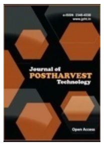

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REVIEW ARTICLE

Molecular basis of biotic and abiotic stress management attributes of plant growth promoting rhizobacteria

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ABSTRACT

Food scarcity is becoming a global issue as the world's population grows. New agricultural strategies that help enhance agricultural crop production and productivity are urgently needed to meet the growing food demand of the world's population. There are various stresses prevalent that prominently reduce the plant productivity. These stresses can be either biotic or abiotic. To ensure food supply to growing population worldwide, the damage caused by these stresses should be minimized. Plant growth promoting rhizobacteria (PGPR) are root-colonizing non-pathogenic bacteria, which found surrounding the roots and have beneficial effects on growth of plant. PGPR act as a source of hormones, vitamins and growth factors that enhance plant growth and yield. PGPR could be a alternative tool for sustainable agriculture as they can induce resistance against various biotic and abiotic stresses. Some PGPR increases tolerance against abiotic stresses like drought, salinity, temperature, oxidative stress, nutrient deficiency and metal toxicity. Several activities of PGPRs such as production of antibiotic compounds, bacteriocins, synthesis and secretion of cell wall degrading enzymes, induction of systemic resistance (ISR) and production of volatile organic compounds are effective in control of many biotic stresses such as plant pathogens. Several PGPR strains such as Pseudomonas spp., Bacillus spp. are proved to be an effective biocontrol agents against plant pathogens. This review emphasized on the role of PGPR for management of various biotic and abiotic stress.

Keywords: PGPR, abiotic, biotic, stress, ISR

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INTRODUCTION

Worldwide growth in population raises demands for increase in global food production and reduction in agriculture yield loss caused by various biotic and abiotic factors are major concerns. These problems may soon result in a scarcity of food to feed the world's rising population. The demand of food at global level is rising rapidly, so according to demand the food production must be increased by about 70% till 2050 (McKenzie and Williams, 2015). Hence agricultural output must considerably rise during the next few decades. The rhizosphere is that part of the soil ecosystem where plant roots, soil and the soil biota interact with each other. These interactions are frequently beneficial to plants, improving soil fertility and enhancing harmful toxins breakdown. The term 'rhizosphere' refers to the narrow region of soil immediately around the root

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system, while 'rhizobacteria' refers to a group of rhizosphere bacteria capable of colonizing the root environment. Plant growth-promoting rhizobacteria (PGPR) are naturally occurring soil bacteria that colonize plant roots aggressively and promote plant growth. Soil contains many categories of bacteria but rhizosphere bacteria are 2-5 % only. Joe Kloepper coined the term PGPR (Plant Growth Promoting Rhizobacteria) and also defined them (Kloepper, 1978). Rhizospheric soil surrounding the roots is influenced biologically, physically and chemically by the plant root. This soil is highly suitable habitat for the proliferation of PGPR and depict a potential impact on plant health and soil fertility. Root exudates contain plenty of amino acids, organic acids and monosaccharides serve as the primary source of nutrients and growth for PGPR.

PGPR can be classified into two major types based on their location in rhizosphere. First Extracellular PGPR can be detected in the rhizosphere or the gaps between root cortex cells and second intracellular PGPR which are present inside the root cells, generally in specialized nodular structure. In general PGPR works in three different ways 1.facilitating the uptake of particular nutrients from the soil, 2. Synthesizing certain compounds for the plant growth 3. Inhibiting or preventing the plant pathogens. PGPR can enhance plant growth by broad range of mechanisms like induced systemic resistance (ISR), systemic acquired resistance (SAR), biological nitrogen fixation, rhizosphere engineering, phosphate and zinc solubilizing, resistance against biotic and abiotic stresses, siderophore production and promoting profitable plant microbe’s symbiosis. PGPR can also develop abiotic stress tolerance towards temperature (high temperature/heat and low temperature/ cold), salinity, osmotic stress, water related stresses (excess of water/flooding and very less water/drought), metal toxicity and towards ROS (Reactive Oxygen Species). A vast range of bacterial groups being considered as PGPR include *Azospirillum, Pseudomonas, Rhizobium, Arthobacter, Azotobacter, Serratia, Thiobacillus, Agrobacterium and Bacilli*. These bacteria are present in the soil around the root systems of different plants. PGPR can inhibit wide range of disease causing agents through elicitation of chemical and physical changes concerned to plant defense (Bhattacharyya and Jha, 2012) and the process is known as “induced systemic resistance” ISR. There are 3 identified pathway of induced resistance in plants: (A) Salicylic acid pathway, (B) Jasmonic acid pathway, (C) non-pathogenic root associated bacteria induced pathway. PGPR release different compounds in the rhizosphere that act as elicitors and some of them are sensed by the plant roots as signals that trigger defense responses (Van Loon, 2007). Elicitors are belongs to different chemical groups like lipids, polysaccharide, glycoprotein, glycopeptides, siderophores and antibiotics (Salomon et al., 2014). When elicitors are perceived by plant roots, signal transduction pathways are activated to trigger the production of different defense enzymes, phytoalexins, pathogenesis related protein (PR protein) and cell wall impaction (Glazebrook, 2005).

The systemic defense responses that are initiated by beneficial micro-organisms are regulated by a signaling network in which the plant growth regulators (PGR) salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) play vital role (Timmusk and Wagner, 1999). A possible relation between ISR and abiotic stress responses induced by PGPR *Paenibacillus polymyxa* in *Arabidopsis thaliana* (Riadh et al., 2010). Similarly the PGPR strain *i.e. Paenibacillus syringae* protect *A. thaliana* plants from the foliar pathogens and also provide resistance against salt stress. PR1 gene expression was involved in the initiation of ISR and SA-dependent pathway. Rhizobacteria can enhance accumulation of secondary metabolic products (phenolics, flavonoids, phytochromes), osmoprotectants (proline, glycine-betaine, glycerol), exudation of sugars, amino acids, vitamins and polyamines in plants. These products improve the resistance and tolerance of plants against biotic and abiotic stress. Rhizobacteria are more helpful in improvement of agricultural crops. PGPR could be used as an alternative strategy for sustainable agricultural manners.

Abiotic stress is a main limiting factor for decline in agriculture productivity. Worldwide out of 5.2 billion hectares of agriculture land 3.6 billion hectares are affected by soil degradation and salinity (Hong et al., 2020). Presently, the world population is increasing continuously and it is very hard to balance crop production according to the needs of the growing population.

