of rhizobacteria to produce IAA differs significantly between plant species due to the difference of IAA producer, culture conditions, stage of bacterial growth, and substrate availability in the culture medium (Bessai et al., 2022). Indole-3-acetic acid plays a key role in the regulation of plant growth and development. IAA affects plant cell division, extension, and differentiation, stimulates seed and tuber germination; increases the rate of xylem and root development, controls processes of vegetative growth, initiates lateral and adventitious root formation, mediates responses to light, gravity and florescence, affects photosynthesis, pigment formation, biosynthesis of various metabolites, and resistance to stressful conditions (Govindasamy et al., 2010; Mahanty et al., 2017; Pal, 2019). Additionally, bacterial IAA increases surface area and root length by providing the plant with sufficient nutrients from the soil. Also, Rhizobacterial IAA loosens cell walls of plants and as a result the amount of root exudates increases and facilitates the uptake of root exudates that is responsible for nutrition of rhizospheric bacteria. Hence, Rhizobacterial IAA is known as an effector particle in plant–microbe interactions in pathogenesis and phyto-stimulation (Nazir et al., 2018). The type of plant may affect response of plant to IAA depending on the complexity of specific tissue. The rate of IAA produced by the plant (endogenously) is essential in limiting bacterial IAA that either enhance or destroy growth of plant. Endogenous IAA in plant root may be optimal or suboptimal for plant growth, and extra IAA that is synthesized from bacteria may change the IAA level to either optimal, promoting plant growth or supra optimal, inhibiting plant growth (Glick, 2012). Development and growth of plant are affected by IAA concentration, whereas, low concentrations promote plant growth while high concentrations inhibit it (Kaya et al., 2021). The influence of exogenous IAA on the roots structure of *Arabidopsis thaliana* is determined by its concentration in which it is simulative for the main root (MR) and lateral roots (LRs) in the range of 1.0–5.0nM and is inhibitory for the formation of LRs when the concentration is 12.5nM, while it blocks growth of both the MR and LRs at 25.0nM (Tsukanova et al., 2017). Experiments applied with artificial auxin illustrate that the influence of auxins on growth of root may be related to the position of hormone submission. Inoculation of auxins to the root tips was found to stimulate the lateral root initiation, while shoot application of auxin promotes the development of lateral root. In accordance, the response of different plants to auxin depends on the position where of PGPR is applied either through leaf spraying or seed injection (Kudoyarova et al., 2019). IAA production is affected by growth phases, culture condition and various environmental conditions (Liu et al., 2019). Tryptophan present in root exudates is considered as the highest precursor for biosynthesis of IAA (Idris et al., 2007). Higher production of IAA takes place in all conditions where tryptophan is added to the culture media (Spaepen & Vanderleyden, 2011). IAA biosynthetic pathways are similar in plant and bacteria where it occur through L-tryptophan dependent (Trp dependent) and L-tryptophan independent, in the absence of tryptophan (Trp independent) pathway (Dimkpa et al., 2012; Kochar et al., 2013). The intermediate stages and genes in Trp independent pathway remain unknown and predominantly found in Cyanobacteria and Azospirilla (Fu et al., 2015). In tryptophan-independent pathway, the main precursor is indole-3-glycerolphosphate. Conversely, there is no enzyme described in this pathway (Sun et al., 2018). L-tryptophan dependent pathways for IAA biosynthesis from L-tryptophan is described in (Fig. 5): (i) the beneficial rizobacteria which promote plant growth such as *Rhizobium*, *Bradyrhizobium*, and *Azospirillum* tend to use indole-3-pyruvate pathway (IPyA) for IAA production (Minakshi et al., 2020). (ii) tryptamine pathway and Tryptophan side-chain oxidase pathway observed *in Pseudomonas fluorescens* CHA0 (Iftikhar & Iqbal, 2019). (iii) phytopathogenic bacteria can mainly synthesis IAA through indole-3-acetamide pathway (Bar & Okon, 1993). This pathway takes place via two steps; (i) conversion of tryptophan by tryptophan-2-monooxygenase *(IaaM)* to indole-3-acetamide (IAM) which is encoded by the *iaaM* gene, (ii) IAM is converted to IAA by an IAM hydrolase (*IaaH*), encoded by *iaaH* gene. Moreover oxygen is necessary for the first step with the releasing of H_2O and CO_2. This pathway occurs in *Pseudomonas syringae, Pantoea agglomerans, Rhizobium* and *Bradyrhizobium* (Spaepen et al., 2007; Bar & Okon, 1995). Besides acting as phytohormones, indole stimulates plant growth. It is one of the most essential nitrogen-containing heteroaryl compounds, present widely in biological system playing a vital role in biochemical processes. Indole derivatives are shown to be neutral medicinal compounds and participants in drug strategy as nonsteroidal anti-inflammatory drugs, e.g. Indomethacin and indoxole (Essa et al., 2018).

