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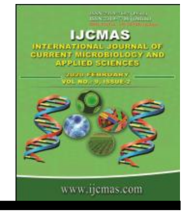

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Enhancement of Plant Growth by Using PGPR for a Sustainable Agriculture: A Review

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A B S T R A C T

Biotic and abiotic stresses exert a serious impact on crop productivity throughout the world. The alternate strategy is to introduce tolerant microbes into plants under stress conditions. Intensive research attempts are underway to improve plant growth, enhance tolerance level against these stresses and protect plants by using plant growth promoting rhizobacteria (PGPR) which have a great potential for sustainable crop production. PGPR play a direct role in maintaining better plant health by nitrogen fixation, phosphate solubilisation, phytohormone production etc. and indirectly by siderophore production, antibiotic production, ACC deaminase activity, Induced Systemic resistance etc. The microbes provide plants resistance to stress by enhancing the activity of the antioxidant enzymes and other non-enzymatic antioxidants.

Keywords

Biotic and abiotic stress, PGPR, Sustainable

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Introduction

Our nature is embedded with full of treasures with not only expensive products like gold, diamond, minerals etc. but also with some priceless things which are having literally even more value than all of this. Apart from these things which are so important for the survival on this earth like air, water and soil, nature is aiding things which are equally important for a sustainable future. Yes, it is in fact beyond our imagination that even small organisms surviving in soil can be useful for the plants. There are group of natural entities like beneficial soil microbial flora which are dwelling in the rhizosphere and on the surface of the plant roots which impose overall well-being of the plants are categorized as Plant Growth Promoting Rhizobacteria (PGPR). Researchers are studying these microbes for the past 30 years to understand the mechanics and usefulness employed by these PGPR to support plant growth. The plant-beneficial rhizobacteria may decrease the global dependence on hazardous agricultural chemicals which destabilize the agro-ecosystem. Microbial populations are ubiquitous and are present in diverse ecological niches, including extreme environments, present in both lithosphere and hydrosphere, where they can thrive easily and their metabolic abilities play a significant role in geochemical nutrient cycling (Aeron *et al*., 2011).

Agriculture is hit badly by both biotic and abiotic factors. Plant pathogens, such as bacteria, viruses, fungi, and parasites heavily damage the yield. The annual agriculture yield losses due to the disease cause by these pathogens are at least 30% globally (Fisher *et al.*,2012). Among all, two-third of total diseased plants is infected by fungi. Agricultural land management, greater use of chemicals including fertilizers, judicious and safe pesticides and herbicides uses, more farm mechanization, greater use of transgenic crops are some of the solutions to boost the yield. But these solutions are effective in short time because we have limited number of resources. The fertilizers will affect our environment adversely. The farm mechanization is not acceptable to everyone due to its high cost. The use of transgenic crops is restricted due to some ethical concerns and resistance breakdown. Thus, we need a long term, safe, sustainable, eco-friendly biological solutions. Expanded use of PGPR is one of the ultimate solutions in our hand which will complete all the mentioned criteria. We should praise our nature for gifting us with such a noble creature.

Rhizosphere and associated communities

Bacterial populations are widely distributed over the soil and some adheres with the plant's roots, interact with it. The term 'rhizosphere' was coined by Hiltner (1904) who describes it as a zone which is dominated by root exudates. Later on, it was defined as that portion of the soil which is specially affected by plant roots and/or in association with roots and roots hairs, and plant-produced materials (Andrade *et al*., 1997). This area cover the soil packed by the roots, extending a few millimetres from the root surface and can consist of the plant root epidermal layer (Bringhurst *et al*., 2001). Further the definitions were updated that it is the modulation of root's parameters like physical, chemical and biological with respect of growth and activity (Sivasakthi *et al*., 2014). The bacterial populations in the rhizosphere are 100-1000 times higher than the rest of the soil. The probability of finding these bacteria is higher in the rhizosphere because they possess unique ability to alter their metabolic activities and consumes the roots exudates efficiently. Also, 15% of the root surface is covered by microbial populations belonging to several bacterial species (Govindasamy *et al*., 2011; Jha *et al*., 2010). Plant photosynthetic product (about 5 to 30%) is secreted by roots in form of different sugars which in turn is utilized by microbial populations (Glick, 2014). Subsequent metabolic activities of these bacteria in the rhizosphere accelerate mineral nutrient transport and uptake by plant roots (Glick, 1995). The rhizosphere serves as an ecological niche for PGPR. Generally, about 2–5% of rhizosphere bacteria are PGPR (Antoun and Prevost, 2006; Jha *et al*., 2010; Sgroy *et al*., 2009; Siddikee *et al*., 2010).