PGPRs increase stress specific adoptive responses against several environmental stresses in plants (Srivastava and Singh, 2017). Globally pathogens and pests are causing wheat losses of 21.5 percent, rice losses of 30.0 percent, maize losses of 22.5 percent, potato losses of 17.2 percent and soya beans losses of 21.4 percent according to the study published in the journal Nature, Ecology and Evolution (https://www.nature.com/articles/s41559-018-0793-y). The use of plant growth promoting rhizobacteria (PGPR) as biocontrol agent can make plants to be resistant against biotic stresses. Biocontrol of plant diseases is an effective method among various methods of disease control as it is environment friendly. Use of PGPR as biological control agent is one of the effective way for disease control as it reduces the use of chemical fertilizers in fields which are harmful for soil, microbial diversity and environment (Møller and Tester, 2007).

MECHANISM OF PGPR FOR MANAGEMENT OF ABIOTIC STRESS

Salinity stress management

Soil salinity in arid areas is frequently an important limiting factor for cultivating agriculture crops. Most commonly high Na^+ and Cl^- cause the salt stress. Salt stress has major impacts on plant growth, it lowers water potential and produces ion imbalance, ion homeostasis disruptions, and toxicity. Salt stress causes a loss in initial growth and a drop in plant output. The detrimental effects of these stresses as whole can cause death of the plant. Salt stress affects all the vital processes like photosynthesis, protein synthesis and energy and lipid metabolism. Although many methods have been established in the improvement of salt tolerance, but PGPR-elicited plant resistance against salt stress has been found to be highly effective. Salt tolerance in plant, especially to NaCl stress depends on variations in tissues tolerance to Na^+. *Arabidopsis* assigns a large number of mechanisms to achieve tolerance to Na^+ accumulation in the leaf but the relation between Na^+ accumulation in the leaf and whole plant Na^+ is not clearly understood (Glenn et al., 1999). At the cellular level, distinctive Na^+ tissue tolerance could be achieved by differences in the expression or activity of protein involved in vacuolization of cells within the leaf structure (Niu et al., 1995, Apse et al., 1999). Even the over expression of a vacuolar Na^+/H^+antiporter gene AtNHX1 enhances plant salt tolerance, possibly by vacuolar Na^+ compartmentalization that minimize the toxic aggregation of the ion in the cytosol and facilitate growth in the saline environment (Zhang and Blumwald, 2001, Barassi et al., 2006). *Azospirillum* inoculated seeds of Lettuce (*Lectuca sativa*) showed better vegetative growth and germination rates than non-inoculated control plants when exposed to NaCl (Glazebrook, 2005). Groundnut grown under saline field conditions, the plant growth enhancing effects of ACC deaminase possessing *Pseudomonas fluorescens* TDK1 were more pronounced as compare to strains lacking the enzyme. Plant stress is relieved and normal plant growth is restored when ethylene precursor 1- aminocyclopropane-1-carboxylic acid (ACC) is degraded by bacterial ACC deaminase (Saravanakumar and Samiyappan, 2007). The PGPR strain *Pseudomonas putida* GR122 can stimulate plant growth by producing the enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase which hydrolyzes ACC and also promotes early development of canola seedlings under salt stress (Glick et al., 2007). High Na^+/K^+ proportions were also found in salt stressed maize and selectivity for Na^+, $Ca^+$and K^+ was changed upon inoculation with *Azospirillum* (Hamdia et al., 2004). Host gene HKT1 (High-Affinity K^+ Transporter 1) fundamentally identified from wheat roots in a high affinity K^+ ion transporter and control Na^+ import in roots. By tissue-specific regulation of HKT1, the soil bacterium *Bacillus subtilis*GB03 confers salt tolerance in *Arabidopsis thaliana* (Zhang et al., 2007). GB03 suppresses HKT1 expression in roots and increases it in shoots in response to salt stress, lowering Na+ buildup all over the plant. Inoculation with two PGPR strains *Serratia proteamaculans* ATCC 35475 and *Rhizobium leguminosarum* pv. *viciae* 128C56G alleviated the salinity impacts on the antioxidant enzymes, photosynthesis, mineral content and growth of *Lactuca sativa* (Lettuce) grown on saline soils (Han and Lee, 2005).

Drought stress management

Dehydration or water deficit represents a common stress challenge to plant cell under drought condition. Plants use a range of survival strategies to protect themselves against environmental pressures, such as drought. One frequent mechanism is ABA-induced stomata closure to reduce water loss via transpiration (Choudhury and Paul, 2012). Plants increase the synthesis of osmolytes in response to aridity, which elevate the osmotic potential (OP) within cells (Farooq et al., 2009). In response to this stress, osmolyte glycine betaine produced by osmotolerant bacteria may operate in concert with plant-derived glycine betaine, increasing drought tolerance. *Achromobacter piechaudii's* ACC deaminase activity was linked to drought tolerance in tomato and pepper, resulting in major increases in fresh and dry weights (Mayak et al., 2014). Maize seedling inoculated with *Azospirillum brasilense* under water deficiency displayed improved relative and absolute water contents in comparison to non-inoculated treatments (Casanovas et al., 2009). A variety of genes are also activated during drought stress condition which often referred to as “stress genes”. For example, at the transcriptional level the bacteria *Pseudomonas polymyxa* causes induction of drought responsive gene ERD15, isolated from drought stressed *Arabidopsis thaliana* (Gupta et al., 2022). The gene RD29A is one such common stress inducible gene (Habib et al., 2022). The stress hormone ABA levels increase in both drought and salt condition, which activates RD29A. Drought tolerance in barley is controlled by two sets of genes (Guo et al., 2014), (a) the genes that act as regulators in signal transduction (UVP8, CP5and protein kinase CDPKs, STKL) and signaling regulators MSBP and SPDS. (b) Functional genes that enhance drought stress tolerance (NADP-ME and PDH), biosynthesis and translocation of glycine–betaine for osmoprotection (CSMO and an APP), scavenging ROS for detoxification (ADOR, ALDH, GSTand SPDS). Root colonization of plants with rhizobacterial *Pseudomonas chlororaphis* 06 induces resistance to drought stress. Drought tolerance exhibited by the bacteria was interrelated with reduced water loss caused by high percentage of stomatal closure. They observed that *Pseudomonas chlororaphis* 06 produces a volatile metabolite 2R, 3R-butanediol (diastereo-isomer of Butane-2, 3-diol) compound which are responsible for stomatal closure and subsequently drought resistance. They also reported that the induced drought tolerance required SA (Salicylic acid) as free SA content is increased following treatment with 2R, 3R-butanediol to the drought stressed *Arabidopsis* plants and hence induction of resistance to drought in *Arabidopsis* by *P. chlororaphis* 06 is through a SA-dependent mechanism. Beneficial PGPR also help plant to cope with flooding stress (C). Rice (*Oryza sativa)* seedlings inoculated with an ACC deaminase synthesizing strain of *Pseudomonas fluorescens* REN1 showed enhanced root elongation under consistently flooded conditions (Etesami et al., 2013).