Cytokinins (CK)

Cytokinin is a group of plant hormones that may be applied endogenously through meristematic tissues, shoot apex and root tips of devolving plant or exogenously by PGPR. Approximately, there are 20 types of ordinary plant cytokinins (Farman et al., 2019). It is reported that, greater concentrations of cytokinin have a positive influence on the development of shoot compared to root. The major type of cytokinin are trans-zeatin [6-(4-hydroxy-3-methyl-trans-2-butenylamino) purine], i6Ade [6-(3-methyl-2-butenylamino) purine], cis-zeatin [6-(4-hydroxy-3-methyl-cis-2-butenylamino) purine], and dihydrozeatin [6-(4-hydroxy-3-methyl-butylamino) purine (Goswami et al., 2016). While the mechanism of action of cytokinin is not yet clear enough, cytokinins have a significant role in chloroplast biogenesis; preserve cellular proliferation and differentiation, cell division, anthocyanin production and photomorphogenic development. Also, Cytokinins affect compassion of vascular cambium, multiplying of root hairs, they may prevent the senescence of premature leaf also development of lateral root and elongation of primary root (Egamberdieva et al., 2017; Kenneth et al., 2019). Furthermost abundant cytokinins are adenine-type, where the site N_6 of adenine is replaced by either an isoprenoid, for example as in zeatin, or an aromatic side chain, as in kinetin. Furthermore, zeatin is generally formed by PGPR. There are two different pathways by which it can be produced,the tRNA pathway where zeatin is a recycled product of isopentenylated tRNA by rotation of tRNA containing *cis*-zeatin, and the adenosine monophosphate (AMP) pathway, in which zeatin is manufactured from an isopentenyl donor such as AMP, adenosine monophosphate, adenosinediphosphate (ADP), or dimethyl-allyl-diphosphate (DMAPP), or adenosine triphosphate (ATP) by isopentenyl transferases (Goswami et al., 2016). Cytokinins and gibberellins or both can be synthesized by PGPR such as *Pantoea agglomerans, Azotobacter* spp*.*, *Rhodospirillum rubrum*, *Rhizobium* spp., *Pseudomonas fluorescens, Bacillus subtilis,* and *Paenibacillus*. Some species of pathogenic microorganisms are also capable of producing cytokinins. Even though the production rate of cytokinin by PGPB is low compared to phytopathogens, cytokinin from PGPB is simulative for plant growth compared to that from pathogens which is inhibitory for plant growth (Glick, 2012). Cytokinin and auxin participate in the interaction between plant regulators and stress response. Application of these two phytohormones offers good result in algae in addition to vascular plant under abiotic stress. When cytokinin and auxin are applied exogenously inside green alga *Acutodesmus obliquus* can mitigate toxicity of lead (Pb) decreasing oxidative process by stimulating the enzymatic and non-enzymatic antioxidants system that accelerate the sulfure uptake pathway, leading to the synthesis of Glutathione (GSH) and enhancing tolerance to Pb stress (Piotrowska-Niczyporuk et al., 2020).