Due to accumulation of variety of plant exudates, such as amino acids and sugars, the zone is acquainted with nutrients as compared to rest of soil providing source of energy and nutrients for microbes (Gray and Smith, 2005). A range of microorganisms including bacteria, algae, fungi, protozoa and actinomycetes colonize the roots of plants.

They live independently or in association with another organism. A popular symbiotic association exist between fungi and roots of plants (mycorrhizal) which facilitate the plant to absorb more water and nutrients by increasing the root surface area (Nadeem *et al*., 2014), the microorganisms in turn get shelter.

Plant Growth Promoting Rhizobacteria (PGPR)

The bacteria that colonized the root, improve plant growth and yield by the addition of some growth factors and hormones are called as PGPR (Kloepper and Schroth, 1978). A rhizosphere bacterium is considered to be a PGPR when it affects the plant in a positive way upon inoculation, thus showing a different active characteristic to the existing rhizosphere communities. In 1998, Bashan and Holguin, revised the definition because there are bacteria which demonstrate a positive interaction over the plant although they are outside the rhizosphere environment. During the Fourth International Congress of Bacterial Plant Pathogens, conducted in France, the importance of rhizobacteria for the plant health was showed by Kloepper and Schroth (1978). PGPRs can act as solid tools for the sustainable agriculture and can produce a new era for the management of diseases.

Classification of PGPR

PGPRs are associated differently with respect to the plant root cells, either outside the root i.e. in rhizosphere, on the rhizoplane or can be confined to the spaces between cells of the root cortex, or inside the roots particularly in the root cortex and thus can be grouped into extracellular plant growth promoting rhizobacteria (ePGPR) and intracellular plant growth promoting rhizobacteria (iPGPR) respectively (Martinez-Viveros *et al.,* 2010). *Agrobacterium, Arthrobacter, Azotobacter, Azospirillum, Bacillus, Burkholderia, Caulobacter, Chromobacterium, Erwinia, Flavobacterium, Micrococcous, Pseudomonas* and *Serratia* belongs to ePGPR (Gray and Smith, 2005). Endophytes and *Frankia* species belongs to iPGPR. Endophytes include large number of soil bacterial genera such as *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium and Rhizobium* of the family Rhizobiaceae that are closely associated in the formation of root nodules (Wang and Maetinez-Romero, 2000). Among all the recognised genera of PGPR, *Bacillus* and *Pseudomonas* predominates (Podile and Kishore, 2006).

Mechanism of PGPR

PGPR affect plant growth in two different ways, indirectly or directly (Figure 1). Indirect mechanisms, as the name suggest are those that do not affect the plant in a straight way and happen outside the plant, while direct mechanisms are those that occur inside the plant and directly involved in the plant's metabolism (Antoun and Prevost, 2006; Glick, 1995; Siddik *et al*., 2010; Vessey, 2003). Biological nitrogen fixation, phosphate solubilization, phytohormone and siderophore production are some of the direct whereas production of defence enzymes and antibiotic, modulation of plant stress markers, induce systemic resistance (ISR) and competition for the rhizosphere are some of the indirect mechanism .The direct mechanisms include those in which either the bacteria will produce the growth regulators, ultimately incorporate in plant system and thus affect the balance of plant growth regulators or they act as a sink of plant release hormones that will induce plant metabolism leading to the overall growth of the plant (Glick, 2014; Govindasamy *et al*., 2011).