Temperature stress management

Heat stress management

Extreme temperature as consequence of global climate alteration also has adverse effect on crop productivity (Driedonks et al., 2016, Fischer et al., 2002, Drigo et al., 2008). Elevated temperature stress negatively influences flowering, photosynthetic rate, plant water relations and fruit set in both tropical and temperate crops (Selvakumar et al., 2012). The positive effects of different bacterial strains on soyabean growth and physiology under suboptimal root zone temperatures and found that bacterial stimulation is interactively dependent on temperature (Khan et al., 2019). The impacts of inoculation with rhizobacterial strain *Burkholderia phytofirmans* PsJN on 18 clones of potato grown-up under two diverse temperatures (20 °C day, 15 °C night, 33°C day, 25 °C night) tested (Bensalim et al., 1998). Results of measurements such as stem length, root and shoot biomass at high temperature indicate that colonization of the potato by rhizobacteria might play an important role in their adaptation to heat. Grapevine plants inoculated with *Burkholderia phytofirmans* accumulated significantly large amounts of carbohydrates compared to control plants (Barka et al., 2006). The activation of genes responsive to heat stress is mediated by heat stress transcription factors (Hsfs). The plant Hsfs have a highly difficult gene family comprising of more than 20 members and are thought to modulate transcription during long-term heat stress response (Baniwal et al., 2004, Nover et al., 2001). In tomato, HsfA1a acts as a master regulator for induced thermo-tolerance and cannot be replaced by any other Hsf (Mishra et al., 2002). Thermo-tolerance of *Pseudomonas putida* NBRI0987 is due to over-expression of stress sigma factor S and enhanced biofilm formation at high temperature (Srivatava et al., 2008). Heat shock proteins that stabilize the membrane are induced under stress conditions and confer thermo tolerance to extreme temperature. The thermo-tolerance conferred by the strain is because of the formation of exo-polysaccharides (Gouesbet et al., 2002). *Paraphaeosphaeria quadriseptata* rhizospheric fungus also improved thermo-tolerance in *Arabidopsis thaliana* through stimulation of HSP101 and HSP70 proteins (McLellan et al., 2007).

Cold stress management

Cold stress adversely affects plants growth and development thereby preventing expression of full genetic potential of plants either by limiting metabolic activity or by inducing inhibition of water uptake. Chilling stress may immediately result in mechanical enforce, changes in activities of macromolecules and reduced osmotic potential in the cell. PGPRs can play a significant role in helping plants to endure cold tolerance as several genes that provide resistance to abiotic stresses on host plants also induced due to PGPR activities. A gibberellins producing PGPR, *Serratia nematodiphila* increases pepper (*Capsicum annum*) growth under low temperature stress conditions. The treated plants contained more GA4 and ABA and less salicylate and jasmonate. When grapevine are inoculated with rhizobacterial strain *Burkholderia phytofirmans* PsJN, it modulates carbohydrate metabolism for alleviation of chilling injury in grapevine (*Vitis vinifera*) plantlets when it applied low temperature stress (Kang et al., 2015).

Burkholderia phytofirmans PsJN-inoculated grapevine plants accumulated more carbohydrates than control plants (Fernandez et al., 2012). Plants ability to survive cold can be boosted by exposure to low, non-freezing temperatures. During cold acclimation, physiological changes such as increases in sugar, proline and anthocyanin levels can be observed. The concentration of proline and phenols, rates of photosynthesis and starch deposition were improved due to cold stress (Barka et al., 2006). The inoculation of rhizobacterial strain *Pseudomonas vancouverensis* OB155 and *P. frederiksbergensis* OS261 increased expression of cold acclimation genes and antioxidant activity in tomato (*Solanum lycopersicum*) plants (Subramanian et al., 2015). Plant cells could percieve cold stress through membrane rigidification caused due to reduced fluidity of the cellular membranes (Chinnusamy et al., 2007). COR (COLD RESPONSIVE) genes are induced by membrane rigidification process and provide cold acclimation in crops like Alfalfa (*Medicago sativa*) and *Brassica napus* (Örvar et al., 2000, Sangwan et al., 2001). The transcription factor ICE1 (Inducer of CBF Expression1) binds to MYC recognition sites in CBF (C-repeat binding factors) promoters and activates CBF3 expression. The mitogen-activated protein kinase (MAPK) cascade plays a fundamental role in different abiotic stresses. The MAPKs modulates the defense pathways activated by biotic and abiotic factors. Overexpression of rice OsMAPK5 gene and improved abiotic stress tolerance including cold tolerance was observed (Xiong and Yang, 2003). An overexpression of this MAPK gene in transgenic rice makes it tolerant to cold. Another gene from rice, which is intron less (OSISAP1) and encodes a zinc-finger protein, is induced by abiotic stresses including chilling stress (Mukhopadhyay et al., 2004).

Nutrient deficiency and metal toxicity stress management

Anthropogenic activities have assembled significant amount of heavy metals in both soil and water environment. Heavy metals are introducing into the environment by metal and ore processing industries, metal-containing fertilizers, mining activities, herbicides, pesticides and sewage sludge (Marrugo-Negrete et al., 2017). Huge-amount count of heavy metals into soil environment is responsible for food chain contamination, decreased crop productivity, changes in physical and chemical properties of soil and soil microbial characteristics. Metal and organic contaminant removal by PGPR is an attractive, low cost, non-destructive and environment friendly method (Park et al., 2011). Plant growth-enhancing activities for example hormone production (IAA, GA), siderophore production, nitrogen fixation, and phosphate solubilization can all be used to help with phytoremediation of contaminated environments (Whiting et al., 2001). Heavy-metal resistant bacteria inhabiting in rhizosphere may play an important role in metal tolerance and accumulation by plants. Increment of nickel (Ni) release from non-labile sources and increased accumulation in *Alyssum murale* has been observed (Abou-Shanab et al., 2003). They assessed the effect of inoculation of three different PGPR species namely *Sphingomonas macrogoltabidus, Microbacterium liquefaciens* and *M. arabinogalactanolyticum* on nickel phytoextraction and solubilization. The maximum extraction (32.4%) was observed with *M. arabinogalactanolyticum.* Enhanced zinc dissolution and accumulation in shoot of *Thlaspic aerulescens* after inoculation of bacteria. Application of these bacteria in soil with immobile zinc (Zn) can boost the production of plants suffering from zinc deficiency (Whiting et al., 2001). The three *Brassica rapa* MT genes (BrMT1, BrMT2and BrMT3) are differentially regulated under various Heavy metal (HM) stresses (Ahn et al., 2012).