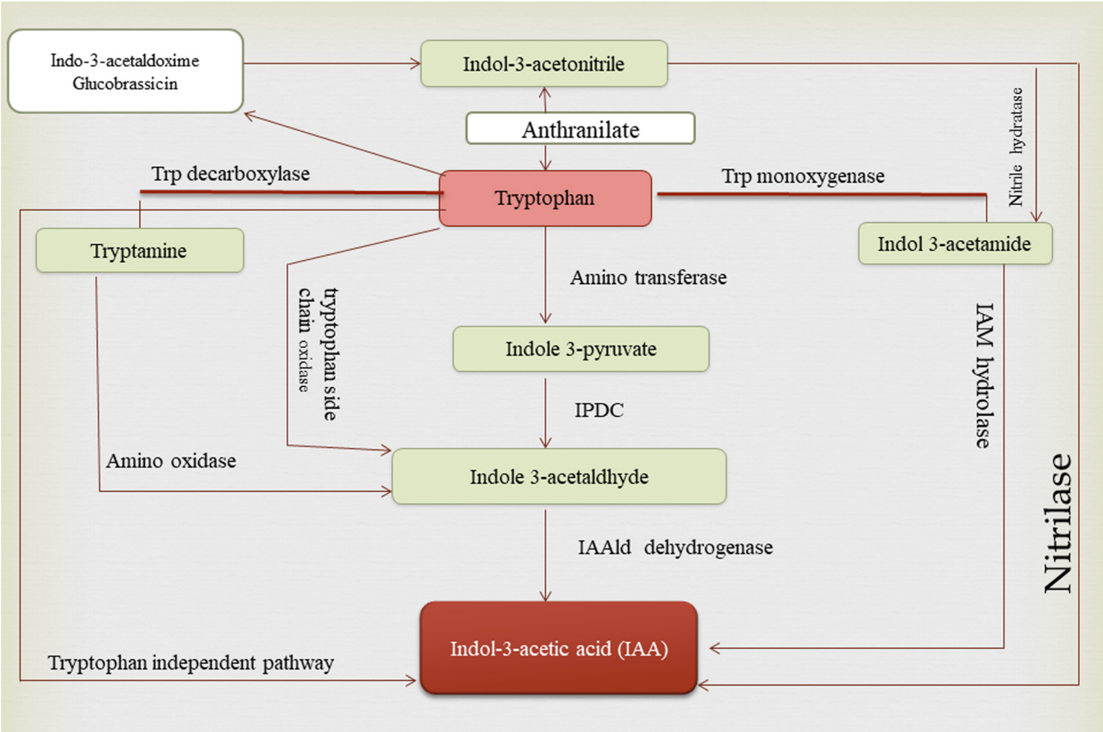

Fig. 5. Outline of the different pathways to synthesize IAA in bacteria. The intermediate referring to the name of the pathway or the pathway itself is underlined with a dashed line. IAAld, indole-3-acetaldehyde - IAM, indole-3-acetamide - IPDC, indole-3-pyruvate decarboxylase - Trp, tryptophan (Spaepen et al., 2007)

Gibberellins

Gibberellins (GAs) are a phytohormones produced by PGPR which affect developmental progression in higher plants, for example germination of seeds, flowering, fruit setting and elongation of stem (Goswami et al., 2016). They have an essential role in the enlargement of stem tissue, root elongation and extension of lateral root (Kenneth et al., 2019). There are nearly 130 gibberelin molecules produced by fungi, bacteria and plant (Cassán et al., 2014). Scientists consider that gibberellin increases the concentration of root hairs that absorb nutrient and water which takes part in the development of larger fruit size, inhibit dormant stage of the bulb, enhance Parthenon carps and improve number of bud, while the absence of it cause plant dwarf (Stamenković et al., 2018). Moreover, gibberellins affect the host plant through signaling factors. Many studies reported that GA produced by *Bacillus or Azospirillum* spp. stimulates growth of plants (Pérez-Montaño et al., 2014). When GA is applied on different plants such as wheat, tomato plus barley, it shows rising in the grain production via decreasing resistance of stomata and improving water deficit (Kannojia et al., 2019). Application of PGPR depending on gibberellic complex showed that high concentration of gibberellins existed uneconomic device, even though low concentrations of gibberellins up to 5 - 10g/ha are sufficient to achieve high crop yield (Rocha et al., 2020).

Ethylene

Ethylene is an essential plant hormone which is more effective at low concentration and elaborated in a numerous physiological processes including; growth of root hair, and apical meristems of the root and the shoot (Tsukanova et al., 2017). Ethylene is classified as senescence or retarding hormone due to its inhibitory role on growth of plant at high concentrations (Odoh, 2017). Ethylene can simply diffuse to adjacent cell due to its gaseous characteristic. Hence production of ethylene mainly occurs at the site of its action. The previous studies illustrate that biosynthesis of ethylene is normally promoted during fruit maturing, and senescence of leaf (Riyazuddin et al., 2020).