Direct mechanism of PGPR

Nitrogen fixation

Bacterial strains which are able to fix atmospheric nitrogen can be classified into two parts. The one which act symbiotically (root/legume association), got the specificity and infects the root of the plants to produce nodules e.g. *Rhizobium* strains. Other group of bacteria are free living which does not possess specificity (Oberson *et al*., 2013). Examples of such free-living nitrogen fixers include *Azospirillum, Azotobacter, Burkholderia, Herbaspirillum, Bacillus, and Paenibacillus* (Goswami *et al*., 2015; Heulin *et al*., 2002; Seldin, 1984; von der Weid *et al*., 2002). These free living nitrogen fixers although not closely associated with plants as they do not penetrate the root of plants but able to fix the nitrogen for better nitrogen absorption to the plants. This relationship is called as non-specific or loose symbiosis. The amount of nitrogen fixed ranges between 20 and 30 kg per hectare per year (Stacey *et al*., 1992). *Azotobacter* and *Azospirillum* are the most widely used species in agricultural trials. They are first reported in 1902 and are the most widely use strains till date (Bhattacharya and Jha, 2012). Application of *Azotobacter chroococcum* and *Azospirillum brasilense* inoculants in agriculture, especially in cereals has resulted in significant increases in crop yields (Oberson *et. al*., 2013).

Based on nitrogenase activity, *Bacillus azotofxans, Bacillus macerans*, and *Bacillus polymyxa*, were identified as nitrogen fixers, (Seldin *et al*., 1984). However, after reclassification, these organisms are now classified in *Paenibacillus* genus. *Paenibacillus odorifer, Paenibacillus graminis, Paenibacillus peoriae,* and *Paenibacillus brasilensis* have been described as nitrogen fixers (Heulin *et al*., 2002; von der Weid *et al*., 2002). Symbiotic nitrogen fixing bacteria such as rhizobia are closely assosciated with root hairs. The rhizobia and the nod factors (lipo-chitin oligosaccharides) interact to change the cell division processes in the root hair cells resulting in curling of the root hairs. The nod factors operate within these curled root hairs, leading to the formation of infection threads through which these rhizobia make their way to enter inside leguminous crops (Broughton *et al*., 2000; William *et al*., 2000) and are reported to possess *nif* gene cluster which are responsible to code for nitrogenase enzyme, a key enzyme involved in nitrogen fixation. These are widely use in biofertilizers for the past 20 years and are very important for agriculture (Goswami *et al*., 2015; Heulin *et al*., 2002).

Phosphate solubilisation

Despite abundant reserve of phosphorous, plant is unable to take these phosphorous directly. Plants are only able to absorb mono- and dibasic phosphate which are the soluble forms of phosphate (Jha *et al*., 2012; Jha and Saraf, 2015). Hence, they are among the most limiting nutrients after nitrogen for the plants. The key mechanism of phosphate solubilization is based on production and secretion of organic acid by microbes *i.e.* PGPR (Han *et al*., 2006). Sugars (Glucose, fructose, mannitol and other form of carbohydrates) from root exudates are metabolized to produce organic acids by these noble creatures living in the rhizosphere (Goswami, 2014). The acids released by the micro-organisms has a property to act as a good chelators of divalent Ca cations or decrease the pH which facilitates the release of phosphates from insoluble phosphatic compounds (Pradhan and Shukla, 2006). Further, these microbes have the ability to release enzymes specially phosphatases (Tarafdar *et al*., 1988; Yadav and Tarafdar, 2003; Aseri *et al*., 2009) and phytases (Moughal *et al*., 2014) which bring about enzymatic reaction to transform the organic P into soluble forms of P through the process of mineralization (Figure 2). Since 1903, these microorganisms are known to act as a chief agent of phosphate solubilisation (Kucey *et al*., 1989).