Nutrient elements like phosphorus (P), potassium (K), iron (Fe), zinc (Zn) and copper (Cu) have less movement in the soil. Element phosphorus (P) is an insoluble form of phosphorus can be mobilized by plant exudates such as phosphatase enzymes and organic acids. Carbohydrates present in plant exudates also indirectly allow to phosphorus mobilization by serving as a carbon source for phosphate-solubilizing microorganisms. In maize (*Zea mays*), inoculation with *Bacillus polymyxa* BcP26, *Pseudomonas alcaligenes* PsA15, and *Mycobacterium phlei* MbP18 enhanced growth and nutrient uptake, respectively (Egamberdiyeva, 2007). Due to microorganisms binding free Cd ions into complex forms that barley cannot absorb, when inoculated with the commercially available PGPR, barley plants grown on cadmium (Cd)-contaminated soil obtained a 120 percent greater grain yield and a twofold decrease in Cd concentrations in grains. *Klebsiella mobilis* CIAM 880 reported (Pishchik et al., 2002). *Brassica juncea* inoculated with IAA- and siderophore-producing bacteria, chromium (Cr) uptake was not changed, whereas chromium tolerance was improved (Kumar et al., 2009). Many PGPRs releases metal-chelating substances into the rhizosphere, such as iron-chelating siderophores. Plant uptake several metals, including iron, zinc, and copper, has been found to be affected by siderophore-producing bacteria. Both monocot and dicot plants use microbial iron–siderophore complexes as an iron source (Egamberdiyeva, 2007, Dimkpa et al., 2009).

Oxidative stress management

Almost all type of abiotic stress leads to dehydration and osmotic imbalance of the cells through alters in the plant's biochemical and physiological status. The initially effect of abiotic stress in plants is imbalance of ions and hyper-osmotic stress which increases the accumulation of reactive oxygen species (ROS) such as H_2O_2, O_2^{2-} and $OH^{\cdot}$. The production of reactive oxygen species (ROS) and antioxidant defences causes cellular structural disturbance and physiological alterations such as denaturation of proteins, lipids, carbohydrates, and DNA.As a result of the structural and physiological alterations, photosynthesis is inhibited, and metabolic dysfunction occurs, resulting in diminished growth and fertility, premature senescence, and low yield. These ROS molecules also damage the root meristem function by destroying chlorophyll (de Souza et al., 2012). Excessive production of ROS causes toxicity, resulting in protein damage, inhibition of several key enzymes in metabolic processes, and oxidation of macromolecules such as lipids and DNA, all of which can lead to cell death (Juan et al., 2021). Plants produces the protective antioxidant enzymes include superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), tryptophan decarboxylase (TDC), reductase, redoxin and phenylalanine ammonia-lyase (PAL). These enzymes can scavenge ROS and keep them under control. Superoxide dismutase is a metalloenzyme that catalyses the conversion of the superoxide radical to H_2O_2. It protects cells from oxidative damage.

Ascorbate peroxidase plays an important function in the defence against reactive oxygen species (ROS) and can catalyse the breakdown of H_2O_2 generated by SOD. By promoting the breakdown of H_2O_2 into H_2O and O_2, catalase helps to lower ROS levels (Yang et al., 2009). PGPR increases drought tolerance in plants by producing IAA, cytokinins, antioxidants, and ACC deaminase. PGPR also protects the plant in saline conditions by lowering membrane destabilising action.in plants by production of IAA, cytokinins, antioxidants and ACC deaminase (Gao et al., 2008). In saline condition, PGPR also protect the plant by reducing membrane destabilizing activity. PGPR increases ROS scavenging enzymes including catalase ascorbate and peroxidase, which may help plants to cope-up with the negative effects of ROS in salinity and drought. Thus, increase in ROS-scavenging enzymes as a means of ISR (Induced Systemic Resistance) can also provide resistance to plants against abiotic stresses (Gururani et al., 2013).

Various types of abiotic stresses and their physiological effects on plants are shown in figure 1. These stresses are managed by different PGPRs as studied on various crops and plant defense genes induced under different abiotic stress is shown in table 1 and table 2 respectively.

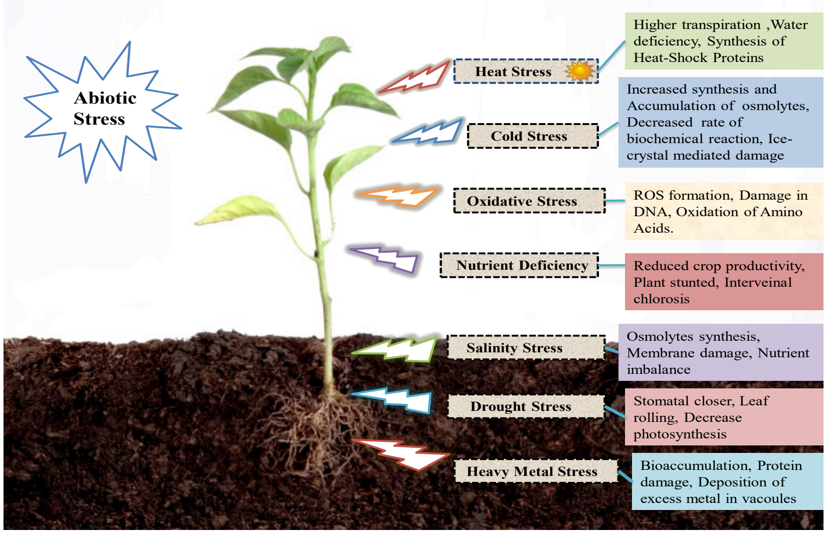

Fig. 1: Various abiotic stresses and their physiological effects on plants.