Ethylene prevents elongation of root and auxin transfer, it also stimulates abscission and senescence of different organs, and leads to fruit maturing in addition to inhibition of nitrogen fixation in legume (Vachero et al., 2013). Ethylene produced in reaction to various stresses is called "stress ethylene". The high level of ethylene production is related to different environmental stresses including high temperature, extraordinary light, drought, the presence of toxic heavy metals and organic contaminants as well radiation, wounding, insect predation, high salt and presence of different pathogens. Plant produces a slight peak of ethylene as defensive response when exposed rapidly to stress. Under continuous stress a second far higher peak of ethylene is released after few days. The Second peak of ethylene induces harmful effects such as senescence, abscission, chlorosis, and this leads to inhibition in plant growth and existence (Glick, 2012). Under various stress as cold, flooding, drought and even the heavy metal presence, plant produces the precursor of ethylene [1-amino cyclopropane-1-carboxylate (ACC)], which is transformed into ethylene by ACC oxidase and increases the level of ethylene (El-Tarabily et al., 2019). To overcome the inhibitory effect of ethylene, enzyme 1-amino cyclopropane-1 carboxylic acid deaminase is required. This enzyme degrades ACC the main precursor of ethylene produced in plant into α-ketobutyrate and ammonium which supplies plant with nitrogen (Kenneth et al., 2019) as shown in (Fig. 6). ACC deaminase activity is broadly dispersed between various genera for e.g. *Achromobacter, Enterobacter Agrobacterium, Pseudomonas, Alcaligenes, Azospirillum, Bacillus, Acinetobacter, Burkholderia, Rhizobium, Ralstonia, and Serratia* (Idris et al., 2007). Under environmental stress, PGPR synthesizes ACC deaminase which stimulates the uptake of plant nutrients by degrading plant ACC, thus inhibit ethylene accumulation, and supporting plant to tolerate water stress (Ojuederie et al., 2019; Javed et al., 2020).