Phtyohormone production

The soil microorganisms especially those residing in the rhizosphere are assosciated with production of phytohormones like auxins, gibberellins, cytokinins, ethylene, and abcisic acid (Arshad and Frankenberger, 1998). These phytohormones play an important role in plant growth and development process such as plant cell enlargement, division, and extension in both symbiotic and non-symbiotic associations of roots (Glick, 2014; Patten and Glick, 1996). Auxin basically impacts the growth and development of whole plant but as IAA is produced in the rhozospheric zone, it mainly affects the root system (Salisbury, 1994) by increasing its size and weight, branching number, and the surface area in contact with soil. Consequently, it accelerates the nutrient exchange process by the roots which strengthen nutrition balance and growth build-up of the plant (Ramos-Solano *et al*., 2008). L- tryptophan is known to be the precursor of IAA. Most of these PGPRs make use of L-tryptophan which is secreted in root exudates for the production of IAA through L-Tryptophan dependent pathway. Although some like *Azospirillum brasilense*, produces more than 90% of IAA through L-tryptophan independent pathway and remaining 10% IAA is produced by utilizing L-tryptophan. However, the exact mechanism and enzymes used for IAA synthesis by this route is still unrevealed (Jha and Saraf, 2015; Spaepen *et al*., 2007).

Pseudomonas, Azospirillum, Bacillus, Proteus, Klebsiella, Escherichia, Pseudomonas, and *Xanthomonas* includes some of the microorganism which are responsible for cytokinins production (Maheshwari *et al*., 2015). Zeatin and kinetin are two major Adenine-type cytokinins, in which N6 position of adenine is substituted with an isoprenoid and an aromatic side chain respectively. Zeatin can be synthesized in two different pathways: the tRNA pathway and the adenosine monophosphate (AMP) pathway.

Seed germination, stem elongation, flowering, and fruit setting are some of the function of gibberellic acid (Hedden and Phillips, 2000). *Rhizobium meliloti, Azospirillum* sp., *Acetobacter diazotrophicus, Herbaspirillum seropedicae and Bacillus sp.* are some of the important microorganism capable of producing gibberellic acid.

Indirect mechanism

Siderophore production

Iron is quite abundant in soils but is frequently unavailable for plants or soil micro-organisms**.** Fe^{+3} is the oxidized form that reacts to form insoluble oxides and hydroxides such as Fe(OH)3 which are difficult to be utilize by the plants and micro-organisms. Siderophores (sid= iron, phore = bearer) are low-molecular weight (<1 kDa), high affinity iron chelating compounds which functions to deliver iron to the plant cell (Hider and Kong, 2010).

Pseudomonas fluorescens and *Pseudomonas aeruginosa* release pyochelin and pyoverdine type of siderophores (Haas and Defago, 2005). These siderophores producing microorganism improve Fe uptake and hinder the growth of pathogen (generally fungi) as a result of competition for scavenging iron (Shen *et al*., 2013).

Defence enzymes

Different strains of PGPR possess the ability to secrete cell wall degrading enzymes like β-1,3-glucanase, chitinase, cellulase, lipase and protease which degrade the cell wall of fungi (Chet and Inbar, 1994). Chitinase breaks the chitin, second largest abundant organic molecule and a major component of the fungal cell wall. Another defence enzyme, β-1,3-glucanase is produce by *Bacillus cepacia* which destroys the cell walls of *R. solani, P. ultimum,* and *Sclerotium rolfsii* (Compant *et al*., 2005). The mycelia of the fungal pathogens *Rhizoctonia solani* and *Fusarium oxysporum* co-inoculated with an effective biocontrol strain *Serratia marcescens* B2 alter hyphal proliferation resulting in swelling, curling or bursting of the hyphal cell (Someya *et al*., 2000).

Antibiotic production

Antibiotic produce by PGPR act as good biocontrol**.** These antibiotics includes 2,4-Diacetyl Phloroglucinol (DAPG), Phenazine-1-carboxylic acid (PCA),Phenazine-1-carboxamide (PCN), Pyoluteorin(Plt), Pyrrolnitrin (Prn), Kanosamine, Zwittermycin-A, Aerugine, Rhamnolipids, Pseudomonic acid, Azomycin, antitumor antibiotics FR901463, and Karalicin. Most of them are produced by the genus *Pseudomonas* such as *Pseudomonas fluorescens* and *Pseudomonas aeruginosa*. These antibiotics are known to possess antiviral, antimicrobial, insect and mammalian antifeedant, antihelminthic, phytotoxic, antioxidant, cytotoxic, antitumor, and PGP activities (Hammer *et al*., 1997). Moreover antibiotics released by the PGPR are thought to be one of the major possible mechanism employ by the antagonists against phytopathogens (Glick *et al*., 2007). The reduction in take all disease of wheat (*Gaeumannomyces graminis f.sp tritici*) and wilt (*Fusarium oxysporium*) is due to colonization of *Pseudomonads* producing phenazine through their redox activity (Chin-A-Woeng *et al*., 2003).The antibiotic, pyrrolnitrin produce by BL 915 strain of *Pseudomonas fluorescens* against *Rhizoctonia solani* manage damping-off of cotton plants (Hill *et al*., 1994). Another antibiotic, DAPG (2,4-Diacetyl Phloroglucinol) produce by pseudomonads, disrupt the membrane and inhibit the zoospore of *Pythium* (de Souza *et al*., 2003).