Table 1. PGPRs for management of different abiotic stress

Types of Stress	PGPR	Crop plant	Reference
Salt	*Azospirillum*	Lettuce (*Lectuca sativa*)	Hoque et al., 2022
Salt	*Pseudomonas syringae*	Maize (*Zea mays*)	Nadeem et al., 2007
Salt	*Pseudomonas fluorescens*	Groundnut (*Arachis hypogaea*)	Ghorai et al., 2015
Salt	*Azospirillum*	Maize (*Zea mays*)	Hamdia et al.,2004
Drought	*Achromo bacterpiechaudii*	Tomato (*Lycopersicum esculentum*), pepper (*Capsicum annuum*)	Mayak et al.,2004
Drought	*Azospirillum brasilense*	Maize (*Zea mays*)	Rodríguez-Salazar et al., 2009
Drought	*Azospirillum*	Wheat (*Triticum aestivum*)	Gupta et al., 2022
Flooding	*Pseudomonas fluorescens*	*Rice (Oryza sativa)*	Etesami et al., 2014

Heat stress	*Burkholderia phytofirmans*	*Grapevine (Vitis vinifera)*	Rashidet al., 2021
Cold stress	*Pseudomonas vancouverensis*	*Potato (Solanum tuberosum)*	Subramanian et al., 2015
Cold stress	*Serratia nematodiphila*	Pepper (*Capsicum annum*)	Kang et al., 2015
Nutrient deficiency	*Bacillus polymyxa, Mycobacterium phlei, Pseudomonas alcaligenes*	Maize (*Zea mays*)	Saha and Mazumdar, 2022
Iron toxicity	*Bacillus subtilis, Bacillus megaterium, Bacillus* sp.	*Rice (Oryza sativa)*	Asch and Padham, 2005

Table 2: Important plant defense genes induced under abiotic stress

Abiotic Stress	**Host gene expressed under stress**	**Reference**
Salt	HKT1	Ali et al., 2019
Salt	PR1	Zarrougui et al., 2022
Salt	AtNHX1	Hussain et al., 2008
Drought	RD29A	Liu et al., 2020
Drought	ERD15	Wang et al., 2021
Drought	UVR8, CP5, CDPK, STKL, MSBP, NADP-ME, PDH, MSBP, SPDS, APP, ADOR, ALDH, GST	Sarma et al., 2012
Flood	REN1	Etesami et al., 2014
Heat	HSP101 and HSP70	Tiwari et al.,2022
Heat	HsfA1a, HsfA4and HsfB1	Haider et al., 2021
Cold	COR genes	Ritonga et al., 2020
Cold	OsMAPK5	Hong et al., 2020
Cold	OSISAP1	Kanneganti and Gupta 2008
Metal Toxicity	BrMT1, BrMT2 and BrMT3	Ahn et al., 2012

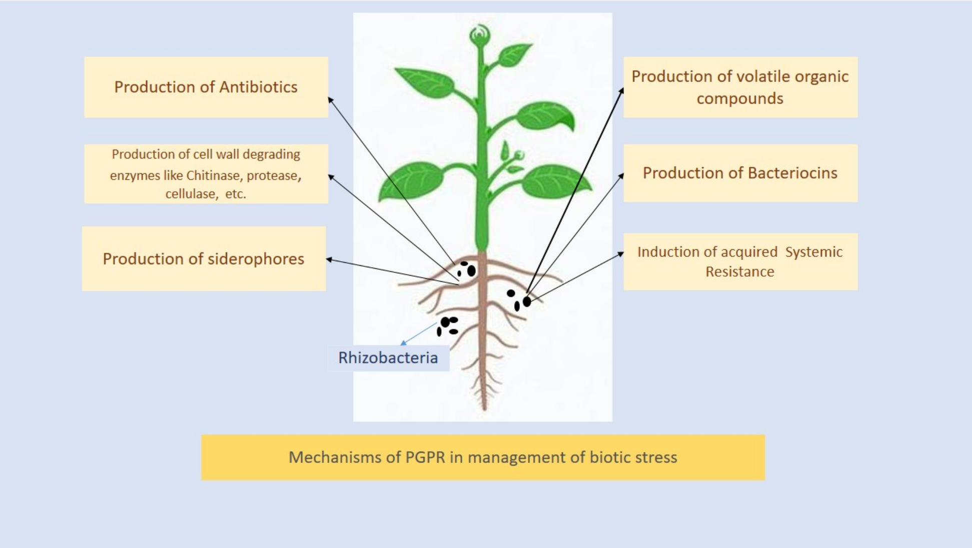

Figure 2: Mechanisms of PGPR for management of biotic stress.

Mechanism of PGPR for management of biotic stress

PGPRs shows several activities that helps plants to tolerate biotic stress such as- production of antibiotic compounds (antibiosis), production of cell wall degrading enzymes, production of bacteriocins, synthesis and release of volatile of organic compounds and induction of systemic resistance. PGPRs plays key role in biocontrol of plant disease through its antagonistic activities against pathogens. PGPRs shows direct suppression of pathogens via antibiosis, competition with pathogens for resources, synthesis of hydrolytic enzymes, such as chitinases, glucanases, proteases and lipases that can lyse pathogenic fungal cells as shown in figure 2 (Suryadi et al., 2019) and also have capacity to stimulate resistance in plants against pathogens.

Antibiosis

Antibiotics are defined as “heterogenous group of low molecular weight organic compounds which are produced by microorganisms and have capacity to inhibit growth and metabolic activities of other groups of microorganisms” (Fernando et al., 2007). Interactions between multiple groups of soil micro-organisms like– predation, antibiotics production and competition for resources etc (Karimi et al., 2017). There are 6 classes of biocontrol antibiotic compounds based on their mode of action– Phenazine, Phloroglucinols, Cyclic lipopeptides, Pyrrolnitrin, Pyoluteorin and Hydrogen cyanide (Premachandra et al., 2016). These antibiotic compounds inhibit the cell wall synthesis in pathogens also effects cell membrane structure and prevent the formation of initiation complex on ribosome. The genetics of *Pseudomonas* was studied and observed that there is direct relationship between suppression of disease and antibiotics production (Kannojia *et al.*, 2019).