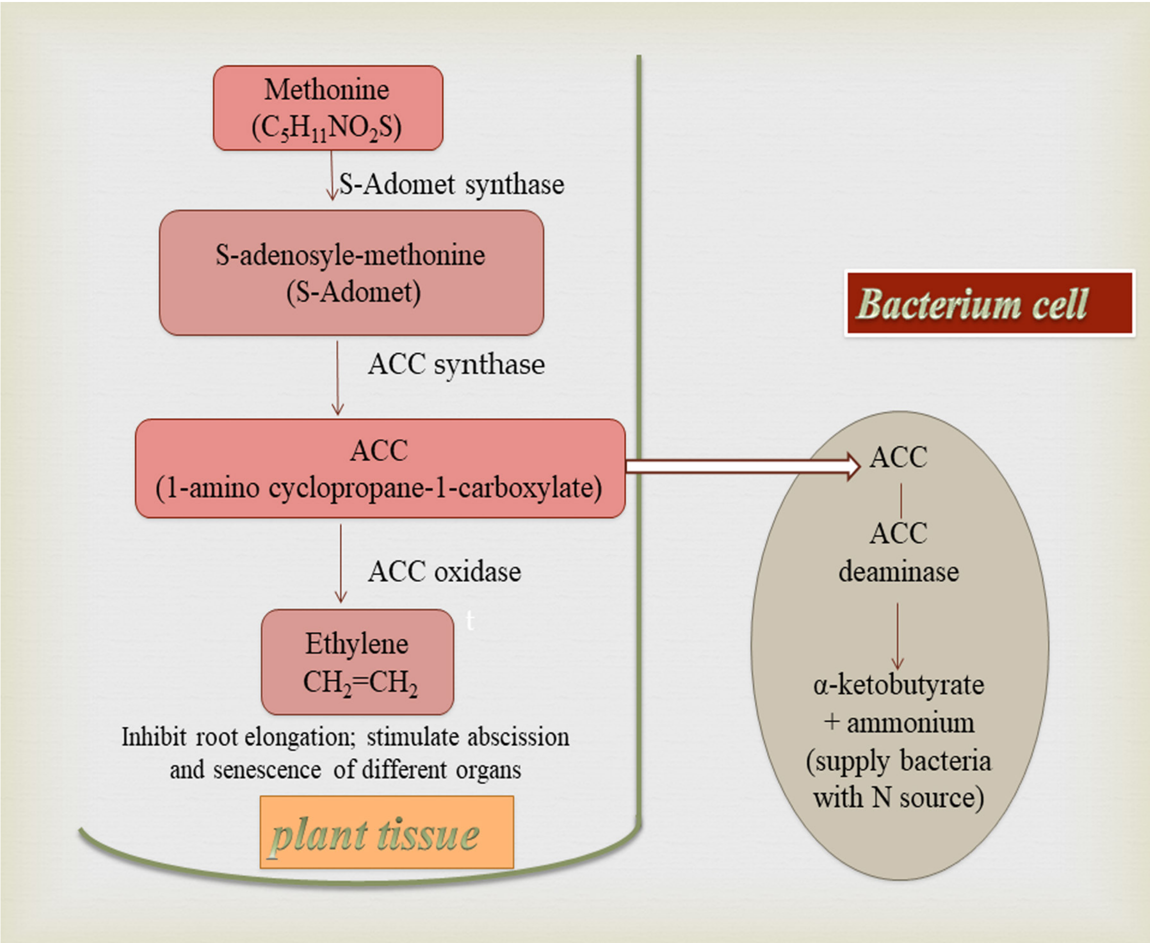

Fig. 6. A possible mechanisms of ACC deaminase produced by PGPR to reduce ethylene level under environmental stress (Adapted from Kang et al. 2010)

Bioprotectants (Biocontrol)

The excessive use of chemical pesticides to kill unwanted weeds, fungicides which destroy phytopathogenic fungi and insecticides to control insects has a negative effect on environment and human health (Ahemad & Khan, 2013). Plant diseases cause economical loss via reducing crop yield, affecting crop quality and contamination of soil and plant with toxic chemicals. Therefore, researchers explore new approaches and eco-friendly methods to control plant diseases (Saraf et al., 2014; Carmona-Hernandez et al., 2019; Khalil, et al., 2023). PGPR has an essential role in protection of crops against phytopathogens in addition to improvement of soil health conditions (Fernando et al., 2005, Abdelmoneim et al., 2023). Also, usage of PGPR help in understanding the goals of world agriculture production to feed the world growing populations (Sayyed et al., 2019) . Genus *Bacillus* has numerous advantages, as it is widely used in agricultural biotechnology. A number of *Bacillus*–based products are promoted as microbial fungicide, pesticide or fertilizer. *Bacillus* based bio-fungicides are commonly used in conventional agriculture compare to application of biofertilizers (Pérez-Montaño et al., 2014). *Pseudomonas* genus is a Gram negative bacteria which act as the main member of the indigenous antagonistic groups in humid stress (Schmidt et al., 2014). The modes of action of the PGPR against plant phytopathogen include production of siderophore, synthesis of cell wall lytic enzymes, and induced systemic resistance (ISR) (David et al., 2018; Debasis et al., 2019).