ACC (1-aminocyclopropane-1-carboxylic acid) deaminase activity

Apart from the major function of ethylene, ripening, an over production under stress condition (Abeles *et al*., 1992; Arshad and Frankenberger, 2002; Etesami *et al*., 2015; Jha and Saraf, 2015) result in inhibitory effect on root growth. To combat this situation, an interesting phenomenon is exhibited by PGPR which perform ACC deaminase activity, regulating this important hormone and thus modulating the growth and development of plant (Arshad and Frankenberger, 2002; Glick, 2005). PGPR convert SAM (S-adenosylmethionine) to ACC by the enzymes ACC synthetase which is activated through production of IAA. Moreover, the ACC release by the root exudates are taken by the microorganism as a source of nitrogen and are further converted into ammonia and α-ketobutyrate by bacterial ACC deaminase activity which checks the production of ethylene. Therefore, in this way, ACC deaminase producing PGPR act as soldier against the adverse effect of ethylene under stress condition (Glick, 2014). ACC deaminase activity performing microbes bind non-specifically to a wide range of plant surfaces as compared to those which have less ACC deaminase activity (Glick, 2005).

ACC deaminase are possessed by a range of microbes including gram negative bacteria

(Babalola *et al*., 2003), gram positive bacteria (Belimov *et al*., 2001; Ghosh *et al*., 2003), rhizobia (Ma *et al*., 2003). PGPR such as *Azospirillum lipoferum* (Blaha *et al*., 2006), *Bacillus* (Belimov *et al*., 2001), *Pseudomonas* (Belimov *et al*., 2001; Blaha *et al*., 2006; Hontzeaset *et al*., 2004), *Ralstonia solanacearum* (Blaha*et al*., 2006), *Rhizobium* (Ma *et al*., 2003; Uchiumi *et al*., 2004) are actively involved in ACC deaminase activity. These ACC deaminases containing PGPR are fascinating researcher to exploit them at molecular level through genetic manipulation (Belimov *et al*., 2002; Safronova *et al*., 2006; Sergeeva *et al*., 2006) and thus creating a vision to utilize them more precisely.