Several bacterial genera produce phenazines, which are nitrogen-containing heterocyclic coloured compounds with antifungal activity such as - *Pseudomonas, Burkholderia, Brevibacterium, Streptomyces, Nocardia, Erwinia, Vibrio, Pelagiobacter* and some Actinomycetales like *Streptomyces* (Kennedy et al., 2015, Mavrodi et al., 2013). Phenazines acts by generating reactive oxygen species (ROS) and uncouples oxidative phosphorylation. Phenazines produced by *Pseudomonas,* show redox activity which damages the phytopathogens like – *Fusarium oxysporum* and *Gaeumannomyces graminis* (Chin-A-Woeng et al., 2003). Antibiotics like Pyrrolnitrins (monochlorinated heteroaromatic pyrrole rings) and Pyoluteorins (dichlorinated heteroaromatic pyrrole rings) are produced by various PGPRs such as *Pseudomonas* spp*., Burkholderia* spp. And *Serratia* spp (Salomon et al., 2014). Pyrrolnitrins act by inhibiting respiratory electron transport and protein synthesis and they combine with cell membrane phospholipids to affect membrane transportation (Haas and Défago, 2005). Antibiotic pyrrolnitrin, produced by *Pseudomonas fluorescence* BL915 strain was effective against *Rhizoctonia solani*, which causes damping off in cotton plants (Hill et al., 2018).

The benzenetriol 2, 4-di-acetyl-phloro-glucinol (DAPG) has two ring hydrogens substituted by acetyl groups. In *Neurospora crassa*, DAPG generated by *Pseudomonas fluorescens* alters mitochondrial structure, cause a loss of membrane potential and an increase in cytosolic Ca^{2+} (Troppens et al., 2013). DAPG have effect on cell membrane of *Pythium* spp. and it is also effective against Oomycetes (De Souza et al., 2003). With the help of a membrane-bound flavoenzyme (HCN synthase), HCN (hydrogen cyanide) is produced by the oxidation of glycine, this oxidation results into HCN and CO_2. Cytochrome C oxidase and several other metallo enzymes are inhibited by HCN (hydrogen cyanide) (Blumer and Haas, 2000). HCN and pyrrolnitrins produced by *Pseudomonas chlororaphis* strain PA23 have repellent and nematicidal activity against *Caenorhabditis elegans* (Nnadi et al., 2015). Majority of *Bacillus* spp. produces several antibiotic compounds like – polymyxin, circulin and colistin are effective against gram positive and gram negative bacteria and also controls pathogenic fungi (Tariq et al., 2017).

Production of cell wall degrading enzymes

The production and secretion of CWD (Cell Wall Degrading) enzymes from PGPR is an important aspects for bio-control of soil borne pathogens (Singh et al., 2014). These enzymes disrupts the structure of pathogens cell wall (Budi et al., 2000). Chitinolytic and antifungal activities in *Serratia marcescens* against pathogens like *Rhizoctonia solani, Fusarium oxysporum* (Someya et al., 2000). β- 1, 4-N-acetylglucoseamine and chitin are major components of cell wall of fungal pathogens (Oak and Jha, 2019). β- 1, 3-glucanase and chitinase degrades and cause the lysis of cell wall and inhibits the growth of pathogens. β- 1, 3 -glucanase enzyme which is produced by *Streptomyces* spp. cause lysis of cell wall of pathogenic fungus *Fusarium oxysporum* (Anitha and Rabeeth, 2010). Chitinolytic activities in *Bacillus licheniformis, B. cereus, B. circulans, B. thuringiensis* (Sadfi et al., 2001). *Micromonos poracarbonacea* produced cellulase, which inhibits the growth of *Phytophthora cinnamoni* causal agent of root rot disease in *Banksia grandis* (Richter et al., 2011).

Production of siderophores

Siderophores are low molecular weight iron chelating organic substances that have ability to solubilize iron from rhizospheric zone. PGPR produces the siderophores, which binds with iron and form iron-siderophore complex. These complexes are taken up by PGPR through a particular receptor found on the bacteriums outer cell membrane. Following this, iron is released into the cell and is now available to stimulate bacterial development. By producing siderophores, PGPRs suppress the growth of plant pathogens like fungus and bacteria. Siderophore makes iron unavailable for phytopathogens and inhibits their growth. Plants are usually not affected by these localized reductions in the concentration of iron because most of the plants can grow at very low iron concentration than microorganisms. Deficiency in concentration of iron limits the growth of pathogen by blocking major processes like- nucleic acid synthesis and sporulation (Saha et al., 2016).

Siderophores like- Pseudobactin produced by *Pseudomonas putida* B10 have capability to control growth of the pathogenic fungus *Fusarium oxysporum* in iron deficient soil (Shanmugaiah et al., 2015). Siderophores produced by *Pseudomonas* strain B324 have ability to suppress *Pythium* which causes root rot disease of wheat (Kannojia et al., 2019). Pyoverdine produced by *Pseudomonas* have ability to suppress *Fusarium oxysporum* that cause wilt disease of potato (Duijff et al., 1999). Siderophores produced by PGPRs such as- *Bacillus, Kochuria* and *Pseudomonas* have strong inhibitory activity against phytopathogens like *Fusarium oxysporum, Pyricularia oryzae, Sclerotium* spp (Chaiharn et al., 2009).

Volatile organic compounds

Volatile Organic Compounds (VOCs) are low molecular weight compounds have molecular weight less than 300 g and enough vapor pressure under normal conditions that is produced by catabolic pathways such as glycolysis, lipolysis and proteolysis (Schulz and Dickschat, 2007). Volatile Organic Compounds (VOCs) are continuously synthesized and released into atmosphere by anthropogenic and biogenic sources. 2, 3-butanediol synthesized by PGPR strains *Bacillus subtilis* GB03 and *Bacillus amyloliquefaciens* IN937a have ability to promote plant defense system and reduce biotic stress (Ryu et al., 2004). For biocontrol strategies VOCs are better alternative because these are environment friendly and provide long term protection against pathogens to crop plants (Bhattacharyya and Jha, 2012). VOCs produced by PGPRs have plant growth enhancing, antimicrobial, nematicidal and ISR inducing activity in crop plants (Raza et al., 2021). C13 VOC produced and released by *Paenibacilluspolymyxa*E681 strain, have activity against *Pseudomonas syringae* (Park et al., 2013).

Bacteriocins

Bacteriocins are different from antibiotics and have relatively limited target range and only lethal to bacteria closely related to producing strain (Riley and Wertz, 2002). At least one form of bacteriocin can be synthesizing by all bacteria (Goh and Philip, 2015). Several bacteriocins produced from gram-negative bacteria appear to be the result of recombinations within existing bacteriocins. The colicin proteins produced by some strains of Escherichia coli that are lethal to related strains are the most representative bacteriocins produced by gram negative bacteria. Some other examples of bacteriocins produced from different bacterial strains include pyocins from *Pseudomonas pyogenes* strains, cloacins from *Enterobacter cloacae*, marcescins from *Serratia marcescens* and megacins from *Bacillus megaterium* (Cascales et al., 2007).