Siderophores

Iron is the most plentiful element existing in the soil, after nitrogen, phosphorus and potassium. It is essential for metabolism, development and existence of all cell types on the earth; also it participates in the formation of chlorophyll biosynthetic pathways (Fernando et al., 2005). Iron is hardly found in a free form, so it becomes unavailable to plants (Hayat et al., 2012). Under iron deficiency, microorganisms are able to develop extremely specific pathways known as siderophores which make iron available to plants (Beneduzi et al., 2012). PGPR are able to solubilize and facilitate the uptake of iron through different mechanisms such as bioleaching, biomethylation and chelation (Uzoh & Babalola, 2020). Siderophores are low molecular weight (<1kDa) secondary metabolites acting as iron chelating compounds and are produced in rhizospheric soils only under iron deficiency (Hayat et al., 2012; Ghosh et al., 2020). Microbial siderophores are useful to agricultural sciences as well as biological control. These siderophores have high binding affinity to ferric ions as they are compounds with minor peptide molecules with side chains and functional groups that bind to ferric ions and make it available for living cells (Gupta et al., 2015). Plants also develop their own mechanism to obtain iron; in dicots through reductase protein from root membrane that transform insoluble Fe^{3+} into the more soluble Fe^{2+} ion, while in the case of monocots by synthesis of phyto-siderophores (Kumar et al., 2015). Researchers reported that, there are about 500 various types of siderophores, 270 of which are well described while the rest are not yet determined (Pii et al., 2015). Siderophores are categorized to four main groups based on their structure, types of ligand and functional group as catecholates, hydroximates and carboxylate (Sayyed et al., 2013; Arora & Verma, 2017). Catecholates produced only by bacteria for e.g. Enterobactin from *E. coli* and dihydroxybenzoic acid from *Azotobacter vinelandii*, hydroximates are produced by fungi and bacteria for e.g. Acinitobactin from *Acinitobacter baumanii*, also carboxylate compounds for e.g. rhizobactin from *Rhizobium meliloti*, and mixed type for e.g. pyoverdine from *Pseudomonas aeruginosa* (Sayyed et al., 2013). PGPR have high affinity to bind iron and can survive in much lower concentration of iron than fungal pathogen (Saha et al., 2016). Bacteria that produce siderophores affect plant either directly by increasing plant growth and enhancing nutrition or indirectly by suppressing phytopathogen via sequestration of Fe^{+2} in the environment (Souza et al., 2015). Rhizobacteria that are efficient to utilize siderophore of the same genera are known as homologous siderophore, while others utilize those produced by another rhizobacteria of different genera known as heterologous siderophore. Siderophores produced by plant-associated bacteria bind ferric ions from the surrounding rhizosphere and suppress the proliferation of fungal pathogen due to competition for binding iron (Kumar et al., 2020). As iron deficiency inhibits growth, decreases synthesis of nucleic acid, suppresses sporulation and causes modification in cell morphology of phytopathogen thus, siderophores play role in biological control of diseases (Pandya & Saraf, 2014). Pyoverdine siderophores synthesized through several *Pseudomonas* species has a distinct role in controlling of *Pythium* and *Fusarium* species. Pyochelin and its precursor salicylic acid are another type of siderophores produced by *Pseudomonads* spp. Pyochelin synthesized via *P. aeruginosa* 7NSK2 participates in the protection of tomato plants from *Pythium* (Akhtar & Siddiqui, 2010). Rhizobia strains have the ability to produce siderophores that stimulate production of peppers, carrots, tomatoes and lettuce (García-Fraile et al., 2015). There is another type of siderophores known as iron-load siderophores or heterologous siderophores which is produced by many organisms and utilized by others. Normally *Pseudomonas putida* has the ability to utilize heterologous siderophores produced by other organisms and increase the availability of iron to plant (Pahari et al., 2020), for example, inoculation of mung bean (*Vigna radiata L.* Wilczek) with the siderophore-producing *Pseudomonas* strain GRP3 improves growth, increases chlorophyll contents, and decreases chlorosis under Fe-restricted conditions compared to un-inoculated controls (Ali et al., 2017). Recently, researchers reported that bacteria which have the ability to produce auxin and siderophore together are good applicants for phytoremediation of heavy metals contamination. But, the presence of metals may suppress auxin produced by bacteria consequently, bacteria are involved in stimulation of plant growth will be less effective (Peralta et al., 2012; Manoj et al., 2020).

Antibiotic and hydrogen cyanide (HCN)

Antibiotics are low molecular weight secondary metabolites that play a role in plant defense mechanism (Reetha et al., 2014). These metabolites are able to inhibit phytopathogen even at low concentrations. Antibiotics are the most effective tool in biological biocontrol, however, there is certain disadvantages of using them related to antibiotic resistance from phytopathogen. So, it is necessary to select a potent biocontrol strain that produces one or more antibiotics (Karthika et al., 2020). There are six antibiotic groups including phloroglucinols, pyrrolnitrin, cyclic lipopeptides, pyoluteorin, phenazines, and hydrogen cyanide acting as inhibitors for root diseases (Gupta et al., 2015). Various kinds of antibiotic are synthesized by PGPR for e.g. xanthobaccin, kanosamine, zwittermicin A and oligomycin A, which are produced by *Stenotrophomonas*, *Streptomyces*, and *Bacillus* spp (Ahemad & Kibret, 2014). Also amphisin, oomycin A, tropolone, phenazine, Pyrrolnitrin, 2, 4-diacetylphloroglucinol (DAPG), cyclic lipopeptides and Tensin are synthesized by *Pseudomonas*. The purpose of antibiotics is not only in biocontrol defense but also very important against certain pathogenic diseases (Mazhar et al., 2016). Hydrogen cyanide (HCN), a toxic gas, suppress the growth of pathogenes by inhibiting the cytochrome oxidase enzyme in the mitochondria, and prevents the production of ATP (adenosine-5′-triphosphate) which is the energy transferring molecule in the cell (Anand et al., 2020). Production of HCN mainly based on the composition of amino acids in the substrate. Glycine is the main precursor for production of microbial cyanide which extends the largest influence compare to other amino acids (Schippers et al., 1990). Proline also increases the production of microbial cyanide but less than Glycine. Production rate of microbial hydrogen cyanide differs with different crops due to the variation in composition of amino acids present in their root exudates. Moreover, environmental factors as intensity of light and water deficiency may affect the rate and composition of root exudates and this consequently may affect HCN production (Compant et al., 2005). HCN gas acts as biocontrol agent, it causes death to phytopathogen because it suppresses terminal movement of electrons in the respirational chain, ending oxidation process and inhibiting the energy supply to the organism (Pahari et al., 2020). HCN can chelate the excess microelements (e.g., Fe, Cr, Cu, Mn) in the soil leading to increase the availability of phosphorous for rhizobacteria and plant hosts. Thus, improve the plant growth promoters (Rijavec & Lapanje, 2016). Researchers reported that low dose of HCN may not affect the biocontrol process, but is convoluted in geochemical process of metal chelation which increases the availability of nutrients for rhizobacteria and their host plant (Abd El-Rahman et al., 2019).