Fig.1 Mechanism of PGPR

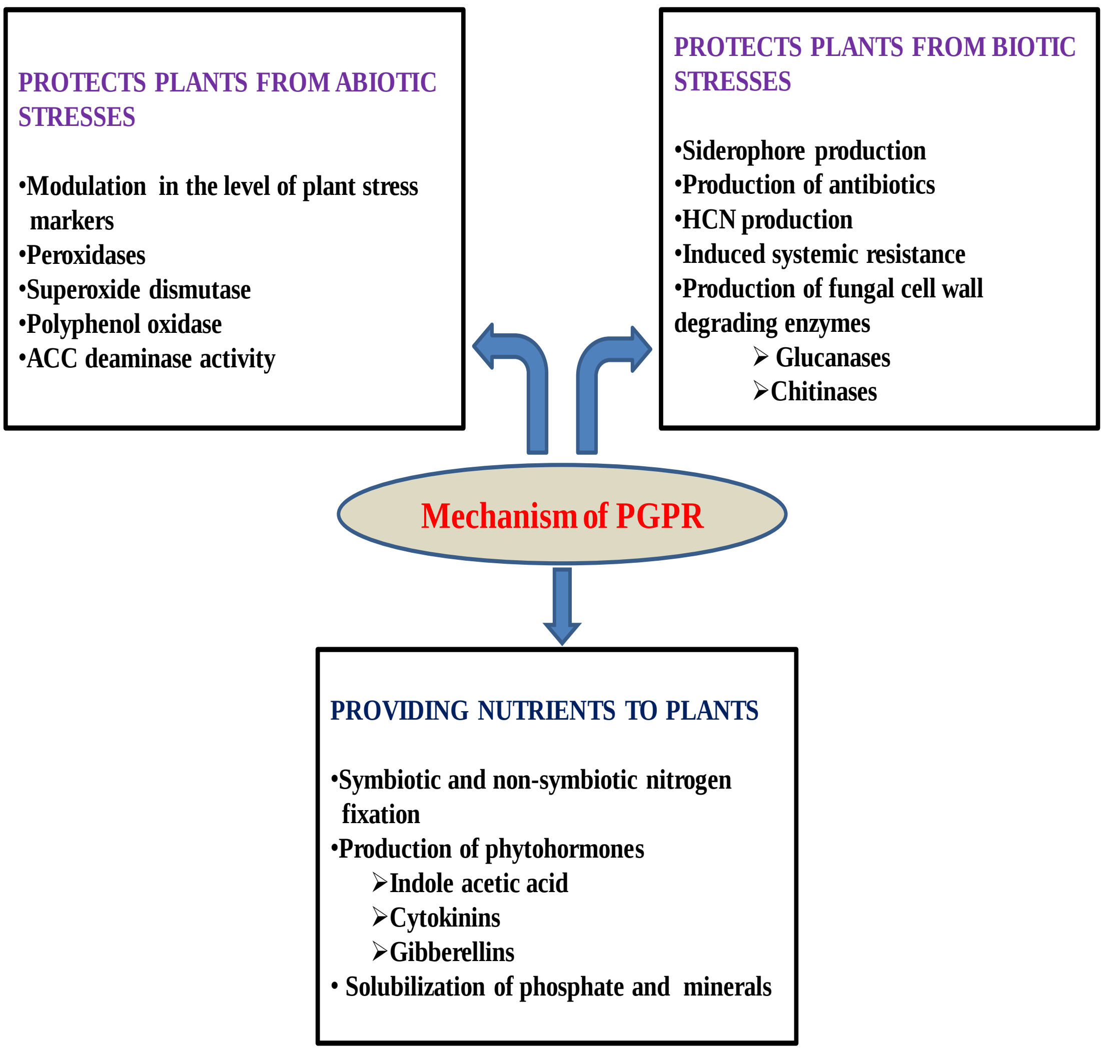


Fig.2 Schematic representation of solubilization of soil phosphorous by PGPR

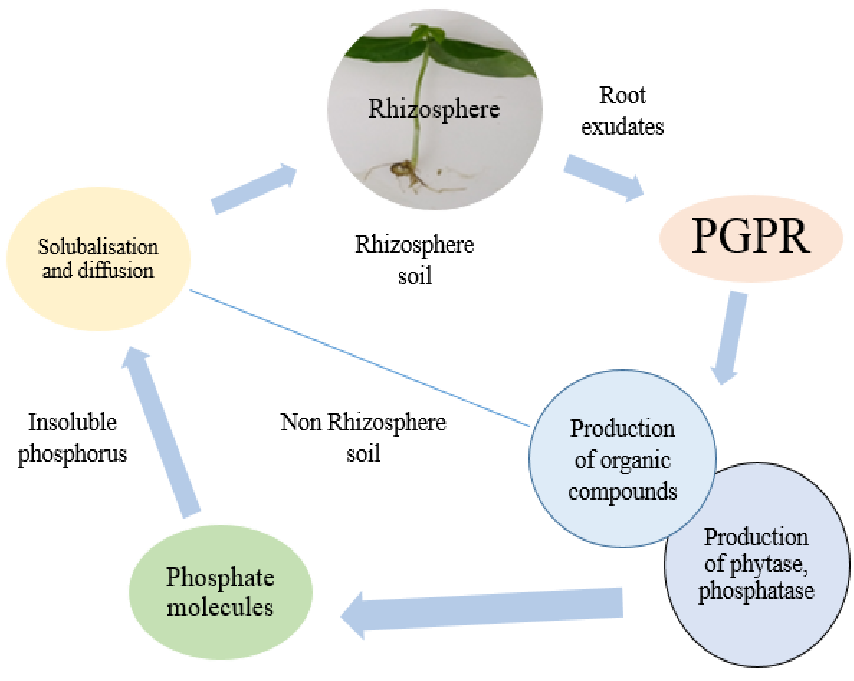
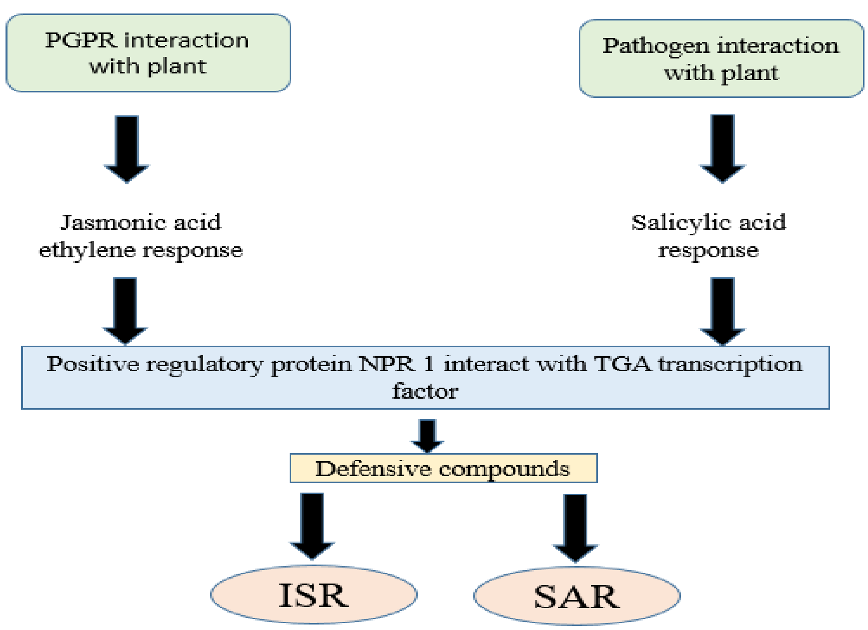


Fig.3 Signal transduction pathways leading to pathogen induced systemic acquired resistance (SAR) and rhizobacteria-mediated induced systemic resistance (ISR) in *Arabidopsis thaliana* (Van Loon *et al*., 1998).



PGPR produces a wide range of low molecular weight metabolites with antifungal activity. Some *Pseudomonads* can synthesize hydrogen cyanide to which these pseudomonads are themselves resistant, a metabolite that has been linked to the ability of those strains to inhibit some pathogenic fungi.

Induced Systemic Resistance

The non-pathogenic PGPR activates Induced systemic resistance which operates to several pathogens simultaneously, thus proving resistance to wide range of pathogens (Figure 3). Rhizobacteriain the plant roots produce signal, which spreads systemicallywithin the plant and increases the defensive capacity of the distant tissuesfrom the subsequent infection by the pathogens(Thakker *et al*., 2011) . *Pseudomonas* and *Bacillus* spp. are the rhizobacteria most studied that trigger ISR (Kloepper *et al*., 2006).

In conclusion, sustainable agriculture is the need of the world as of late due to the unfavourable impact of synthetic substances utilized in farming. In the present situation, using PGPR in agriculture are one of the most appropriate decisions for plant development advancement so as to mitigate various sorts of stresses which are experienced by the plants and also to conquer the utilization of synthetic composts and pesticides. The rhizosphere is a huge supply of organisms, where PGPRs are most generally found and are involved in overall well being of the plant. The exudates of plant roots generally collaborates them and help in root-colonizing activities. For that reason, PGPR is considered as 'A gift of nature for bright future'. PGPR and their interactions with plants are exploited commercially (Podile and Kishore, 2006) and can be a huge future scope for sustainable agriculture. These noble and beneficial creatures have been introduced in several crops like maize, wheat, oat, barley, peas, canola, soya, potatoes, tomatoes, lentils, radicchio and cucumber (Gray and Smith, 2005). Thus, PGPR offers an excellent attractive alternative to chemicals and can maintain or even increase the yield of crop which is the need of time.

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