Nematodes management

Rhizobacteria control plant parasitic nematodes in the rhizosphere through a variety of mechanisms. The mechanism of nematode suppression can be categorized mainly in two major headings viz., direct and indirect antagonism. Direct antagonism is exhibited by producing enzymes, toxins and other metabolic products while indirect effect by regulating nematode behavior, altering root diffusates. These mechanisms induce the production of repellents by host that adversely affects the host recognition, alteration the nematode feeding site development or sex ratio inside the root tissue, promoting plant growth, competing for essential nutrients and inducing systemic resistance (Mhatre et al., 2019). The biocontrol Potential of PGPR against plant parasitic nematodes is shown in table 3.

Table 3: Biocontrol Potential of PGPR against plant parasitic nematodes

PGPR strain	Agriculture crop	Nematodes	Reference
Bacillus subtilis	Tomato	*Rotylenchulus reniformis*	Jonathan et al., 2009
Paenibacillus polymyxa and Paenibacillus lentimorbus	Tomato	*Meloidogyne incognita*	Son et al., 2009
Pasteuria sp.	Cotton	*Rotylenchus reniformi*	Schmidt et al., 2010
Streptomyces sp.	Eggplants	*Meloidogyne incognita*	Rashad et al., 2015
Pseudomonas fluorescence	Mungbean	*Heterodera cajani*	Meena , 2010
Pseudomonas fluorescens	Tomato	*Meloidogyne javanica*	Siddiqui, 2006
Pseudomonas fluorescens	Okra	*Meloidogyne incognita*	Singh et al., 2014
Pseudomonas fluorescens and *B. Subtilis*	Rice	*Meloidogyne graminicola*	Narasimhamurthy et al., 2017
Bacillus polymyxa +VAM	Tomato	*Meloidogyne incognita*	Liu et al., 2012
Pseudomonas fluorescens	Banana	*Helicotylenchus multicinctus*	Selvaraj et al., 2014
Bacillus tequilensis and *Bacillus flexus*	Basil	*Meloidogyne incognita*	Tiwari et al., 2017
Bacillus sp.	Yellow melon	*Meloidogyne incognita*	Medeiros et al., 2009
Bacillus subtilis	Carrot	*Meloidogyne incognita*	Rao et al., 2017

INDUCED SYSTEMIC RESISTANCE (ISR)

The induced resistance is a condition of enhanced defensive capacity by plant, when it is stimulated by stimulator (Abbasi et al., 2021). Systemic resistance induced by pathogenic organisms and exogenous chemicals is termed as SAR (Systemic Acquired Resistance) whereas the resistance in plants triggered by strains of PGPR is termed as Induced Systemic Resistance (ISR). ISR is induced by non-pathogenic PGPRs, while SAR is induced systematically after infection with pathogen. SAR requires salicylic acid as its signal molecule and associated with pathogenesis-related (PR) proteins, whereas ISR is not dependent on salicylic acid but involves jasmonic acid and ethylene signaling (Doornbos et al., 2011). The application of PGPR as a systemic resistance inducer in crop plants against multiple diseases (Ramamoorthy *et al.*, 2001). Induced Systemic resistance in plants is activated by certain molecules, which are secreted by (PGPRs) microbes, termed as “Elicitors”. Elicitors are usually cell wall components such as polysaccharides, flagella and some signalling molecules like salicylic acid, cyclic lipopeptides, siderophores, antibiotics, N-Acyl homoserine-lactones (AHLs) etc (Van Loon and Bakker, 2005). Several defense enzymes which are associated with ISR include phenylalanine ammonia lyase (PAL), chitinase, b-1, 3-glucanase, peroxidase (PO), polyphenol oxidase (PPO), superoxide dismutase (SOD), catalase (CAT), lipoxygenase (LOX), ascorbate peroxidase (APX) and proteinase inhibitors (Narayanasamy, 2013, Van Loon, 1997).

PGPR triggers ISR either by strengthening the physical structure of cell wall or by changing the physiological and biochemical reactions of host plant. During these process the synthesis of defense chemicals like chitinase, peroxidase, proteinase, inhibitors etc. also occurs (Ramamoorthy et al., 2001, Nandakumar et al., 2001). ISR has been studied in several crop plant species for examples in *Arabidopsis thaliana*, bean, cucumber, radish, tobacco, carnation etc (Saikia et al., 2003). Table 4 shows list of PGPR strains triggers induced systemic resistance (ISR) against phytopathogens in different crop plants.

Table 4: PGPR strains inducing systemic resistance (ISR) against different pathogens

PGPR strain	Host Plant	Pathogen	Reference
Pseudomonas fluorescence (WCS417r)	Tomato	*Fusarium oxysporum*	Singh et al., 2022
P. fluorescence (Pf1)	Rice	*Xanthomonas oryzae*	Ramadass et al., 2021
P. putida (KKMI)	Sugarcane	*Colletotrichum falcatum*	Viswanathan, and Samiyappan, 2012
P. fluorescence and Bacillus licheniformis	Grapevine	*Bacillus cinerea*	Salomon et al., 2014
P. putida(BTP1)	Bean	*Bacillus cinerea*	Ongena et al., 2004
P. fluorescence (Pf1)and *Bacillus subtilis*	Chillies	*Colletotrichum capsici*	Sundaramoorthy et al., 2012
P. fluorescence (FP7)	Mango	*Colletotrichum gloeosporioides*	Udhayakumar et al., 2019
Bacillus subtilis (GB03)	*Arabidopsis*	*Erwinia carotovora*	Sharifi et al., 2016

Molecular mechanism of ISR Signaling

Molecular studies on *Arabidopsis thaliana* proved that both ISR and SAR are connected via “NPR1gene”. *Bacillus* spp. triggers ISR in *Arabidopsis thaliana* by the production of 2, 3-butanediol and *Pseudomonas* spp. produce 2, 4-diacetyl-phloroglucinol for induction of ISR (Iavicoli et al., 2003). *Pseudomonas fluorescence* and *Bacillus licheniformis* triggers ISR in Grapevine plants by the production of different terpenes (Salomon et al., 2014).