Lytic enzymes

PGPR are capable of lysing phytopathogens cell wall and protect plant against biotic and abiotic stress through enzymatic activity. These lytic enzymes include β-gluconases, lipase, cellulase, chitinase, protease, dehydrogenase and phosphatases (Mostafa et al., 2009; Bajracharya, 2019). In addition, catalase (CAT) acts as an oxygen-scavenging enzyme having a key role in defending the cell from the inhibitory effect of hydrogen peroxide (H_2O_2) (Yasmin et al., 2016). These enzymes can also degrade inorganic substances and plant remains to get carbon source (Tariq et al., 2017). Numerous researches illustrate that PGPR acts as biocontrol agent including *Pseudomonas fluorescens* LPK2 that inhibit wilt disease arises from *Fusarium oxysporum* by production of chitinase and gluconase, also *Serratia marcescens* produce chitinase which suppresses mycelial mass of *Sclerotium rolfsii*. PGPR also suppress growth of *Phytophthora capsici* and *Rhizoctonia solani* which are the most harmful plant pathogens over the world (Pahari et al., 2020).

Induced systemic resistance (ISR)

Induced or acquired resistance increases the level of plant resistance without changing in its genome by using external agents which may be either a chemical activator or extract of microbial cell (Labuschagne et al., 2010). Induced resistance is divided into main types; ISR is a phenomenon that induces the resistance to infectious disease by local infection or treatment with microbial components or products. It also enhances the physiological condition of the plant to react more efficiently to biotic stress. Systemic Acquired resistance (SAR) is developed in plant tissues, enhancing plant resistance to the subsequent attack by pathogens (Kuć, 2001; Kamle et al., 2020). ISR is active against different types of pathogens in which some bacteria interact with plant roots turning it impervious to some phytopathogenic bacteria, fungi or virus. It is excited by nonpathogenic bacteria and starts in the root spreading to the shoot without causing observable symptoms to the host plant (Pérez-Montaño et al., 2014). In contrast, SAR is stimulated by necrotic pathogenic bacteria, especially when the pathogen motivates over sensitive reaction and limited in a native brown necrotic scratch or dry tissue (Compant et al., 2005). PGPR destroy life cycle of soil borne pathogen as they have the ability to stimulate ISR through metabolic pathways including jasmonic acid (JA) or ethylene (Beneduzi et al., 2012; Gogoi et al., 2020). Furthermore, defense responses in ISR depend on JA and ethylene signaling inside the plant which protects plant against different phytopathogens, while salicylic acid plays a vital role in SAR. In some cases, ISR and SAR may overlap (Paul & Lade, 2014). ISR involves the synthesis of phytoalexins, phenolic compounds, pathogenesis-related proteins, and production of reactive oxygen species, which help in the development of different physical barriers as alternation of cuticles. These processes are energy-dependent that support plants to keep their defense mechanisms always active. Conversely, direct induced resistance mechanism occurs rapidly and is energy independent (Singh et al., 2020b). Induced systemic tolerance (IST) known by PGPR causes chemical and physical changes inside plants that stimulate tolerance to abiotic factors. While biotic stress is excluded from IST because theoretically it is a portion of natural control and induced resistance (Farag et al., 2013; Carlson et al., 2020).