As an indication of active defence, infected plants produce more jasmonic acid and ethylene (DeLaat and Van Loon, 1982). *Pseudomonas fluorescence* WCS417r strain triggers ISR in numerous plant species. *Pseudomonas fluorescence* WCS417r strain induce ISR in *Arabidopsis thaliana,* by Jasmonic acid / Ethylene signalling pathways with NPR1gene regulation (Duijff et al., 1998, Pieterse et al., 1996). When the JA response mutant jar1 (Staswick *et al.*, 1992) and the ethylene response mutant etr1 (Bleecker et al., 1988) are treated with WCS417r strain, they do not exhibit ISR, indicating that the ISR-signalling pathway requires components of the JA and ethylene response (Knoester et al., 1999, Pieterse et al., 1996). SAR and ISR follows different signalling pathways but both are blocked when tested in regulatory mutant npr1 when the Arabidopsis JA response mutant jar1 and the ET response mutant etr1 were tested for ISR development against *Pseudomonas syringae* pv. Tomato after colonisation of the roots by WCS417r bacteria, both mutants were unable to develop ISR, indicating that ISR signalling is dependent on these phytohormones (Pieterse et al., 1998). The signal transduction pathways of pathogen induced SAR and rhizobacteria mediated ISR in *Arabidopsis thaliana* are presented in figure 3.

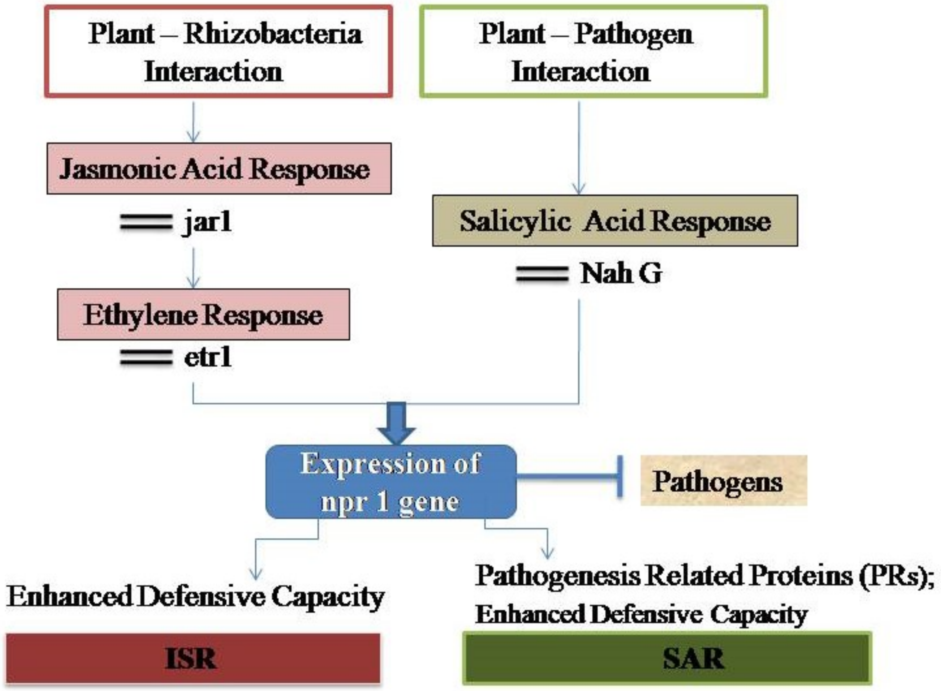

Figure 3: Signal transduction pathways leading to pathogen induced systemic acquired resistance (SAR) and rhizobacteria induced systemic resistance (ISR) Source: Van Loon *et al.*, 1998

Methyl jasmonate (MeJA) and the ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) also promote resistance against *Pseudomonas syringae* pv. Tomato DC3000 (it is a phyto pathogenic bacteria of tomato and *Arabidopsis thaliana*) in SA non-accumulating NahG plants. Methyl jasmonate (MeJA) induced protection is blocked in *jar1*-1, *etr1*-1 and *npr1*-1 plants, whereas aminocyclopropane-1-carboxylate (ACC) induced protection is affected in *etr1*-1 and *npr1*-1 plants, but not in *jar1*-1 plants. WCS417r strain mediated ISR follows a signaling pathway in which constituents from the Jasmonic acid and ethylene response pathways are involved to trigger a defense reaction which is controlled by NPR1 gene like in SAR. *Arabidopsis* plants which expressed *Pseudomonas fluorescens*-mediated ISR, shows enhanced resistance against *Fusarium oxysporum* and *Pseudomonas syringae*, but there is not any sign of activation of the SAR marker genes PR-1, PR-2 and PR-5 (Van Loon et al., 1998, Van Wees et al., 1997).*Arabidopsis* mutant npr1 for the induction of ISR and reported that mutant npr1 plants were unable to express *Pseudomonas fluorescens* mediated ISR indicating that like pathogen induced SAR, rhizobacteria mediated ISR is also NPR1-dependent defense response (Pieterse et al., 1996)**.**

CONCLUSION

The use of chemicals in agriculture such as fertilizers, pesticides, herbicides, insecticides etc. are proved harmful for both soil fertility and human health. Thus, to minimize these negative impacts effective alternatives needs to be discovered which make availability of various nutrients e.g. nitrogen, phosphorus, potassium, zinc and iron etc., provide phytohormones (IAA, gibberellin and cytokinin), secrete antibody and enzymes that help the plant and rhizosphere in abiotic stress and disease control. The plant growth promoting rhizobacteria present in the rhizosphere of plants are very much correlate with the plant roots, various research studies have documented their positive direct and indirect impact on plant growth. It is an eco-friendly strategy for plant protection against plant stress. Different PGPR till date has been used significantly in the improvement of growth and yield of different crop plants in addition to boosting plant’s immunity and managing biotic and abiotic stresses. Stress caused by biotic and abiotic factors like drought, salinity, temperature, oxidative stress, nutrient deficiency, metal toxicity, plant pathogens, insects and nematodes significantly reduce the plant productivity. PGPRs are a sustainable option to overcome the loss caused by these stresses. In addition, PGPR enhanced the fertility of soil through decomposition of organic matter, mineral solubilization and production of phytohormones. The aim of the present review is to increase the yield of healthy crops by managing plant biotic and abiotic stresses. Thus, successful application of beneficial rhizobacteria provides an efficient and cost effective alternative to conventional methods for increasing growth and productivity of crop plants.

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