Polysaccharides and bio-film formation

Rhizobacteria have the ability to produce a wide range of polysaccharides for example extracellular polysaccharides (exopolysaccharides, EPS), structural polysaccharides and intracellular polysaccharides. EPS is essential for formation of biofilm (Noumavo et al., 2016). Microorganisms producing EPS are able to restore important nutrients to plant for better growth and development, also protect it from invasion of phytopathogen (Gupta et al., 2015). PGPR plays an important role in agricultural and waste water management through Quorum sensing (QS) in their biofilm mode (Yadav et al., 2019). QS is a communication process between the cell, which organizes genes expression then causes phenotypic changes in the activity of organism from non-virulent to virulent as a response to population density by production of proteins and specific chemical or autoinducer (Desouky et al., 2017; Hamed et al., 2021). The mechanism of bacterial quorum sensing is dependent on two groups of signal molecules: peptide derivatives especial for Gram-positive bacteria and fatty acid derivatives broken by Gram-negative bacteria. The most important signal molecule in PGP Gram-negative bacteria especially *Pseudomonas* is N-acyl-L-homoserine Lactones (N-AHLs), which is responsible for organization of different actions such as biofilm formation, production of antibiotics, synthesis of exoenzyme and replication. The PGPR *Pseudomonas aureofaciens* can inhibit growth of *Fusarium* by quorum sensing–dependent and AHL-based manufacturing of an antifungal antibiotic phenazine. EPS takes part in development of soil aeration and forms a defensive barrier to protect plant against invasion of phytopathogen (Noumavo et al., 2016). Furthermore, EPS has a vital role in mitigation of soil salinity through binding of free cations like f Na^+ present in root zone and make it unavailable to plant (Abbas et al., 2019). Furthermore, it stimulates bacterial colonization to plant root and soil particles thus; improving soil structure and crop yield (Banerjee et al., 2019).

Conclusion

Soil is the main natural resource for agriculture and food deficiency and it is important to maintain human life on earth. The misapplication of chemical fertilizers, herbicides and pesticides affect soil quality, environmental balance and also modify the food chain and human health. So it is necessary to investigate another strategy which alternate chemical fertilizers and are ecofriendly, economic and increase crop yield. Inoculation of crops with PGPR may enhance sustainable agricultural production. PGPR increase soil fertility through production of biological N_2 fixation and phosphate solubilization, enhance plant growth and increase crop production by synthesis of phytohormones and reducing ethylene level, suppress phytopathogens that cause plant diseases and stimulate tolerance to biotic and abiotic stress. Unfortunately, in vitro results couldn't be well achieved in vivo due to the unstable interaction between the host plant and PGPR under unfavorable conditions. Thus, it is important to find out and select the best PGPR strains that are optimally active and supply the expected results under environmental conditions. Finally, the researchers must offer sufficient scientific information to understand farmers the role of PGPR and their mechanisms of action to improve crop productivity and its importance as biosafety approach instead of agrochemical compounds.

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دور البكتريا المحفزة لنمو النبات في الزراعة الصحية والمستدامة

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تلعب الزراعة التقليدية دورًا حيويًا في تلبية المتطلبات المتزايدة على الغذاء الناتجة عن الزيادة المستمرة في عدد السكان. في الوقت الحاضر، يستخدم المزارعون كميات متزايدة من الأسمدة الكيماوية والمبيدات الحشرية التي لها تأثير سلبي على جودة التربة والنظام البيئي وصحة الإنسان. وبالتالي فمن المهم البحث عن أساليب أخرى لتقليل استخدام الأسمدة الكيماوية وتعزيز إنتاجية المحاصيل. يعد تلقيح المحصول بالبكتريا المحفزة لنمو النبات (PGPR) لزيادة الإنتاج الزراعي المستدام استراتيجية أخرى صديقة للبيئة ويمكن تنفيذها على المدى الطويل. PGPR هي مجموعة من البكتيريا قادرة على استعمار جذور النباتات وزيادة نموها وإنتاجيتها فهي تساعد في زيادة امتصاص الماء، وقمع مسببات الأمراض، وكذلك تعزز امتصاص العناصر الغذائية من التربة. نوقشت في هذه المقالة التطبيقات البيوكيميائية التي يمكن من خلالها للبكتيريا الجذرية أن تحفز نمو النباتات ؛ (1) المنشطات الحيوية: ممثلة في هرمونات نباتية معينة تم تصنيعها بواسطة PGPR على سبيل المثال: الأوكسينات أو إندول حمض الخليك (IAA) ، والسيتوكينينات، حمض الجبريليك (GA) وغاز الإيثيلين، (2) الإخصاب الحيوي: من خلال المساعدة في امتصاص العديد من العناصر الغذائية من البيئة على سبيل المثال التثبيت البيولوجي للنيتروجين، إذابة الفوسفات وإنتاج حامض الحديد، (3) عوامل الحماية الحيوية أو المكافحة الحيوية: عن طريق منع أمراض النبات من خلال إنتاج المضادات الحيوية، والإنزيمات المحللة أو إنتاج سيانيد الهيدروجين(HCN) أو كلاهما.